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[1] CWS, Western & Northern Region,
Edmonton, Alta. T6B 2X3

[2] CWS, Pathology Section, Ottawa, Ont.;
current address:
Agriculture Canada, Ottawa, Ont. K1A 0Y9

[3] Wildlife Management Division,
Department of Renewable Resources,
Government of the Northwest Territories,
Coppermine, NWT X0E 0E0

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Abstract

The mortality of migratory barren-ground caribou (*Rangifer tarandus groenlandicus*) on the calving grounds of the Beverly caribou herd, District of Keewatin, Northwest Territories, was investigated in 1981, 1982, and 1983. Two hundred and eighty-seven dead or incapacitated newborn caribou calves were found and necropsied between 31 May and 20 June 1981, 8 and 23 June 1982, and 6 and 17 June 1983. Wolf (*Canis lupus*) predation was the single most important cause of newborn calf mortality (68.5%), followed by atelectasis (fetal and neonatal) (14.2%), pathophysiological disorders (6.7%), separation or abandonment (6.2%), pneumonia (4.0%), and grizzly bear (*Ursus arctos*) predation (0.4%).

The samples of cows that died shortly before, during, or after calving in 1981–83 are too small to allow evaluation of the causes and magnitude of mortality among breeding females of the Beverly caribou herd.

Management measures to help safeguard against the deaths of newborn calves, including maintenance of wolf numbers and minimization of human activities on the calving grounds, are discussed.

Résumé

La mortalité chez le Caribou migrateur de la toundra (*Rangifer tarandus groenlandicus*) dans les aires de mise bas de la harde de Beverly, district de Keewatin, territoires du Nord-Ouest, a fait l'objet d'une étude qui s'est poursuivie en 1981, 1982 et 1983. Deux cent quatre-vingt-sept faons morts ou invalides ont été trouvés et ont fait l'objet d'une autopsie entre le 31 mai et le 20 juin 1981, entre le 8 et le 23 juin 1982 ainsi qu'entre le 6 et le 17 juin 1983. La prédation par le Loup (*Canis lupus*) a constitué la plus importante cause de mortalité chez les faons nouveau-nés (68,5 %); il y avait ensuite l'atélectasie (foétale et néonatale) (14,2 %), les désordres physiopathologiques (6,7 %), la séparation ou l'abandon (6,2 %), la pneumonie (4,0 %) et la prédation par le Grizzli (*Ursus arctos*) (0,4 %).

Il n'y a pas eu assez de biches qui sont mortes juste avant, pendant ou après la mise bas de 1981 à 1983 pour permettre d'obtenir une évaluation des causes ainsi que de l'importance de la mortalité chez les femelles gestantes de la harde de Beverly.

Le document traite de mesures de gestion visant à assurer la survie des faons nouveau-nés, notamment du contrôle de la population de Loups et de la minimisation des activités anthropiques dans les aires de mise bas.

Introduction

This 3-yr study was initiated in 1981 in response to the concern of the Beverly and Kaminuriak Caribou Management Committee[1] over the decline of the Beverly herd of migratory barren-ground caribou (*Rangifer tarandus groenlandicus*) during the 1970s.

Prior to this study, not enough was known about the causes and extent of natural mortality in the Beverly herd to enable initiation of any management of predation or harvest. Natural mortality is the least understood aspect of caribou management because of the difficulties of quantifying it. The natural mortality of calves until they are 1 yr old is of particular concern to wildlife managers, not only because it is frequently high (e.g., Kelsall 1968; Skoog 1968), but also because the number of 1-yr-old calves is a measure of the potential maximum to which a herd can increase in numbers.

In this study, caribou carcasses were located by visual searches of the calving grounds, then examined for causes of death. Emphasis is placed on the causes of death of newborn calves on their calving grounds at or about the time of calving; these have not been previously described for the Beverly herd, although incidental observations have indicated that calf mortality was extensive in some years (Heard and Decker 1980). The management implications of our results are evaluated, and recommendations for managers are developed.

[1]The Beverly and Kaminuriak Caribou Management Committee officially became the Beverly and Kaminuriak Caribou Management Board on 3 June 1982. The board represents the federal, provincial, and territorial governments together with the native users of those two caribou herds and was established to direct and advise on management of the caribou.

Study area

1. Topography and vegetation

Our study area was the northern portion of the Beverly calving grounds that have been used during the 14 yr between 1957 and 1983 for which there are data (Fleck and Gunn 1982) (Figs. 1 and 2). The characteristics of the topography, snowmelt patterns, and vegetation have been compiled for the calving grounds north and south of Beverly Lake (Fleck and Gunn 1982).

Four dominant glacial landforms contribute to the varied topography that is characteristic of the calving grounds (Fleck and Gunn 1982). Much of the area consists of fields of drumlins and lines of eskers oriented northwest-southeast. North of Sand Lake is a flat extensive outwash sand deposit that also extends southeast to the north end of Sandhills Lake. West of Deep Rose Lake is a smaller outwash sand deposit and a glacial till plain studded with boulders. There are also many boulders on the drumlins.

Fleck and Gunn (1982) initially classified five vegetative communities based on similar percentages of structural forms for the northern Beverly calving grounds (lichen, dwarf shrub, tussock - short sedge, tussock-moss, and tall sedge - moss). The xeric and mesic drumlin areas are dominated by lichen communities. Graminoids and mosses dominate the more hydric lowlands. Using topography, moisture regimes, and landforms, Jingfors *et al.* (1982) reclassified the vegetative communities into four range types: lichen uplands (38.8% of total surface area), dwarf shrub (24.1%), meadow (12.3%), and rock/sand barrens (4.0%). Numerous lakes and ponds account for the remaining surface area (20.8%).

When the cows arrive on the calving grounds in late May, the ground is snow-covered except for the tops of some ridges. In early June, the lichen uplands and rock/sand barrens become snow-free, exposing the fruticose lichens, but phenological development is relatively slow; for example, the dominant rush (*Luzula confusa*) does not start greening until the third week of June (Jingfors *et al.* 1982). In the meadows, however, greening of the graminoids starts even while the roots and lower stems are still frozen in the ground. As the tussocks of *Eriophorum vaginatum* emerge from the snow in early June, the plants have new green growth of floral heads and leaves. The preference of the caribou for greening plant tissue explains the selection of the meadow range type by foraging caribou during calving and postcalving (Jingfors *et al.* 1982). Caribou bed in both lichen uplands and meadows during early June; however, as the melt progresses and the depth of standing water increases, the caribou prefer to bed on the drier lichen uplands.

2. Beverly caribou herd

The Beverly herd of migratory barren-ground caribou calves on tundra ranges in the west-central District of Keewatin, NWT, and calving usually peaks between 4 and 10 June (Fleck and Gunn 1982; see Fig. 1). Post-calving summer ranges are found in both the District of Keewatin and the District of Mackenzie, NWT; winter ranges occur for the most part in the southern District of Mackenzie and some years extend into northern Saskatchewan (Kelsall 1968; Thomas 1969; Fleck and Gunn 1982) (see Fig. 1). A detailed annotated bibliography of all aspects of the biology of the Beverly herd (and the adjacent Kaminuriak herd) has been compiled by Williams *et al.* (1983).

The breeding cows and the other caribou associated with them arrived on essentially snow-covered calving grounds by the third week of May in each year of this study (Clements 1982, 1983; Bradley and Gates 1984). Most calving took place during the first two weeks of June. In 1981, calving peaked on 2-5 June on the eastern section of the calving grounds and on 7-9 June in the southwest (Jingfors *et al.* 1982). In 1982, calving peaked on 9-10 June on the central portion (high-density stratum) (Stephenson *et al.* 1983) and on 11-12 June in the east (medium-density stratum) (Gunn *et al.* 1983). In 1983, only one general high (peak) period of calving was discerned, 8-14 June.

The calving grounds were similar in size and were located in just about the same area each year (see Fig. 2). In 1981, the highest density of breeding cows occurred in

Figure 1
Known winter range, direction of spring migration, and calving grounds of the Beverly barren-ground caribou herd, 1950-79 (after Fleck and Gunn 1982) and 1981-83 (this report)

