From: Big Game of North America
Ed. P. Lambert

Chapter 6
Appx K July 1974

CARIBOU

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In May, 1792, an explorer, David Thompson, described the caribou crossing the Nelson River (Parker 1972a): ". . . the herd the first day to one hundred and twenty miles in length and the herd of the second day to half as much more, making the whole length of the herd to be one hundred and eighty miles in length, by one hundred yards in breadth . . . by the above space, allowing each deer, ten feet by eight feet, an area of eighty square feet, the number of Rein Deer that passed was 3,564,000 an immense number."

Such assemblages still can stagger the imagination. Each July the bulk of the Porcupine caribou herd gathers on the Arctic plain adjacent to the Beaufort Sea, where densities reach 19,000 animals per square kilometer (50,000 per square mile). This postcalving aggregation must be one of the great remaining natural marvels of this world—equal to zenithal flights of the passenger pigeons and massings of American bison. Such sights, or even knowledge thereof, add perspective to our lives, a tonic and humbling experience. Surely our stewardship on Earth requires our continued coexistence with this splendid animal.

ECOLOGY

Life history

Caribou *(Rangifer tarandus)* have roamed the North for more than one million years. The earliest evidence is from central Germany about 440,000 years ago (Banfield 1961). At present, five subspecies are recognized in North America and a sixth, formerly of the Queen Charlotte Islands, British Columbia, is extinct (Figure 19).

Caribou belong to the deer family (Cervidae) in the Order Artiodactyla. They are an even-toed ruminant with a four-compartment stomach. Caribou are medium-sized deer, with males larger than females. Males of the larger subspecies, found in central Alaska, northern British Columbia and Ungava, Quebec, weigh 181–272 kilograms (400–600 pounds), and those of the smaller subspecies in the Northwest Territories and the Arctic Slope of Alaska, 124–169 kilograms (275–375 pounds). Respectively, females usually weigh about 91–136 kilograms (200–300 pounds) and about 91 kilograms (200 pounds). The above represent average fall weights. Males can