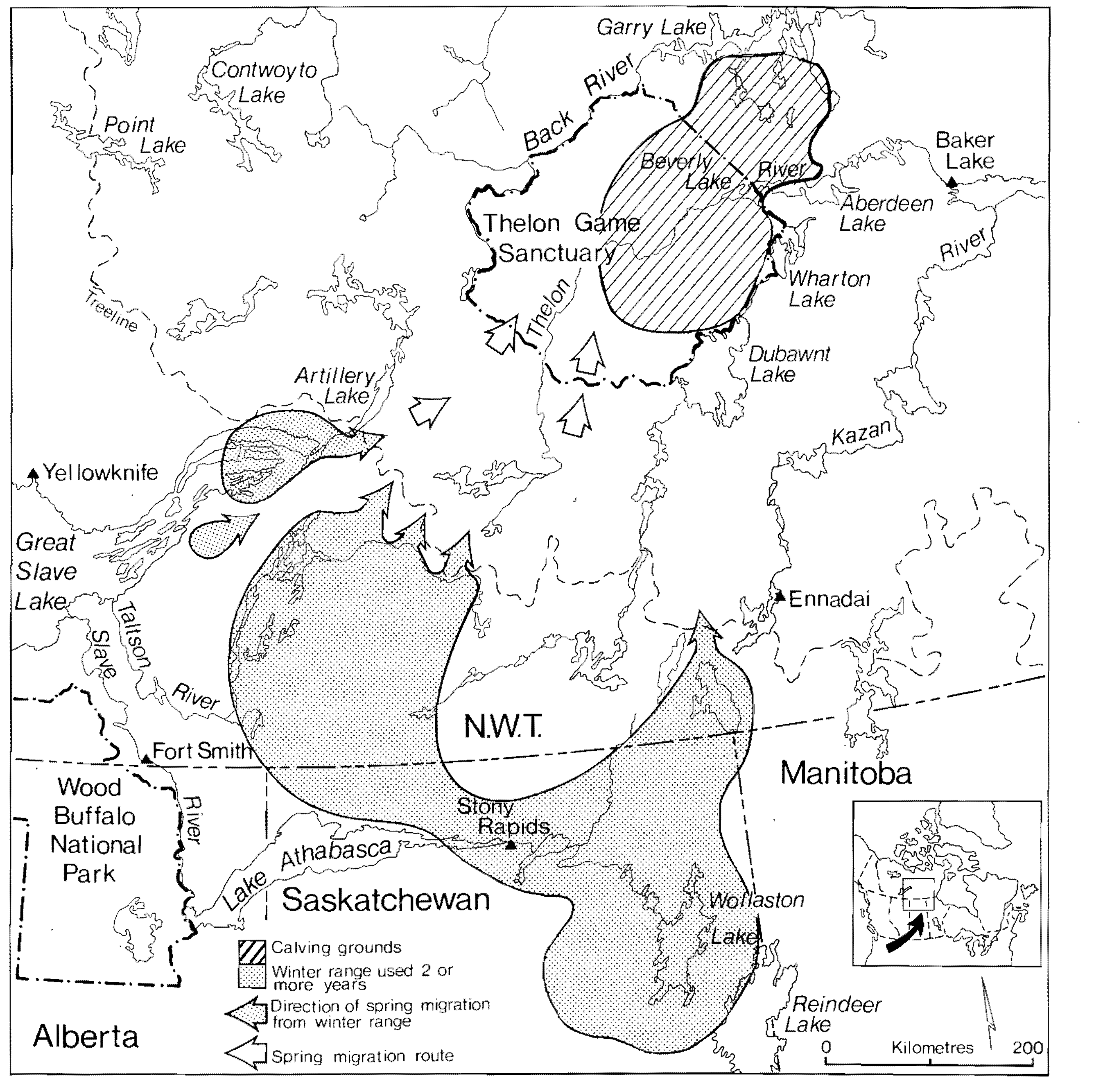
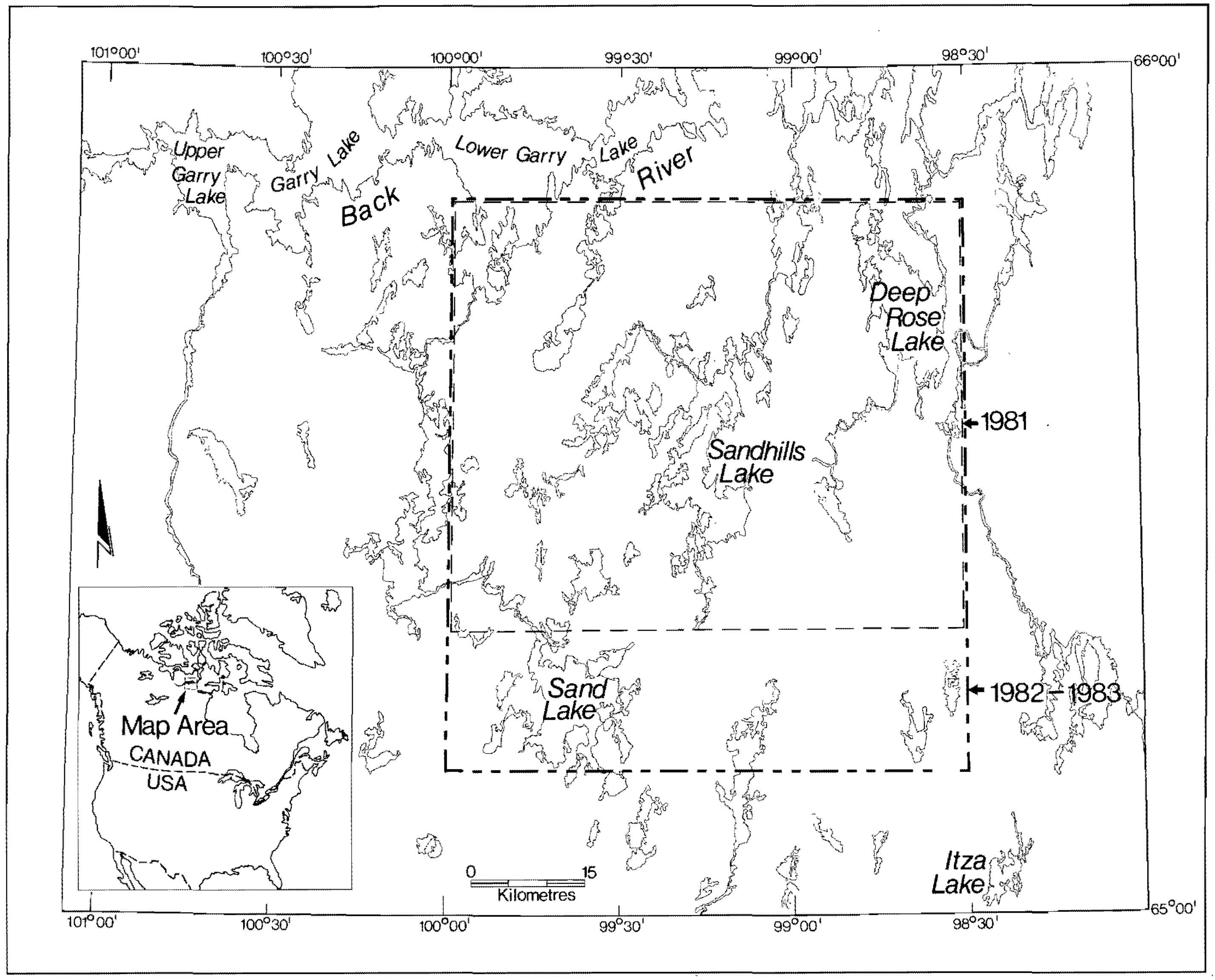


Figure 2
Areas searched by helicopter for dead caribou in May–June 1981, June 1982, and June 1983, Beverly calving grounds, Northwest Territories



the northeast around Deep Rose Lake, with the medium density immediately to the west and south to Sandhills Lake, and the lowest density farther to the west, towards Sand Lake. In 1982, the high- and medium-density areas were reversed, and the low-density area remained about the same (Stephenson *et al.* 1983). In 1983, the relative densities remained much as in 1982, but the high-density area appeared to come farther south, to the north end of Sand Lake. The general impression was that the main core (highest density) of breeding cows moved progressively southwest from the Deep Rose Lake area in 1981 to the north end and northeast side of Sand Lake in 1983.

In June 1982, the NWT Wildlife Management Division (NWTWMD), from a visual aerial survey of the Beverly calving grounds, estimated that breeding cows totalled 42 858 ± 4474 (SE) (Stephenson *et al.* 1983). It also carried out aerial photography subsampling of caribou on the Beverly calving grounds in June 1982 (NWTWMD, unpubl. data) that greatly increased the estimate of herd size beyond that which would have been obtained from extrapolation of the visual calving grounds estimate. Application of a correction factor based on the difference between the number of animals photographed and those visually counted or estimated on a given unit of area gave total herd size estimates of 150 000 – 240 000 (or about 195 000 ± 54 000 (SE); NWTWMD, unpubl. data). If we assume that about 60% of the herd consists of females 1 yr of age or older and that about 70% of these females are breeders, we can estimate that between 63 000 and 101 000 calves were produced in 1982. We believe that this level of calf production also occurred in 1981 and 1983.

3. Weather, June 1981–83

The weather during calving and early postcalving was mostly favourable to the survival of newborn calves in all 3 yr of the study. For the most part, temperatures were seasonally moderate to mild (Fig. 3); precipitation was seasonally light, with three exceptions in 1981 and two in 1982; and winds were mostly seasonally moderate to light (Fig. 4).

Daily maximum temperatures averaged highest in June 1981 and lowest in June 1982. In 1981 and 1983, daily minimum temperatures were similar and paralleled each other throughout the first three weeks of June. In June 1982, daily minimum temperatures showed more variation and most often remained lower. Temperatures in the first week of June were markedly higher in 1981 than in 1983, and even more so than in 1982 (Fig. 3). (Vegetation greened earliest in 1981 and latest in 1982.)

The relative lack of precipitation during the peak of calving in the first week of June in all 3 yr was apparently beneficial to the survival of newborn calves. The potentially lethal combination of precipitation, strong winds, and relatively low temperatures during the calving periods appeared most severe on 10 and 11 June in both 1981 and 1982 and on 4 June in 1983. The most severe day during the first week of postcalving was 19 June 1982, when strong winds were associated with the heaviest rainfall at relatively low temperatures; the only other apparent severe day was 16 June 1981, when the second heaviest rainfall occurred.

Strong winds (30+ $km \cdot h^{-1}$) were recorded slightly more often in 1983 than in 1982 or 1981, but in all 3 yr were less than 20% of all winds recorded (Fig. 4).

Figure 4
Frequency of occurrence of wind velocity classes at the Itza Lake base camp, Northwest Territories, June 1981–83

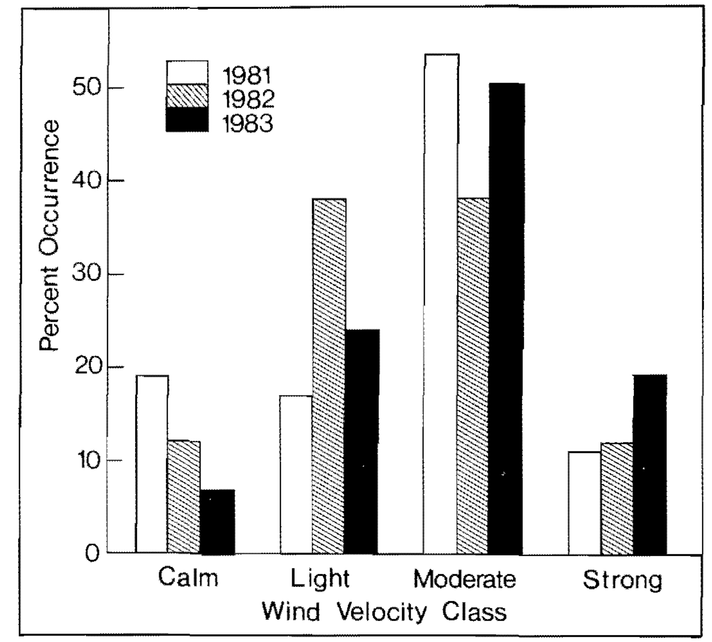
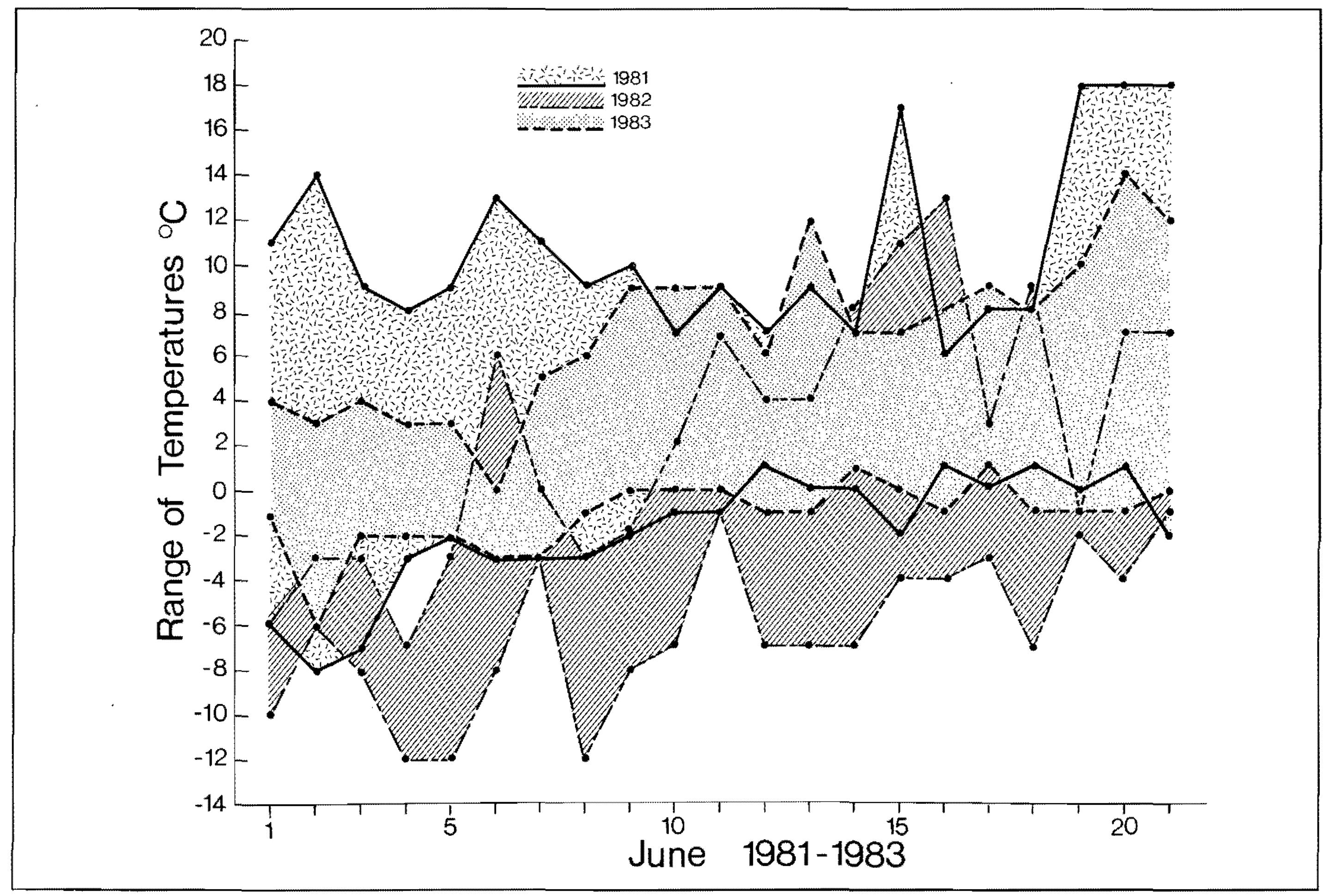