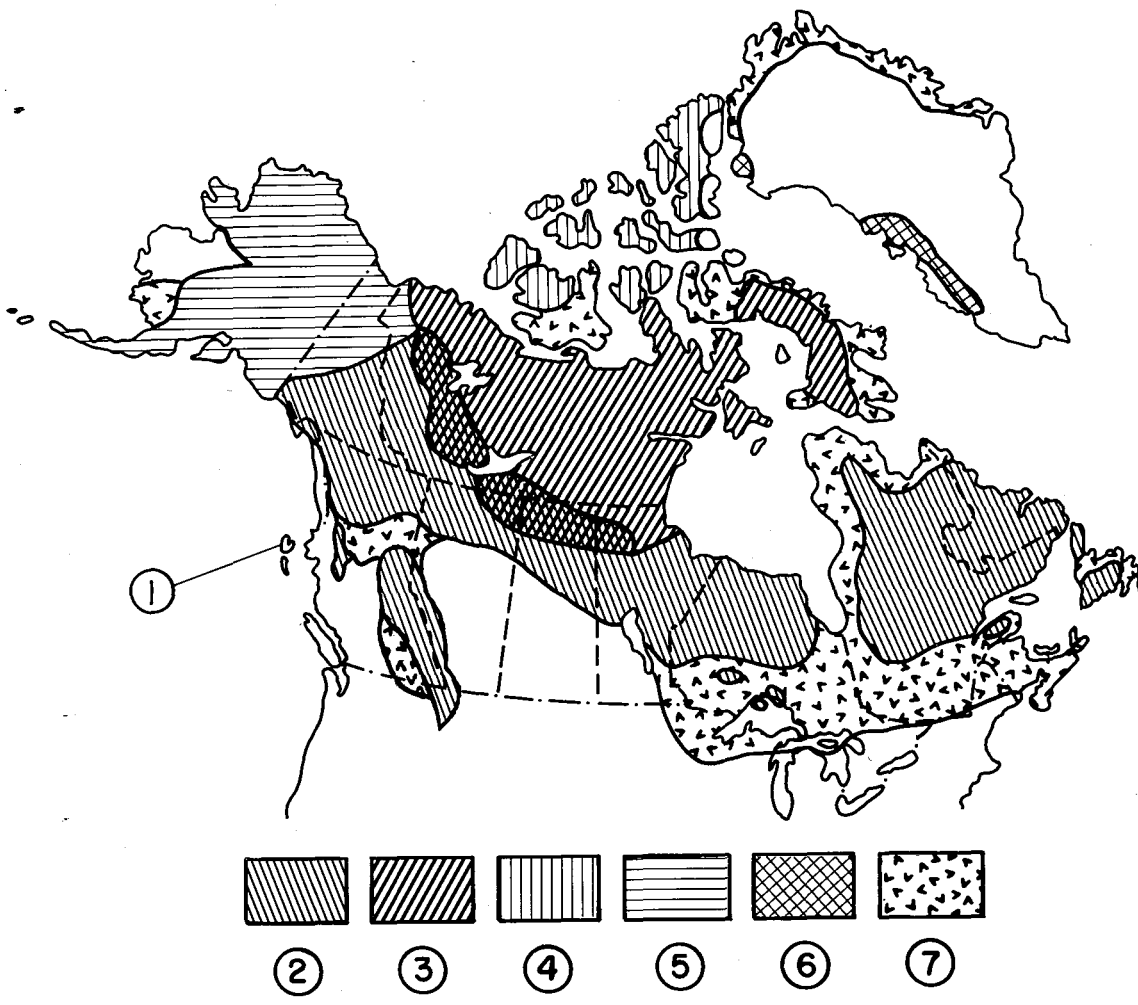


Figure 19. Past and present distribution of caribou (after Banfield 1961): 1. *Rangifer tarandus dawsoni* (extinct); 2. *R. t. caribou;* 3. *R. t. groenlandicus;* 4. *R. t. pearyi;* 5. *R. t. granti;* 6. *R. t. eogroenlandicus;* and 7. former range.

lose as much as 25 percent of their weight during the autumn rut, as do females during some winters.

Caribou are unique among deer in that both females and males commonly have antlers. In northern populations, nearly all females have antlers, but many females in Ontario, Quebec and Newfoundland are "bald." As many as 95 percent of females in one Newfoundland herd had no antlers. The antlers of males are tall, commonly 102 centimeters (40 inches) or longer, often with beams flattened (palmate) and as many as 40 or more points. A brow tine is recognized as the "shovel" over the face. The bez tine is a handlike structure that forks from the main beam above the brow tine.

The caribou breeding season is much shorter than that of other deer. Actually, the majority of breeding occurs in a one-week period in either the middle or end of October. If a female fails to conceive, she can experience a second or third heat period at intervals of 10–12 days. Gestation is about 227–229 days, with the calves born in May or June. About 90 percent of the young are born during a 10-day period. Dates of breeding and parturition vary among herds, but are remarkably constant within herds. For example, in the Nelchina herd in Alaska

the peak of calving always has been from May 24–28; in the Interior herd, Newfoundland, from May 28–June 1; and for various herds in the Northwest Territories, from about June 10–14.

Caribou calves weigh about 5–9 kilograms (11–20 pounds) at birth and are precocial and able to follow their dams within one hour of birth. This mobility is an important adaptation which reduces mortality, since calves are highly vulnerable to predation at birth on the exposed tundra. The first few weeks of life are critical ones; often 25 percent or more of calves die before one month of age.

Population dynamics

The productivity of caribou is low compared to the other cervids in North America. Twinning is almost unknown, and puberty in females is normally not reached until 29–41 months of age. Age-specific pregnancy rates for the Kaminuriak herd were the following: yearlings, 2 percent; two years, 48 percent; three years, 82 percent; and four years or older, 91 percent (Dauphine 1976). However, the pregnancy rate is high for mature females and constant among geographical regions: Kaminuriak herd, 90 percent pregnant; Beverly herd, 78 percent; Nelchina herd, 89 percent; Western Arctic herd, 78 percent; and the Interior herd, 85 percent.

The pregnancy rate remained high in Newfoundland over an 11-year period, even though winter nutrition varied greatly. In one year, some calves starved and in another winter females lost 26 percent of their November weight by June. To the contrary, adult Peary caribou on some Arctic islands starved during the winter of 1973–1974 and again in 1975, and subsequently had low reproductions with only 7 percent pregnancy rates both years (Parker et al. 1975, Thomas et al. 1976).