Figure 3
A comparison of daily maximum–minimum temperatures experienced at the Itza Lake base camp, Northwest Territories, June 1981–83



Methods

1. Fieldwork

In 1981–83, we flew nonsystematic searches for dead caribou in a Bell-206B turbo-helicopter at about 10–30 m above ground level (agl) at speeds of 90–160 $\text{km}\cdot\text{h}^{-1}$. Three observers usually rode with the pilot. The sharing of the helicopter with another project crew in 1981 and 1982 often influenced the timing and area of some searches, as did the prevailing weather.

The study design called for us to locate large numbers of cows and recently born calves, as well as groups of maternal cows and their calves, during early postcalving. We overflew cows during calving, when they were relatively scattered. Once the cows and their newborn calves had left, we returned to those areas and searched more intensively. We also flew along the peripheries of large aggregations of caribou throughout the study period.

When we searched a particular area, the helicopter was flown back and forth so that sections searched were completely overlapped on each successive pass. The strip widths searched were highly variable (usually < 50 m), being governed by prevailing topography, the influence of sky conditions on observability, and individual observer search patterns.

We recorded all sightings of wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*).

In all 3 yr, we used maximum–minimum thermometers at the base camp at Itza Lake (Fig. 3) to record daily highs and lows at ground level (hung 0.3 m agl and shaded from above but open to surrounding air circulation). In 1981 and 1982, we also had a Glaisher's 20.3-cm bucket-type rain gauge at the base camp for recording daily precipitation. Each day, at about 08:00 and 20:00, we recorded temperature; estimated wind speed (calm [0–1 $\text{km}\cdot\text{h}^{-1}$], mild [2–9 $\text{km}\cdot\text{h}^{-1}$], moderate [10–29 $\text{km}\cdot\text{h}^{-1}$], and strong [30+ $\text{km}\cdot\text{h}^{-1}$]); wind direction; type and intensity of precipitation; and cloud cover.

2. Diagnoses and analyses

2.1. Determining cause of death

When a carcass was spotted, we landed and searched the immediate area on foot. We recorded the posture of the carcass, noting whether or not it was in a natural resting position, the presence of scuffed vegetation, and the presence and types of tracks, hair, feathers, and scat.

We noted body temperature, condition of the umbilicus, and extent of rigor mortis before we posted or labelled and bagged the carcass. Calf carcasses were examined on site (1981) or returned to our base camp (1982, 1983). Carcasses of cows were examined on site (except for one that was slung by helicopter back to the base camp).

Each carcass was skinned, and the contents of the body cavities were removed. General condition of body tissues (e.g., colour, consistency, softness); postmortem imbibition on mesentery or omentum; imbibition of bile on liver; firmness of kidneys; presence, colour, and clotting of blood in heart; and other conditions of the carcass when found were used to estimate approximate time of death.

We performed detailed field necropsies on the caribou carcasses. All data were recorded on a field form; the 1981 form was redesigned in 1982 to allow a more detailed, quantitative record of each case. We numbered each carcass and recorded the following data:
(1) date;
(2) location (by latitude and longitude to the nearest minute: determined from 1:250 000 Geological Survey of Canada topographic maps);
(3) sex (by examination of genitalia: heavily damaged carcasses were listed as sex unknown);
(4) age (estimated by a combination of variables: appearance of carcass; condition of pelage; condition of umbilical cord and cheek teeth; degree of hoof wear; stomach contents; and whole body weight) (Table 1);
(5) weight, to 0.25 kg, as "whole" or "partial";
(6) numbers and kinds of all other nearby animals;
(7) parts of the carcass that were partially or wholly missing as a result of predation or scavenging;
(8) wounds (specific, recorded as punctures, hemorrhages, or traumas);
(9) the condition of the right diaphragmatic, left diaphragmatic, and apical lobes of the lungs (recorded by percentage as normal or with atelectasis or pneumonia);
(10) stomach contents (recorded as "empty"; milk curds only; milk curds and a trace of vegetation; milk curds, well mixed with vegetation; or vegetation only);
(11) the condition of the fourth mandibular premolar (pm4) (checked for state of eruption, presence or absence of staining, and vegetation impacted in the infundibula);
(12) whether or not the carcass had been fed on by predators or by scavengers and the types and locations of entry holes to the body cavities; and
(13) other comments.

We established 10 categories of death: (1) wolf predation; (2) suspected wolf predation; (3) grizzly bear predation; (4) fetal atelectasis; (5) neonatal atelectasis; (6) suspected fetal or neonatal atelectasis; (7) separation or abandonment (malnutrition/starvation complex); (8) pathophysiological disorders; (9) pneumonia; and (10) unknowns. For some purposes we lumped the above 10 categories into four major categories: (1) wolf predation; (2) suspected wolf predation; (3) nonpredator deaths; and (4) unknowns. Grizzly bear predation was omitted because of its rarity.

Table 1
Criteria used for estimating ages of caribou calves at death, Beverly calving grounds, Northwest Territories, 1981–83

Criterion	Estimated age (d)
Appearance of carcass (subjective)	
1. Long-legged and relatively big-headed in proportion to the size of the torso	< 1
2. Legs and head in proportion to torso	> 1
Condition of pelage	
1. Encased in placental sac (lungs completely fetal type)	0
2. Encased in placental sac (lungs only partially distended)	0– < 1
3. Pieces of placental tissue adhering to calf's pelage (especially if lungs only partially distended)	0– < 1
4. Pelage soaked, hair matted down (not related to ambient wetness)	0– < 1
5. Pelage dry	≥ 1
Umbilical cord	
1. Present	0–7
— Fleshy and wet to touch	≤ 1
— Drying and beginning to wither, but still soft	1–3
— Dried and withered	1–7
2. Absent	7+
Degree of hoof wear	
1. Class 1: Hooves yellowish; soft, translucent cartilage on tips (never walked)	0– < 1
2. Class 1–2: Hooves blackish with lighter yellowish translucent or opaque areas; cartilage dark and dried on tips; showed no wear (might have walked but never travelled)	0–3
3. Class 2: Hooves blackish with some semitranslucent areas near tips; showed no wear (walked but never travelled)	1–3
4. Class 2–3: Hooves black; showed slight wear or scratches on 3rd or 4th digits (might have travelled some)	1–3
5. Class 3: Hooves black; showed wear on 3rd and 4th digits (minimum travel)	1–3
6. Class 3–4: Hooves black; 3rd and 4th digits worn; dew claws scratched (travelled)	4–7
7. Class 4: Hooves black; 3rd and 4th digits and dew claws well worn (well travelled)	4–7+
Cheek teeth[a] (milk — pm4, pm3, pm2)	
1. pm4 — not stained, no vegetation impacted in infundibula	< 3
2. pm4 — lightly stained, little vegetation impacted in infundibula	4–7
3. pm4 — well stained with considerable vegetation impacted in infundibula	> 7
Stomach contents	
1. Empty (meconium present in gut) — never nursed, never fed on vegetation	< 1
2. Milk curds, no vegetation	≤ 1
3. Milk curds, with trace of vegetation	1–3
4. Milk curds mixed with a little vegetation	≤ 3
5. Vegetation only (signs of malnutrition and starvation)	< 7
6. Some, little, or no milk; considerable vegetation (no signs of malnutrition or starvation)	7+
Whole body weight[b]	
1. ≤ 9 kg	< 7
2. > 9 kg	7+

[a] m1, m2, and m3 not erupted at birth or during first two weeks of life; m1 erupts at about one month of age (Miller 1974).
[b] Based on whole body weights of caribou calves from the Beverly herd estimated to be less than 7 d old at death in 1981.

2.1.1. Predation

We used type and location of wound(s), occurrence of hemorrhage(s), or frank blood and tissue trauma induced before death to differentiate predation (wound inflicted on living calf) from scavenging (postmortem tissue damage). In some cases the type of entry into the body cavity also helped to distinguish between feeding by wolves and feeding by gulls. "Wolf predation" was determined primarily by the skull being crushed, fractured, or punctured by a canine tooth; and secondarily by the criteria stated above. "Grizzly bear predation" was primarily determined by the carcass remains being cached and covered by soil and litter, or by massive damage to skeletal parts and disarticulation of the head or limbs from the torso. (No wolverines [*Gulo gulo*] or lynx [*Lynx canadensis*] were seen nor was any evidence of their presence on the Beverly calving grounds obtained.) Cases with trauma or hemorrhages but lacking any direct evidence of wounds to critical areas were classified as "suspected" cases of predation. Identification of the predator, if not observed making the kill, was made by evaluating the array of evidence from the death site and the carcass, aided by descriptions from the literature and empirical observations.

2.1.2. Nonpredator deaths

"Fetal atelectasis" was primarily determined by the retention of 100% fetal lung tissue in the thoracic cavity (i.e., complete failure of the fetal lung tissue to convert to air-breathing neonatal lungs). Secondary evidence included the presence of remnants of afterbirth adhering to the pelage or patches of sticky amniotic fluids on the pelage, total absence of wear on the hooves, and an empty stomach. Fetal atelectic lungs were recognized by their relatively small, purplish appearance. The standard test used for verifying fetal lung tissue was submersion in water: if the tissue sank, it was fetal lung; if the tissue floated, it was distended, air-breathing neonatal lung.