The most interesting finding comes from the introduction of 29 reindeer—a semidomestic relative of caribou—to St. Matthew Island, Alaska, in 1944. These 29 animals increased to 1,350 by 1957, then to 6,000 by 1963. This herd increased at a rate of 34 percent per year from 1944–1957, and 28 percent per year from 1957–1963. During the entire period 1944–1963, density increased from 0.08–18 caribou per square kilometer (0.2–46.7 per square mile). This population increase was quite constant and did not follow the normal sigmoid growth curve for animals "pushing" and exceeding their food resources. Even survivors of the eventual "crash" continued to ovulate. In the winter of 1963–1964, the entire herd starved and only 42 animals remained in 1965 (Klein 1968). Until then, the herd did not demonstrate an appreciable increase in mortality or decrease of reproductive rate, despite the dramatic increase of density and depletion of food supplies over the 19-year period. This study strikingly identifies the degree to which some caribou populations have achieved a reproductive rate independent of food supply.

The reproductive rate of caribou is low, but the mortality rate is high. An average of only 50 percent of calves in many herds live to 12 months of age. Calf mortality can exceed 90 percent in herds located where there are high densities of wolves and/or grizzly bears. Adults fare better. The natural annual mortality of adults is about 4–6 percent with few natural predators. In Newfoundland, males had a higher mortality rate (9 percent) than females (4 percent). The natural mortality rate of adults when there are normal densities of predators has not been determined yet, but it probably will average 7–13 percent, depending on predator densities.

At birth, approximately 51–55 percent of calves are male. In Newfoundland where lynx selectively killed male calves, the sex ratio favored females by five to six months of age. However, in the Kaminuriak and Nelchina herds, males predominated in the yearling class. They also were most abundant in the two-year age class of the Kaminuriak herd (Bergerud 1971a, Miller 1974, Skoog 1968). The mean percent of adult males was 39 for eight populations

which either were not hunted or were hunted nonselectively (Bergerud 1974a). Frequent segregation of the sexes makes it difficult to obtain a representative sample of a caribou population.

The percentage of calves in a herd, at birth, is normally about 27–30. Herds with calves representing less than 10 percent of their populations in April probably are declining; herds with 17 or more calves per 100 animals in April likely are increasing (based on the assumption of hunting mortality near 5 percent).

Mortality factors

Caribou calves die from a multitude of factors, including birth defects, accidents, social interactions such as trampling, wind chill, desertion and predation. By far, predation is the most important natural cause of death. On calving grounds in the Northwest Territories, Miller and Broughton (1974) reported that 32 percent of the calves they found dead were killed by wolves. During an 11-year study in Newfoundland, lynx were found responsible for 75 percent of the calves I located dead or dying. When wolves and possibly grizzly bears are abundant, calf mortality during the first year can be about 85 percent; I believe that miscellaneous deaths can account for 30 percent of this loss and that predators cause the remaining 55 percent. Wind chill is the second most common cause of death of newborn calves during inclement weather (*cf.* Kelsall 1968). This cause of mortality can deplete an entire calf crop. The Kaminuriak herd lost much of its 1962 calf crop from this factor (Miller 1974). The extent of this form of mortality depends on both the severity of weather plus the vigor of calves at birth. Following hard winters, the weight of pregnant females is reduced which, in turn, results in calves of reduced size at birth. These small calves have reduced viability and increased susceptibility to mortality from harsh weather; thus, the two variables are involved (Bergerud 1974b, Dauphine 1976). Desertion is possibly the third most common cause of death. Females in large moving herds tend to abandon their calves more frequently than do nonmigratory dams.

Causes of death for adults include drowning, social interactions during breeding, death in parturition, disease, starvation and predation. There now is considerable evidence that white-tailed deer transmit the parasitic meningeal worm *Parelaphostrongylus tenuis* to caribou with fatal results. The declines of caribou in Minnesota, Maine, New Brunswick and Nova Scotia may have been due in part to the northward spread of deer when settlement practices cleared forest lands. The only viable caribou population now coinhabiting range with high densities of deer is in the Shickshock Mountains, Gaspé, Quebec. Altitudinal stratification, with caribou living higher than deer, may be the reason that contact is minimized. If caribou could become resistant to this disease, it might be possible to restore them to many former ranges. This should be an important area of research for wildlife departments.