"Neonatal atelectasis" was determined by the presence of patches of fetal atelectic lung tissue in the partially distended, air-breathing neonatal lungs. Such neonatal atelectic lung tissue appeared as relatively dense, dark purplish blotches of various sizes in one or more of the lobes of the lungs, in contrast to the surrounding distended, lighter, pink, air-breathing neonatal lung tissue. The atelectic condition of the lung tissue was tested by submersion in water (as for fetal atelectasis). Secondary evidence included that listed for fetal atelectasis, but in some cases the pelages were clean, the hooves showed some wear, or the stomach contained milk curds.

"Suspected fetal or neonatal atelectasis" was identified if a carcass exhibited the external appearance of a calf with fetal or neonatal atelectasis but lacked any lung tissue for verification of an atelectic condition, if no other pathological or physiological disorders could be discerned (Table 2).

"Separation or abandonment (malnutrition/starvation complex)" was identified as the cause of death when there was vegetation but no milk in a stomach, no evidence of any trauma or pathological or physiological conditions, and no maternal cow near the carcass (Table 2). The calf was considered to have died from a malnutrition/starvation complex, sometimes involving pneumonia as part of the complex, resulting from the calf's separation from or abandonment by its mother (Table 2).

"Pathophysiological disorder" was used whenever a carcass was diagnosed as having any other type of pathological or physiological disorder, primarily to allow comparisons with other studies.

"Pneumonia" was considered the cause of death when a calf had dark mottled pneumonic patches in its lungs and foamy fluid in its trachea and there was no evidence of separation or abandonment from its mother or other evidence of trauma or pathological or physiological conditions that could be the primary cause of death. A calf showing a malnutrition/starvation/pneumonia complex (the pneumonic condition being minor) was classed as separated or abandoned (Table 2). Pneumonia was recorded separately from other pathophysiological disorders because it supposedly can be a major cause of death of newborn reindeer calves during calving periods with a great deal of inclement weather (Zhigunov 1961).

2.1.3. Unknowns

When a carcass was too fragmentary or too decomposed or no evidence was apparent, the carcass was classified as an "unknown" and omitted from our quantitative evaluations.

2.2. Evaluating whole body weight

We arbitrarily chose 4.0 kg as the threshold viable whole body weight of newborn calves. Our choice was based mainly on our previous knowledge of calf weights from the Beverly and Kaminuriak herds (McEwen 1959; Kelsall 1968; Miller and Broughton 1974; Dauphiné 1976).

Calves that were intact or that had only their eye(s) and/or tongue or less than 0.25 kg of deep muscle tissue or viscera missing were used to calculate average whole body weight and the associated standard error of the mean value on an annual basis.

Table 2
Procedure for determining the most probable cause(s) of death of a calf whose carcass still contains the stomach and/or intestines with no milk present (evidence of malnutrition) and is missing the lungs

Variables to be evaluated

1. Estimated age < 1 d
2. Estimated age 1–4 d
3. Estimated age > 4 d
4. Never nursed — meconium still in intestines; stomach completely empty of solids, and walls of stomach clean
5. Nursed — no meconium present; stomach with at least traces of vegetation present, and particles adhering to stomach walls
6. Never walked — hoof class 1
7. Walked — hoof classes 2–4
8. Pelage not completely cleaned by dam — remnants of afterbirth adhering to, and patches of sticky amniotic fluids still on, pelage
9. Pelage completely cleaned by dam

Evaluation of existing combination of the above conditions and the best subsequent diagnosis

Combination
1 1 1 1
4 4 4 4
6 or 7 or 6 or 7
8 8 9 9

Diagnosis
1st probability = suspect neonatal atelectasis
2nd probability = suspect separation or abandonment

Combination
1 1 1 1 2 2 2 2 2
5 5 5 5 4 4 4 4 5
6 or 7 or 6 or 7 or 6 or 7 or 6 or 7 or 6
8 8 9 9 8 8 9 9 9

Diagnosis
equal probability = suspect neonatal atelectasis
= suspect separation or abandonment

Combination
2
5
7
9

Diagnosis
1st probability = suspect separation or abandonment
2nd probability = suspect neonatal atelectasis
3rd probability = suspect pneumonia

Combination
3 3
5 5
6 or 7
9 9

Diagnosis
1st probability = suspect separation or abandonment
2nd probability = suspect pneumonia

2.3. Estimating carcass utilization

We used three approaches for estimating carcass utilization of calves by predators. The first approach involved listing the major parts of the carcass that were missing: (1) deep muscle tissue; (2) viscera; (3) tongue; and (4) eye(s). The amounts of deep muscle tissue or viscera missing were then rated as being (1) all, (2) most, or (3) some used.

The second and third approaches, based on weight, were restricted to calves that were less than 7 d old at death, because large older calves would have caused greater variation in the overall sample. The second approach was to calculate minimum–maximum estimates of percent utilization of calf carcasses by predators by category of death as follows:

$$\text{Overall \% utilization} = \frac{a(x) - c}{a(x)} \times 100 \text{ to } \frac{b(x) - c}{b(x)} \times 100 \qquad [1]$$

where

a = annual mean viable whole body weight;
b = annual mean viable whole body weight plus two standard errors of the mean;
c = total weight of carcass remains in the category; and
x = number of carcasses in the category.

The third approach was to calculate percent utilization of individual carcasses of calves less than 7 d old at death as the average whole body weight (based on annual samples) minus carcass weight (for calves with more than 0.25 kg of muscle tissue or viscera missing) divided by the annual average whole body weight, all multiplied by 100. We chose five utilization classes to group individuals by cause of death: (1) 1–9%, "minimally used"; (2) 10–34%, "lightly used"; (3) 35–49%, "moderately used"; and (4) 50–69% and (5) 70–90%, both "heavily used." All carcasses lacking only eye(s) or tongues were classed as "minimally used," as was any calf whose carcass weight exceeded the mean annual whole body weight for the class.

Results and discussion

1. Causes of calf mortality

1.1. Predisposition to death by sex and age

In the overall 3-yr sample of 287 calves, 42.9% were males, 35.9% were females, and the sex of 21.1% was undeterminable. The calves of undiscernible sex prevented us from completely evaluating the relative proportions of females and males. However, we statistically tested the probability that the annual distributions of the sex of dead calves represented about an even sex ratio to see whether female or male calves were predisposed because of their sex to early deaths. At birth, the numbers of male compared with female calves is usually similar (i.e., about 50:50; actually, usually slightly in favour of males: Kelsall 1968; Skoog 1968; Bergerud 1969; Miller 1974). The sexes of the newborn calves sampled between 1981 and 1983 were about in accordance with the expected "secondary sex ratio" in newborn caribou. Those results indicate that neither female nor male calves were predisposed to early deaths because of their sex between 1981 and 1983.

Almost all (97.6%) of the 287 calves were estimated to be less than one week old at death, and most (77.0%) were 3 d of age or less. The distribution of the ages of the 280 calves 7 d old or less suggests that 3.24 calves 0–3 d old had died for every calf 4–7 d old (Fig. 5). Thus, newborn calves died at greater rates during the first 3 d of life than during the next 3–4 d of life ($\chi^2 = 78.66$, 1 df, $P < 0.001$).

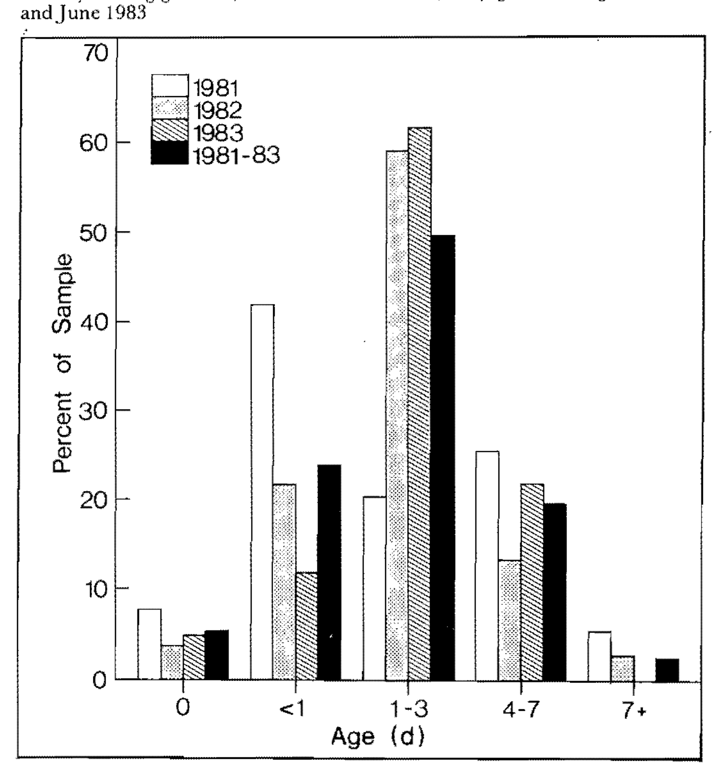
We used counts of cows with calves at heel or cows without calves but with distended udders in June 1981–83 to evaluate overall early calf mortality. We judge that a 10% total loss of calves at about one week or so of age in June is a reasonable approximation for each of the 3 yr of this study. As the counts were not taken exactly at the necessary time (taken on several days on either side) for our specific purpose, the resultant values are considered only as approximations of the overall early calf mortality at about one week of age in each of those 3 yr. All empirical impressions of early calf mortality in all 3 yr during calving and early postcalving support this value. All 3 yr of this study must be thought of as favourable to early calf survival in terms of prevailing weather on the calving grounds; thus, the results do not necessarily relate directly to years when unfavourable weather conditions might detrimentally influence early calf survival. However, we do argue that such years of extremely unfavourable weather would be relatively few over the long run when compared with years when weather did not seriously impact on newborn calves (Miller and Gunn 1986b).

1.2. The importance of adverse weather

Not a single calf's death during the 3 yr of this study could be linked directly or indirectly to exposure to adverse weather. We could not even demonstrate by postmortem examination or associated circumstantial evidence that any of the nine deaths of calves from pneumonia were initially caused by adverse weather. However, even when a detailed field necropsy is performed, separating and identifying the primary cause of death from the proximate cause are not always possible. Because weather on the Beverly calving grounds during calving and early postcalving was mostly favourable to calf survival in all 3 yr of this study, these results cannot be used *per se* to discount the possible role of adverse weather as an important cause of mortality among newborn barren-ground caribou.