Starvation is another cause of death, especially on the Arctic Islands and the Alaskan Peninsula. Skoog (1968) predicted that snow and ice cover would limit populations on the Arctic Islands, and his prediction has been proven correct. In 1972–1974, a large portion of the Peary caribou population died. The population on 20 islands was estimated to number 24,320 in 1961 (Tener 1961), but in 1974, only 2,676 caribou remained (Miller et al. 1977)—a 90 percent loss. This die-off resulted because snow and/or ice prevented the animals from reaching food.

Predation is omnipresent. Recent studies in Alaska showed males more vulnerable than females and that caribou in small groups faced greater risk than more aggregated individuals. Wolves were able to secure an animal from nearly 50 percent of the groups they tested or chased (Haber 1977). Caribou have but one strategy besides herding: running. A 50 percent mortality rate per wolf encounter for single animals leaves something to be desired.

Behavior

We can presume that the extrinsic environment has shaped the behavior of the species. Important environmental factors have been the weather (snow and wind), other animals (insects and wolves), visibility in the habitat (mostly open views for many populations), and the flora (slow-growing lichens). First, the open habitat plus the presence of wolves likely has fostered the caribou's gregarious behavior. Grouping reduces predation (Bergerud 1974c), but is not compatible with a sedentary mode of life because of the slow-growing flora and the variability of food supplies due to snow and wind. Thus, the caribou is a gregarious but nomadic denizen of the Arctic prairies.

Caribou are always moving, usually in large groups. We might say caribou constantly move but pause periodically where there is an abundance of requisites. A brief outline of the annual cycle of movement and aggregating behavior is presented in Table 6 (for details on behavior and movement, see Bergerud 1974c).

Table 6. Annual cycle of behavior and movement of caribou.

Time of year	Life cycle, pause-shift schedule[a]	Group size and composition	Habitat utilized	Factors affecting aggregating and movement behavior
April–May	Spring migration, spring shift	Long columns, pregnant females at front, few males, some yearlings drop out, 50–1,000 per group	Natural channels, areas free of snow, south slopes	Movement starts with bare areas, move faster if start later, 19–55 km/day (10–30 mi/day); move to familiar areas to produce young, tradition involved
Late May–early June	Calving, calving pause	Scattered over calving grounds, alone at birth, yearling and female groups less than 10 per group	Tundra, sedge meadow, drier uplands	Pause to give birth to calves, immediately join other females with young calves; period for female to learn to recognize her offspring
July	Post-calving aggregation, post calving shift	Huge groups of females, yearlings and young calves, up to 80,000 per group	Tundra, new willow-birch growth, wind-swept hills, snow fields	Huge herds form, with sharp boundary line; herds reduce wolf predation on offspring; animals often together because of discontinuous nature of insect-relief habitat
August	Summer dispersal, summer shift	Scattered small groups everywhere, less than 100 animals together	River flats, alpine tundra, birch-willow stands	Insects abate; animals can scatter to find most palatable food, move and then pause
September	Fall shuffle, fall shift	Females start to group, males join female groups	Tundra, open lichen-conifer forests	Movement to bring sexes together
October–November	Rut, fall pause	Random assortment males and females, herds 5–400 per group	Open lichen-conifer forests, bushy areas	Pause for breeding; can start moving while breeding if snow occurs
November	Fall migration, fall shift	Long columns, groups up to many thousands	Open lichen-conifer forests, bushy areas	Movement triggered by first heavy snow; move to areas where food will be easier to find later in winter
December–March	Winter, winter pause	Scattered over range 20–100 per group, males segregated	Sedge lake margins open forests, wind-swept mountains	Little movement if snow cover does not change; widely scattered if little snow and food can be detected over wide area; concentrated and aggregated if area where food can be detected is discontinuous

[a]Pause-shift sequence from Skoog (1968).

HABITAT NEEDS AND PREFERENCES

Caribou have universal tastes, eating a wider variety of plants than other deer species. A partial list of the plants eaten includes 62 lichens and 282 kinds of seed plants (Bergerud 1977). However, caribou show preference for green vascular plants and mushrooms. When these plants cannot be secured, caribou are opportunistic and will eat whatever plants are available. Relative availability then is the prime factor in species utilization.

As the spring thaw advances, caribou quickly change their diet to include new vegetative growth. In mountainous regions, caribou can continue to find new plant growth by shifting altitude and visiting receding snowfields. Grasses, sedges and cottongrass are the most important plant groups eaten. The animals also seek other newly sprouting plants such as willow catkins, larch needles, leaves of alder and Solomon's seal, and sweet gale buds.