As yet, no convincing data exist to support the belief (Kelsall 1968) that neonatal barren-ground caribou frequently succumb at high rates from exposure to adverse weather (Pruitt 1961; Miller and Gunn 1986b). The small samples of dead calves supposedly killed by exposure to

Figure 5
Distributions of estimated ages of 287 caribou calves at time of death, Beverly calving grounds, Northwest Territories, May–June 1981, June 1982, and June 1983



adverse weather that have been reported and the associated circumstantial evidence do not necessarily support the assumptions that the losses were weather-related or that high losses due to adverse weather are common. Healthy newborn barren-ground caribou appear well adapted physiologically and behaviourally to cope with all but the most severe weather at or about the time of calving. Significantly high mortality among newborn barren-ground caribou probably results from the additive effects of several unfavourable conditions: e.g., lack of forage (which would lower the nutritional status of pregnant cows to the extent that their calves would be light and weak) together with unusually bad weather.

1.3. Wolf predation

Wolf numbers were low on the calving grounds in all 3 yr. In 1981, we saw 12 wolves on 10 occasions — eight singles and two pairs. In 1982, we saw 10 wolves on six occasions — five singles and one group of five. In 1983, we saw only three solitary wolves; a fourth one was seen at another party's tent camp on the northwest corner of the calving grounds.

Wolf predation was the most important detected cause of death for newborn caribou calves during their first week of life on the Beverly calving grounds (Tables 3 and 4). Wolves probably killed about 5–7% (50–70% wolf kills × 10% early calf mortality) of the calf crop while the calves were still in their first week of life during June in 1981–83.

Between 1981 and 1983, the 19 calves whose cause of death was classified as suspected wolf predation comprised only 7.4% of the 257 calves that had causes of death assigned to them (Tables 3 and 4). In 1981, the 14 cases of suspected wolf predation increased the wolf kill to 37 calves, thereby increasing the overall importance of wolf predation to 59.7% (based on the 48 calves with known causes of death assigned to them plus the 14 suspected wolf kills). In 1982 and 1983, respectively, the cases of suspected wolf predation only slightly increased the known wolf kill of 69 and 62 calves to an apparent 71 and 65 calves.

The proportion of calves killed by wolves was lower in 1981 than in 1982 and 1983 (Tables 3 and 4); the differences are likely the consequences of differences in the hunting patterns of the wolves and/or the distribution of caribou groups in relation to factors that increase the vulnerability of the calves, e.g., soft, deep snowbanks. We do not believe that these differences can be explained by any annual variation in our sampling efforts. In all 3 yr, our searches bracketed the calving periods, and all known high- and medium-density calving areas were sampled in each year.

Examination of carcasses of wolf-killed calves showed that only a minor portion (12.8%) is likely to have been predisposed to being killed by wolves because of physiological or pathological disorders. Therefore, compensatory mortality seems to be a minor consideration in the evaluation of the impact of wolf predation on newborn caribou calves during calving and early postcalving of the Beverly herd. We assume that most (87.2%) calves one week old or less that were killed by wolves would have otherwise survived.

The age distributions of the wolf-killed calves in 1981 (Fig. 5, App. 1) suggest no selection by wolves on the basis of age ($\chi^2 = 0.04$, 1 df, $P > 0.80$). The age distributions in 1982–83 (Fig. 5, App. 1) indicate, to varying degrees, that wolves did not select newborn calves (< 1 d),

Table 3
Percent frequency of occurrence of causes of death in newborn caribou calves, Beverly calving grounds, Northwest Territories, May–June 1981, June 1982, and June 1983 (suspected cases and unknowns excluded)

	% mortality		
Cause of death	1981 (n = 48)	1982 (n = 90)	1983 (n = 87)
Wolf predation	47.9	76.7[a]	71.3
Neonatal atelectasis	22.9	5.6	2.3
Pathophysiological disorders	6.2	5.6	8.0
Separation/malnutrition	6.3	3.3	9.2
Fetal atelectasis	10.4	4.4	5.8
Pneumonia	4.2	4.4	3.4
Grizzly bear predation	2.1		

[a]The inclusion of 34 wolf-killed calves found on one occasion within a 3-km² area likely causes an overrepresentation of the percentage of wolf-killed calves. Thus, 69.8% is probably a better overall representative value for wolf predation, based on the 53 calf carcasses found outside the 3-km² area.

Table 4
Percent frequency of occurrence of causes of death in newborn caribou calves, Beverly calving grounds, Northwest Territories, May–June 1981, June 1982, and June 1983 (suspected cases included)

	% mortality		
Cause of death	1981 (n = 70)	1982 (n = 92)	1983 (n = 95)
Wolf predation	32.9	75.0[a]	65.3
Suspected wolf predation	20.0	2.2	3.1
Neonatal atelectasis	15.7	5.4	2.1
Pathophysiological disorders	4.3	5.4	7.4
Separation/malnutrition	4.3	3.3	8.4
Fetal atelectasis	7.1	4.4	5.3
Suspected atelectasis[b]	11.4		5.3
Pneumonia	2.9	4.3	3.1
Grizzly bear predation	1.4		

[a]The inclusion of 34 wolf-killed calves found on one occasion within a 3-km² area likely causes an overrepresentation of the percentage of wolf-killed calves. Thus, 69.8% is probably a better overall representative value for wolf predation.
[b]Fetal atelectasis could not be separated from neonatal atelectasis in all suspected cases.

but that there was apparently selection for younger (< 4 d) rather than older (≥ 4 d) calves ($\chi^2 = 17.78$, 1 df, $P < 0.001$, 1982; $\chi^2 = 12.56$, 1 df, $P < 0.001$, 1983). Other explanations are that more calving took place after mid-June than we thought or that late-born calves were especially vulnerable to wolf predation. An analysis of the age distribution of calves during the search period confirmed that wolves killed proportionately more younger (< 4 d) than older (4–7 d) calves ($\chi^2 = 29.82$, 1 df, $P < 0.001$). Regardless of this apparent selection by age, calves remained vulnerable throughout their first week of life.

The sex distributions of the wolf-killed calves (App. 1) (χ^2, 1 df: $P > 0.10$, 1981; $P > 0.30$, 1982; $P > 0.90$, 1983) suggest that the wolves were not selecting calves on the basis of sex, nor were calves predisposed to wolf predation because of their sex. This conclusion holds true even when the sexes of the calves of unknown sex are assigned according to the observed ratio for the calves of known sex in each year (χ^2, 1 df: $P > 0.10$, 1981; $P > 0.20$, 1982; $P > 0.90$, 1983) or the expected 50:50 sex ratio (χ^2, 1 df: $P > 0.70$, 1981; $P > 0.30$, 1982; $P > 0.90$, 1983).

Many authors have argued about the importance of wolf predation on newborn caribou calves, but their evidence was based on only meagre samples of wolf-killed calves, if any (e.g., Murie 1935; Clarke 1940; Murie 1944; Banfield 1954; Harper 1955; Crisler 1956; Kelsall 1957, 1960, 1968; Pruitt 1960; Skoog 1968; Bergerud 1971, 1974*a*, 1974*b*, 1978, 1980; Clark 1971; Kuyt 1972; Parker 1972; Miller 1974, 1982, 1983; Miller and Broughton 1974; Bos 1975; Cumming 1975; Curatolo 1975; Miller

1975; Davis *et al.* 1978; Davis and Valkenburg 1978, 1979, 1981; Davis and Preston 1980; Boertje 1981; Fleck and Gunn 1982; Gasaway *et al.* 1983). Those reports of calf mortality due to predation cannot be directly compared with this study, because they include neonatal mortality of caribou over several weeks or months. Relatively few data are reported on calves estimated to be two weeks of age or less.

The results of this study are most comparable with those of the study of calf mortality in the Kaminuriak herd in June 1970 (Miller and Broughton 1974). In the Kaminuriak study, wolf kills amounted to 19.4% (6/31) for calves 7 d old or less and 25.6% (11/43) for calves 14 d old or less. Wolf predation during the entire period of calving and early postcalving was 31.6% (18/57) for calves seven weeks old or less. Thus, the percentages of newborn calf mortality attributed to wolf predation on the Kaminuriak calving grounds in 1970 were lower than those found in each year of this study on the Beverly calving grounds, although more wolf sightings (n = 19) were made in June 1970 on the Kaminuriak calving grounds than were made on the Beverly calving grounds during any of the 3 yr of this study (n = 12 in 1981; n = 10 in 1982; and n = 3 in 1983).

Essentially all studies in North America considering wolves and caribou calves have offered the same two general conclusions: (1) wolves are important predators of newborn calves; and (2) wolf predation (and predation by all other predators) is most severe in the first week or two of the calf's life (e.g., Murie 1944; Kelsall 1968; Skoog 1968).

Managers and biologists seem to accept that predation is often an important cause of mortality of newborn caribou in North America. For the Beverly herd, the wolf was the principal predator in 1981–83 and was responsible for at least one-half of the early calf mortality. Findings in 1978–79 by Heard and Decker (1980) support this conclusion.

1.3.1. Carcass utilization by wolves

In 1981, 1982, and 1983, 19 of 23, 51 of 69, and 35 of 62 calves killed by wolves were fed on by both wolves and gulls (Miller *et al.* 1988). Of the rest, only two were fed on by wolves only, the remainder being scavenged by gulls (*Larus* spp.) only or remaining unutilized. It was often difficult to separate the amount of carcass utilization by wolves from that by gulls.

The rate of utilization among carcasses in this study varied considerably by year (Miller *et al.* 1988). In 1981, 12 of 20 carcasses of calves killed by wolves were heavily utilized, and four were lightly or minimally utilized. In 1982 and 1983, utilization ranged from 1 to 90%, and overall utilization was low (Table 5).

Table 5
Approximate estimates of utilization by predators or scavengers of 152 carcasses of wolf-killed caribou calves one week old, Beverly calving grounds, Northwest Territories, May–June 1981, June 1982, and June 1983

		No.	% in utilization class[a]				
Year	Sample size	fed on	1–9	10–34	35–49	50–69	70–90
1981	23	20	15	5	20	15	45
1982	67[b]	66	24	34	12	24	6
1983	62	60	22	38	22	12	6

[a]Calculated for carcasses with deep muscle tissue or viscera missing by assuming: % utilization = (average whole body weight − carcass weight) / (average whole body weight) (average whole body weight = 5.70 kg [1981], 6.09 kg [1982], and 5.42 kg [1983]).
[b]In 1982, two wolf-killed calves estimated to be 7+ d old were not included in this estimate.

Table 6
Distributions of caribou carcasses by degree of clumping and by death category, Beverly calving grounds, Northwest Territories, May–June 1981, June 1982, and June 1983

Clumping		No. of calves by death category					
Clump size	No. of clumps	Wolf predation	Suspected wolf predation	Non-predator causes	Unknown	No. of adult cows	Total
1981							
1	70	13	13	30	9	5	70
2	5	5[a]	1	2		2	10
3	2	6					6
1982							
1	46	17	2	12	12	3	46
2	2	4					4
3	2	3		2		1	6
4	1			2		2	4
14	1	11		1	2		14
39	1	34		4	1		39
1983							
1	51	18		21	4	8	51
2	8	9		4	1	2	16
3	2	4		1		1	6
4	2	7		1			8
5	1	5					5
6	1	5			1		6
7	1	6	1				7
13	1	8	2	3			13

[a]Includes one grizzly bear-killed calf that was found along with its mother, who had also apparently been killed by a grizzly bear.

In all 3 yr, wolves usually took the viscera first, including the stomach contents, followed by (if at all) deep muscle tissue. This suggests that wolves killing newborn caribou calves may be specialized feeders, taking only high-quality milk curds and some viscera. Another possibility is that wolves may totally consume some calves, although we found no evidence of such complete utilization.

1.3.2. Surplus and/or excessive killing by wolves

If numbers of wolves were as low on the Beverly calving grounds as our sightings suggest, we can conclude that each wolf was killing many newborn calves, and that the rate of killing by each wolf is higher than previously generally thought by others. Our finding of 34 calves all killed within a short time on a 3-km² area is the best example of "surplus killing" of newborn caribou by wolves (Miller *et al.* 1985). Our finding in this study that 68.8% (106) of all wolf-killed calves were clumped associations (Table 6), usually with little or no carcass utilization by wolves, is further evidence of excessive killing of newborn calves by wolves.

1.4. Atelectasis[1]

Atelectasis was the second most important cause of death of newborn calves (14.9%, n = 225; 17.5%, n = 257) (Tables 3 and 4). This was due principally to the large number of cases observed in 1981, for which we have no explanation. Dead calves less than 1 d old were overrepresented in 1981 compared with 1982 or 1983 ($\chi^2 = 24.17$, 1 df, $P < 0.005$). However, whether or not there is any cause and effect relationship between this fact and the relatively high number of cases of atelectasis in 1981 compared with 1982 and 1983 cannot be discerned. We found 45 cases of atelectasis: (1) 14 cases of fetal atelec-

[1]Fetal atelectasis: essentially stillbirths, but possibly including some deaths resulting from complications of unknown origin at the time of birth; neonatal atelectasis: premature births, *in utero* complications, or complications at or about the time of birth.

tasis (10 males and four females); (2) 18 cases of neonatal atelectasis (10 females and eight males); and (3) 13 cases of suspected fetal or neonatal atelectasis (six unknowns, four females, and three males).

The relative occurrence of calves with essentially whole body weights of less than 4.0 kg was greater than expected among calves with atelectasis (seven) than among calves that died of other causes (two) (χ^2 = 10.70, 1 df, $P < 0.01$). This high level of nonviable body weights for cases of atelectasis, mostly the neonatal type, seemingly reflects the likelihood of premature births or complications in fetal development being linked with this condition.

Our observed rates of atelectasis (App. 1) are higher than reported hitherto. It is likely that atelectasis (other than observed stillbirths) in dead caribou calves had earlier gone undetected because the lungs were not examined for the condition. For example, pathological examination of lung tissue was carried out on only seven of the 100+ dead calves found on the Beverly calving grounds in 1958: lung tissue from six of the seven calves examined revealed degrees of atelectasis (Kelsall 1960).

Methods used in the most recent study of calf mortality in the Porcupine caribou herd in Alaska are biased against finding stillbirths and neonatal atelectasis (as well as all other types of mortality that occur only, or more often, during the first day or so of life), as the researchers started by capturing and radio-collaring healthy, live calves already usually 1 or a few days old (Mauer *et al.* 1983; Whitten *et al.* 1984). Samples of unmarked calves were small, and atelectasis was not detected or reported. In addition to radio-collaring calves, these researchers also radio-collared cows and followed the fates of their unmarked calves. They were unable to determine the cause of mortality in most instances and detected loss of calves by their disappearances or the presence of radio-collared cows with distended udders with no calves being present. Those data are currently being analyzed; however, preliminary results indicate that calves of radio-collared cows died at a higher rate than the collared calves — thus, atelectasis could have been involved (G.W. Garner, pers. commun.).

1.5. Pathophysiological disorders

Death of calves resulting from pathological conditions or physiological disorders was the third most important cause of death of newborn calves in 1981–83 (6.7%, n = 225; 5.8%, n = 257) (Tables 3 and 4). We found no predisposition to death due to sex for calves in this category (App. 1). Most (86.7%) of the calves in this category were less than 4 d old at death (App. 1).

Specific pathological or physiological conditions (other than pneumonia) were of low occurrence and varied, especially among years. Therefore, all calves that died of such conditions except pneumonia were placed in the collective pathophysiological category to better allow direct comparisons between or among present and future samples.

The most common cause of death (seven of 15 cases) in this category was shock, stress, or drowning from entrapment in frigid waters or slushy mires along the shores of lakes and streams. Six of those seven cases occurred in 1983, when an abrupt warming trend in the second week of June and the seasonal lack of rain on the calving grounds created difficult travelling conditions for calves. The slush mires created by melting deep snowbanks along the shores of lakes, rivers, and streams were death traps for newborn calves in June 1983 for about 10 d, and the six dead calves were found on 10, 11, and 13 June. Calves drowned or died of fatigue, stress, or shock while trying to traverse these slush mires. Although conditions for potential entrapment and subsequent death most likely occur in all or most years on the calving grounds during late calving or early postcalving, they are probably not as bad in most years as they were in June 1983.

Kelsall (1960) referred to calves mired in unseasonable deep snow as one of the examples of how adverse weather and a late season indirectly cause calf mortality. The slush mires would occur regardless of the lateness of the season, however, because snowbanks are always present during calving — the important consideration is whether they are firm or slushy, and how fast they break down after becoming slushy. A late season would likely prevent or at least greatly reduce this type of mortality, because the snowbanks would stay hard packed or refreeze nightly during early June, allowing the newborn calves to traverse them without difficulty. By late June, older calves would be better able to cope with the slushy areas in a late season.

Drowning is likely to be more important as a cause of calf mortality during July and early August when post-calving aggregations are frequently making water crossings on large water bodies. The most significant example of the possible importance of calf drownings comes from Kelsall (1968), who reported the estimated loss of 300 calves among 450 caribou of the Beverly herd that drowned at the narrows in Aberdeen Lake in July 1951.

Other more varied and less frequent conditions leading to deaths placed in this category included:
(1) accidental trauma or intraspecific strife (calf being stepped on or kicked by the maternal cow or some other caribou);
(2) malnutrition/starvation, due to the maternal cow's death, or apparently as a result of odd articulation of the calf's foreleg (probably preventing the calf from keeping up with its mother), or apparently due to the calf's "parrot mouth" condition (probably interfering with or preventing nursing);
(3) broken leg (calf found alive but would have eventually been taken by a predator or succumbed to a malnutrition/starvation complex;
(4) peritonitis, associated with infection of umbilical cord; and
(5) hydrocephalus condition — abnormal displacement of frontal bones of skull (proximal cause of death undetermined because carcass was too decomposed to obtain brain tissue for histopathological examination).

Calves during their first day or two of life readily stumble and can be accidentally knocked over and trodden on or trampled, especially if the animals are frightened or panicked by an approaching predator or human activity. Calves with broken legs are not the only consequence; we also found calves with ruptured livers or subcutaneous hemorrhages, and one calf had a liver abscess that may have started as an internal injury after the calf had been stepped on.

We found only three single dead calves during the 3 yr of this study that exhibited trauma most likely caused by adult caribou. The cause(s) of those traumas could not be positively determined, and no absolute distinction could be made as to whether the fatal injuries were accidental or caused by deliberate acts of aggression. This point is important, as a clear distinction should be made between mortality of a newborn calf due to accidental injury and mortality due to intraspecific strife (e.g., de Vos 1960).

A maternal cow being aggressive to her own calf was rarely seen on the Beverly calving grounds during 1981–83 (cf. Jingfors *et al.* 1982; Gunn *et al.* 1983; Miller and Gunn 1986*a*).

Although Thing and Clausen (1980) and Clausen *et al.* (1980) reported epidemic infection and heavy parasitic loads leading to massive die-offs of caribou calves during their first summer of life in Greenland, we found no evidence of heavy parasite loads and only one possible *Escherichia coli* infection in this study.

The most important cause of fetal mortality in caribou is probably diseases causing abortion, such as brucellosis (e.g., Neiland *et al.* 1968; Skoog 1968; Neiland and Dukeminier 1972). Brucellosis has never been found on a large scale in Canadian barren-ground caribou herds (Broughton *et al.* 1970), but even epidemic levels could have escaped detection. In our study on the Beverly caribou calving grounds, we did not observe retained placentas or excessive hemorrhage from the vulva. A few cases of hygroma, large swelling of the carpal joint (which is common in cattle [*Bovis* spp.] infected with brucellosis), have been reported from the Beverly herd (CWS, Pathology Section, unpubl. data). Over 200 serum samples have been tested from the Beverly herd for brucellosis, and only two positive and two suspicious reactions have been detected (CWS, Pathology Section, unpubl. data). This low level of serological evidence of brucellosis would indicate that brucellosis is not significant in the Beverly caribou in terms of effects on reproduction. In contrast, brucellosis appeared to be a problem in the Arctic herds in Alaska (e.g., Neiland *et al.* 1968; Skoog 1968; Neiland and Dukeminier 1972).

1.6. Separation or abandonment (malnutrition/starvation complex)

We found 14 dead calves that we assigned to this category of death (eight males, six females). Separation or abandonment by the maternal cow leading to the death of the calf from a malnutrition/starvation complex was the fourth most important cause of mortality of newborn calves in 1981–83 (6.2%, n = 225; 5.5%, n = 257) (Tables 3 and 4). We found no predisposition to death due to sex for calves in this category (App. 1). Most (57.1%) of the calves in this category were less than 4 d old at death (App. 1).

We assume that calves die from the lack of their mothers' milk and not from the lack of forage, so we refer to the cause of death as a "malnutrition/starvation complex." Starvation is defined as death caused by the lack of anything to eat (empty stomach), and death by malnutrition as the result of eating food that does not provide enough or any nourishment (forage in the stomach but no milk). Death usually results from malnutrition rather than starvation, which rarely occurs in the wild (cf. Mautz 1978).

Deaths in this category result from a combination of causes. First, the calf becomes separated from its mother, likely through abandonment, wolf harassment, or human activities. Then, if the calf is not killed by a predator, it subsequently succumbs to a malnutrition/starvation complex, which is the proximal cause of death.

Pneumonia can often be a contributing factor to the deaths of newborn calves that have become separated from their mothers (e.g., six of eight calves found in June 1983). The pneumonia follows the general deterioration of the calf as it suffers from malnutrition/starvation. Regardless of the proximal agents (malnutrition, disease, or predator)

Table 7
Percent distribution[a] of pneumonic patches in the lobes of the lungs of nine carcasses of caribou calves that died from pneumonia or a combination of pneumonia and malnutrition, Beverly calving grounds, Northwest Territories, June 1983

			% pneumonic		
			Diaphragmatic lobes		
Sex	Age (d)	Weight (kg)	Left	Right	Apical lobe
Female	1–3	3.75[c]	100	100	20
Female	1–3	5.0	20	100	0
Female[b]	1–3	5.5	10	10	80
Female[b]	1–3	5.75	70[d]	70[d]	70[d]
Female[b]	4–7	3.75	25	95	0
Female[b]	4–7	6.25	20	40	0
Female[b]	4–7	6.5	90	15	50
Male[b]	1–3	4.75	100	5	0
Male	4–7	6.5	100	100	0

[a]Percent distribution was determined by visual estimate.
[b]The primary cause of death of these six calves (five females and one male) appeared to be separation from their maternal cows with subsequent actual death from a malnutrition/starvation complex plus complications from pneumonic conditions.
[c]Partial body weight only — carcass had been extensively scavenged.
[d]Lungs were covered with dark purple blotches (samples were taken for histopathological examinations in the laboratory, and pneumonia was confirmed).

involved in the actual deaths, the primary cause is separation of the calf from the cow.

Separation from or abandonment of calves by maternal cows on the Kaminuriak calving grounds in June 1970 was involved in at least five and as many as 13 cases (Miller and Broughton 1974); at least eight of the calves were probably predisposed to death because of respiratory complications that may also have influenced or even caused their separations from their mothers.

In a recent Alaskan study of mortality in about the first month of life of radio-collared calves in the Porcupine caribou herd, natural abandonment accounted for two of 12 dead calves in 1982 (Mauer *et al.* 1983) and three of 11 in 1983 (Whitten *et al.* 1984). These results are not strictly comparable with ours because the calves ranged in age from a few days to three weeks. In Russia, Baskin (1983) compiled mortality data on domestic reindeer calves from 1934 to 1954. Abandonment by the maternal cow accounted for 16.6% (n = 4797) of deaths of newborn reindeer calves during the first month of life on tundra and 18.0% (n = 4926) on taiga.

We suggest that much of the apparent abandonment of calves is by young, primiparous cows — they are probably the least well nourished and in the poorest physical condition of all the breeding cows, with the possible exception of extremely old cows. Studies by Espmark (1980) on female penned reindeer in Norway support this supposition. In years of severe winters, however, even prime-aged, multiparous cows may be undernourished, although data to support this are still lacking.

1.7. Pneumonia

We found nine calves that apparently died from pneumonia (five females, four males), the fifth most important cause of death for newborn calves in 1981–83 (4.0%, n = 225; 3.5%, n = 257) (Tables 3 and 4). Percent distributions of pneumonic patches in the lobes of the lungs varied widely among carcasses (Table 7). We found no predisposition to death due to sex for calves in this category (App. 1). Most (66.7%) of the calves in this category were less than 4 d old at death (App. 1).

We separate pneumonia from other pathophysiological disorders because pneumonia is supposedly an important cause of mortality of newborn reindeer calves in years of unfavourable weather (Zhigunov 1961). The supposed importance of pneumonia for newborn caribou mortality was suggested as the reason why Kaminuriak herd cows calve on relatively dry, rugged terrain (Parker 1972). Even in years with weather favourable to calf survival during calving and early postcalving, pneumonia may be of some importance as a complicating factor in general body deterioration in combination with poor nutrition.

Pneumonia in newborn caribou in North America has likely often gone undetected because the necessary postmortem examinations were not performed. In 1958, the pathological examination of lung tissue from seven dead calves revealed that one of them had a severe pneumonia (Kelsall 1960). Bergerud (1971) reported only two young calves with pneumonia in 114 dead young calves found between 1957 and 1967 in Newfoundland.

1.8. Grizzly bear predation

Grizzly bears were infrequently seen on the calving grounds in 1981 and 1983, and none was seen in 1982. In 1981, we saw nine grizzly bears: single adults on seven occasions, and a female with a yearling on two occasions. In 1983, we saw only two solitary adult grizzly bears.

The finding of only two grizzly bear-killed calves during this study (Tables 3 and 4) leads to the conclusion that grizzly bear predation is not an important cause of death for caribou calves at the present time. However, consumption of newborn calf carcasses by grizzly bears, whether as a result of predation or of scavenging, is apparently most often so complete that it would go undetected (usually only the odd limb is found, and it is assumed that the rest of the calf's carcass was consumed by a bear).

Although we saw only 11 grizzly bears in this study, there has been (Kelsall 1960; Cooper 1981) a relatively large reservoir of grizzly bears along the Thelon River system west of Beverly Lake and south of the current (1981–83) Beverly calving grounds. When and if numbers of grizzly bears increase on the Beverly calving grounds, some bears will likely learn to hunt both newborn calves and adult female caribou. This could indeed occur if bears expand their May–June range northward or if the Beverly caribou revert to more southerly, previously used calving areas (Fleck and Gunn 1982). This possibility suggests that more effort should be made to record by date the numbers and precise locations of grizzly bears seen on the Beverly calving grounds at or about calving time. (This need for better records also applies to sightings of wolves and all other potential predators of newborn calves). It is impossible to determine from current records the actual locations of reported sightings of most wolves or grizzly bears and their relation to the calving grounds used in that year.

2. Causes of cow mortality

The samples of seven, six, and 11 dead cows necropsied that died shortly before, during, or shortly after calving in 1981, 1982, and 1983 are too small to allow evaluation of the cause and magnitude of mortality among breeding females of the Beverly caribou herd in those years. The high proportion of cows killed by predators (60.9%) may reflect the actual threat of wolves and grizzly bears to parturient or maternal cows at about the time of calving, but cannot be extrapolated.

The seven, nine, and 15 dead cows found during about 44, 41, and 45 h of low-level helicopter flying support our field impression that mortality of breeding females from either predation or birth complications was low relative to the total number of breeding females on the Beverly calving grounds. The mortality of breeding females of the Beverly herd at calving time (subjectively estimated as follows) gives support to our belief that mortality of breeding females was low at calving time.

We located carcasses of only seven, nine, and 15 adult cows compared with 79, 107, and 101 calves during the 3 yr. Assuming that carcasses of cows are no harder to detect than those of calves, and that early mortality of calves at calving time was about 10% of the entire calf crop in each of the 3 yr, then we suggest that the level of mortality of breeding females during the calving period was about 1.0% of the entire breeding female segment of the Beverly herd, in line with our empirical impressions. Although the annual percentages are low, they represent 890, 840, and 1490 breeding females and their offspring removed from the potential growth of the herd, if there were 100 000 breeding cows.

Predation accounted for about 61% (14) of the deaths of the 23 cows for which the causes of death could be determined between June 1981 and June 1983 — nine were killed by wolves and five by grizzly bears. The remaining nine (39%) of the 23 cows died from birth complications and associated pathological problems.

There was no direct evidence to indicate that the 14 cows were predisposed to predation by wolves or grizzly bears. All but one (4%, 10+ yr) of these cows were of prime age (74%, 4–8 yr) or young (22%, 2–3 yr). Only one of the 2-yr-olds was not pregnant.

Our results show the need to include the mortality of breeding females at calving time as part of any formula for evaluating the population dynamics of any migratory barren-ground caribou herd.

3. Representativeness of the samples in 1981–83

A systematic aerial search procedure would allow evaluation of the representativeness of the annual samples of dead calves and cows relative to the overall calf crop and the breeding cow segment. To collect adequate samples we would need (1) accurate counts of the number of breeding cows occupying each segment of the search area during calving and early postcalving; and (2) estimates of the amount of time those animals spent on each of those segments. Obtaining such counts and estimates was not feasible in this study, and we would likely get a smaller sample of dead caribou if we carried out systematic searches over the entire calving grounds in each year. Therefore, we decided to carry out unsystematic aerial searches of segments of known relatively high occupation. Effort expended was not always proportional to the assumed relative use of the segments, because the sampling effort was spread over as large an area of the calving grounds as possible (all known areas of high and medium densities of calving were sampled in each year) to maximize both the size and representativeness of the annual samples.

Our searching efforts were spread throughout early to late calving and into early postcalving to increase the representativeness of the samples by time. Also, although searching new areas over time might have reduced sample sizes, as few carcasses were available in early calving, it increased the level of representation.

We cannot determine the representativeness of the samples of dead calves found in terms of the early mortality of newborn calves of the entire calf crops in 1981–83 in the Beverly herd. We can, however, examine the results of three of our sampling approaches for ways the sample might deviate from mortalities at the population level. The presence of a dead calf can be indicated by a gull or an Arctic fox (*Alopex lagopus*), or by a maternal cow's behaviour. Also, additional wolf kills are often found in the immediate vicinity of a wolf-killed calf or cow (clumped associations; Miller and Gunn 1986*a*).

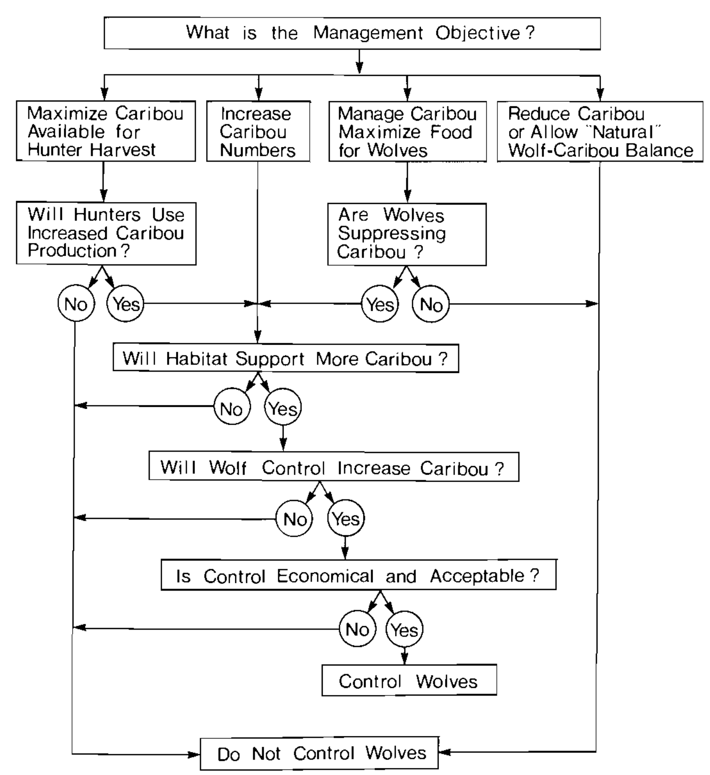
Analyses of our data showed there was no reason to believe that visual clues to carcass locations markedly influenced the proportional representation of wolf kills or nonpredator deaths in 1981–83. Proportionately more calves that died from nonpredator causes had other animals, especially maternal cows, present with them when found by us than did predator-killed calves (χ^2 = 46.19, 1 df, $P < 0.005$).

4. Implications of results for management

4.1. Wolf predation

Wolf predation was the most important cause of early calf mortality in this study, and wolves are the most readily manageable of all of the detected causes of early calf mortality. Estimates of numbers of caribou required to support a wolf on an annual basis (e.g., Clarke 1940; Kelsall 1968; Kuyt 1972) are not applicable to an evaluation of what a single wolf might kill in terms of newborn calves. Existing data indicate that wolves are killing newborn calves in excess of their needs (Miller *et al.* 1985; Miller and Gunn 1986*a*), that they are not subsequently using those kills, and that the impact of even a few wolves on newborn calves can be substantial. Thus, one key to maximizing early calf survival may be to have few or no wolves present on the calving grounds.

Figure 6
Proposed logic for the use of wolf control in caribou management (after Connolly 1978)



There are several pertinent factors to consider before implementation of wolf control (Fig. 6). Management decisions in the interim may be necessary despite a lack of a sound biological understanding of the wolf–caribou relationship.

The main consideration should be that wolf control will not have irreversible impacts on any of the species involved, i.e., the target predator (wolves), the benefiting prey (caribou), or any exposed, nontarget, susceptible animals. If northern mainland Canadian wolves hold spatial territories, these territories must be determined by the availability of prey and therefore have to be mobile and centred on the caribou over time. The possibility that wolves dependent upon migratory barren-ground caribou do not have annual fixed spatial territories is important in the application of any wolf control. Any potential approach to wolf control on the ranges of the Beverly herd will have to be tied to the actual locations of the caribou at any given time and not to fixed land areas.

The management of caribou should include the maintenance of wolf numbers at levels that maximize human utilization of the caribou resource and at the same time conserve the large herds of migratory barren-ground caribou and the wolf populations associated with them. Specific recommendations for wolf maintenance are few, because for the most part they would fall outside the biological scope of this report into the realm of sociopolitical considerations.

It is recommended that no wolf control be carried out on the calving grounds at calving time or during early postcalving, because it would be ineffective, inefficient, expensive, and probably disruptive to cows and newborn calves. The most effective and efficient time to control wolves is most likely in late winter and spring (March – late May) of the year, when many wolves are in close company with the migrating caribou. If poison bait is not used, possibly cash incentives could be offered to trappers and hunters to take wolves at that time of the year. Special aerial shooting teams could be effective on tundra ranges during that period, but costly.

Bergerud (1980) pointed out that the best evidence for the significance of wolf predation in calf mortality comes from improvements in calf survival when wolf control was carried out in Alaska, British Columbia, and the Northwest Territories. Intensive and effective monitoring of recruitments to the caribou herd during and after wolf control will be necessary to demonstrate that the desired effects were produced by reducing wolf numbers.

Wolf control may have a place in an intensive caribou management program, but a possibly more efficient and less costly management exercise would be an annual reduction in the harvest of 3+-yr-old female caribou. Reducing the harvest of 3+-yr-old females by 1000 animals yearly (by shooting more males, if necessary) for a 50-yr period would, we have calculated, theoretically put a yearly average of about 3360 additional 3-yr-old caribou into the Beverly herd at 40% calf survival, or 12 100 at 66% calf survival. Thus, retaining a higher number of breeding female caribou rather than saving the same number of newborn calves over an extended period of time (50 yr) theoretically would result in 4.3 times greater production of 3-yr-old caribou at 40% calf survival, or 2.8 times greater production at 66% calf survival.

4.2. Nonpredator deaths

The three most important causes of death for caribou calves in this study, other than wolf predation, were atelectasis, pathophysiological disorders, and separation/abandonment. Fetal or neonatal atelectasis can probably not be reduced by management actions if those conditions are related, as suggested, to the physical condition of the dam, which is governed by the quality and quantity of her forage intake. The only form of range management that is likely to be practised is forest fire control on the winter range of the Beverly herd. There is, however, no evidence to suggest that Beverly caribou were nutritionally stressed during 1981, 1982, or 1983, when Beverly females had high nutritional status and experienced high rates of pregnancy (D.C. Thomas, unpubl. data). If neonatal atelectasis results from the inspiration of placental fluids at parturition, the possibility exists that any human disturbance at the time of calving could lead to an increased occurrence of neonatal atelectasis. The regulation of human activities associated with mineral exploration on calving grounds has been attempted (Gunn 1984), but exclusion of all human activities is difficult.

The only manageable aspect of death from pathophysiological disorders would be through minimization of human activities that have the potential to force newborn calves into lethal situations (e.g., trampling, entrapment in slush mires, aggressive actions brought on by agitation during fright or flight). Also, because the cow–calf bond in caribou can be prevented, broken, or disrupted by human interference or disturbance, minimization of human activities on the calving grounds at calving and during postcalving should reduce calf separation from or abandonment by maternal cows.

4.3. Summary

In summary, the conclusions we reach are as follows:

(1) Intensive management of caribou should include the maintenance (control) of wolf numbers at levels that allow maximum utilization of the caribou resource by people, while at the same time conserving the large migratory herds of barren-ground caribou and the wolf populations associated with them.

(2) No wolf control measures should be carried out on the calving grounds at calving time or during early postcalving, because such activities would likely be ineffective, inefficient, and exceptionally costly, and could be disruptive to the calving segment of the herd.

(3) The most effective and efficient period for carrying out wolf control would most likely be from March into late May when most wolves are in close company with migrating caribou (including wolves that would go to the calving grounds and those that would remain in wolf denning areas).

(4) An educational program should be started to encourage users to select male caribou at all times of the year rather than female caribou during winter and spring. Significantly reducing the annual kill of females could have marked beneficial effect on the long-term reproduction capacity of the herd. Such action could permit greater annual harvest while at the same time allowing the herd to grow at faster rates. The herd must grow in order to sustain the likely future human demands on it.

(5) The Beverly calving grounds (and all other calving grounds) should be permanently protected against human disturbance to help assure maximum early calf survival or to prevent any marked increases in early calf mortality. A relatively stable calving and early postcalving environment is likely essential for maximizing early calf survival. The general lack, or low levels, of human disturbance in the past cannot be used to predict the probable impacts of man's activities on caribou on calving grounds in the future. The current "Caribou Protection Measures" in use on the Beverly and Kaminuriak calving grounds are at best a stopgap exercise that would be insufficient in the face of the development that would follow a significant find of some nonrenewable resource. Any manager who remains complacent about the possible future impacts of humans on the calving grounds of large migratory herds of barren-ground caribou is running the risk of jeopardizing a valuable renewable resource, perhaps irrevocably.

Conclusions

1. Weather was basically favourable to calf survival throughout calving and early postcalving periods in all 3 yr of the study (1981–83).

2. Neither female nor male calves were predisposed to early deaths because of their sex.

3. Newborn calves apparently died at greater rates during the first 3–4 d of life than during the next 3–4 d of life.

4. Wolf predation was the single most important cause of newborn (≤7 d old) calf mortality (68.5%).

5. Evidence was obtained for "surplus killing" (no utilization of carcass); "excessive killing" (only slight utilization of carcass); and "specialized feeding" (apparent preferences for milk curds and viscera over muscle tissue) by wolves.

6. Wolf predation as a form of compensatory mortality was negligible and thus only a minor consideration in the evaluation of the impact of wolf predation on newborn caribou calves.

7. Wolves are the most readily manageable of all of the causes of early calf death detected in this study.

8. Grizzly bear predation on newborn calves was not significant in this study.

9. Atelectasis was the second most important cause (14.9%) of death of newborn calves (17.5%, including suspected cases).

10. Mortality of newborn calves from pathological conditions or physiological disorders was the third most important cause of death of newborn calves (6.2%).

11. Separation from or abandonment by the maternal cow subsequently leading to the calf succumbing to a malnutrition/starvation complex was the fourth most important cause of death of newborn calves.

12. Minimization of human activities on the calving grounds at calving and during postcalving is a possible management measure that would help safeguard against atelectasis, pathophysiological disorders, and separation/abandonment.

13. Pneumonia was the fifth most important cause of death of newborn calves (3.7%). The relatively low rate of deaths from pneumonia most likely reflects the essentially favourable weather that prevailed during calving and early postcalving in all 3 yr of the study.

14. Wolves were the major predators of adult female caribou on the calving grounds, based on the small sample found (but grizzly bears could be relatively important, at least in some years).

15. Grizzly bear predation was more important on cows than on calves in June 1981 and 1983.

Recommendations

1. We recommend that helicopter searches for dead calves be routinely carried out as part of the aerial survey program on the calving grounds. Because helicopter support is already necessary for obtaining adequate calf/cow counts on the calving grounds in association with aerial calving grounds surveys, additional costs for searching for dead calves would not be great.

2. We recommend that the exact number of predators and their locations by latitude and longitude be routinely recorded during all future surveys of the calving grounds. Better records should be an essential part of any intensive management program, to allow evaluations of kinds and numbers of predators occupying the calving grounds during the calving and postcalving periods.

3. We recommend that future studies of caribou calf mortality at or about calving should include the following elements: (*a*) a large sample of radio-collared calves (preferably at least 100 calves) to quantitatively document the chronology and magnitude of calf mortality and to be compared with the sample of unmarked dead calves; (*b*) a sample of radio-collared pregnant cows for evaluation of rates of reproduction and data on cow and calf mortalities (the animals will serve as "controls" for the collared calf sample); (*c*) systematic aerial surveys of the calving grounds from precalving through calving into early postcalving to determine distributions and size of the breeding segment of the herd on the calving grounds; (*d*) extensive systematic helicopter searches for dead calves and cows, encompassing at least the entire core of the calving grounds from the beginning of calving through early postcalving, to more precisely define the various causes of mortality; and (*e*) large samples from extensive systematic ground counts on cows with calves at heel or cows without calves but with distended udders (also with or without antlers, although this characteristic can be misleading as an indicator of pregnancy at least in some years) to evaluate calf production and survival.

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Appendix

Appendix 1
Distributions of estimated ages of 287 caribou calves at time of death by cause of death, Beverly calving grounds, Northwest Territories, May–June 1981, June 1982, and June 1983

Cause of death by sex	Sample size			No. in age class by cause of death: 0 d			< 1 d[a]			1–3 d			4–7 d			7+ d		
	1981	1982	1983	1981	1982	1983	1981	1982	1983	1981	1982	1983	1981	1982	1983	1981	1982	1983
Wolf predation	23	69	62															
Female								2	1		20	17	4	2	8			
Male							2	5	3	2	18	18	4	7	7		2	
Unknown							3	4		4	6	6	4	3	2			
Suspected wolf predation	14	2	3															
Female							1			1	1	1	1			1		
Male							1						2			2		
Unknown							3	1		2					2			
Neonatal atelectasis	11	5	2															
Female							4	1		3	2							
Male							4		2		2							
Pathophysiological disorders	3	5	7															
Female										1		3	1					
Male								1			2	4					1	
Unknown							1	1										
Separation/ malnutrition	3	3	8															
Female												2	3		3			
Male									1		3	2						
Fetal atelectasis	5	4	5															
Female				1		3												
Male				4	4	2												
Suspected fetal or neonatal atelectasis	8	0	5															
Female							2		2									
Male							1		2									
Unknown							5		1									
Pneumonia	2	4	3															
Female											1	2	1	1		1		
Male											2	1						
Grizzly bear predation	1	0	0															
Female				1														
Unknowns	9	15	6															
Female							2	1			1	2						
Male							3	2		1	3	1		1				
Unknown							1	5		2	2	3						

[a]Some of the calves in this age class that were suspected cases of fetal or neonatal atelectasis were most likely stillborn and would then be 0 d old at death.

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