The most important food in the summer diet are green leaves of deciduous shrubs, especially those of willow, shrub birch and blueberry. Caribou are fastidious feeders, stripping leaves from woody stems and picking only new sprouts and finer stem tips of sedges, herbs and horsetail. In late summer, they actively search for mushrooms.

After the first hard frost, leaves quickly become unavailable and the animals switch to terrestrial lichens and leaves of evergreen shrubs. The most important fruticose lichens eaten include *Cladonia alpestris, C. rangiferina* and *C. mitis*.

In winter, snow depth dictates food availability. Winter greens are especially important if caribou can find them by digging holes in the snow (called feeding craters). The animals also seek the fine twigs of birch, willow and blueberry. Where a sun crust that can support caribou develops on the snow, they will shift from open habitats to forest cover seeking arboreal lichens growing on coniferous trees.

Two environmental needs stand out above all others: (1) to escape or find relief from flying insects in summer; and (2) to find food through deep snow in winter. These two needs largely dictate where caribou will be found.

Caribou are bothered especially by warble and nostril flies. The warble fly lays its eggs on the flanks of caribou. When the larvae hatch, they burrow through the skin and move to the region of the back. The nostril fly lays live larvae in the nostrils of caribou. To reduce insect attacks, caribou seek hilltops with strong winds, snow and ice fields, and cool and shady forests. If the environment does not provide insect-relief habitat, then the animals keep moving, at times running and stampeding. They often stand in dense clumps on hilltops with their heads down and together, hindquarters out. Apparently the simple obstructions of caribou bodies reduce attacks. Animals continually wheeze and shake to ward off insects.

In winter, finding food through deep snow is the all-important need of caribou. We should distinguish between "absolute abundance" of food (the actual food amount present; often what we see and measure on summer range studies) and "relative abundance" of food (the amount of food the animals can find through snow cover). In winter, caribou often are found where there is limited absolute abundance of food, but because of reduced snow depths there is high relative abundance. Caribou seek areas of reduced snow cover, south slopes and windswept mountains to locate food.

Caribou can smell the presence of food under snow, probably to depth no more than 15–18 centimeters (6–7 inches) of continuous snow. They often visit shrubs sticking through the snow because air vents adjacent to the stems let them scent down to greater depths. Even when covered by snow, shrubs bridge the detection gap between the snow surface and buried ground flora.

Summarizing the condition suitable for winter feeding:

1. Irregular terrain—because of wind currents and, thus, variable snow depths—is superior to uniform terrain;
2. Habitats with three vegetation strata (ground, shrub and tree) are superior to ranges with only one or two strata (the trees should be well-spaced);
3. Regions with shallow snow are superior to those with deep snow; and
4. Terrain with hard snow (that will support caribou) is superior to terrain with soft snow if it is deep.

DISTRIBUTION AND STATUS: PAST AND PRESENT

The caribou of the Nearctic are distributed throughout Canada and Alaska in the tundra and taiga biomes (Figure 19). They no longer frequent New Brunswick, Nova Scotia, Maine or Minnesota. A small herd of 20–30 still frequents the Selkirk Mountains in southeastern British Columbia and northern Idaho (Freddy 1974).

How many caribou were there originally? This presumes that there was an upper carrying capacity, a view I question. Populations likely rose and fell. Murie (1935) estimated an Alaskan herd at 568,000 animals in 1920, or 2.2 per square kilometer (5.6 per square mile). Also, in 1962–1967, the Nelchina herd approached 1.9 animals per square kilometer (5 per square mile). Thus, based on habitat available and a density of 1.9 animals per square kilometer (4.9 per square mile), Alaska may have reached 1–2 million caribou (Murie 1935) and northwestern Canada may have had 3.8 million (Clarke 1940). However, numbers were probably much lower, perhaps 0.4–0.6 per square kilometer (1–1.5 per square mile) (Calef 1974), or 3–5 million caribou for all North America.

There were perhaps 1.3 million caribou in the mid-1960s, and in 1977, about 1.1 million. Three large populations now exist, each composed of several subpopulations or herds that have different calving grounds:

1. The Ungava population, ranging over about 260,000 square kilometers (100,000 square miles), calving at three or more locations and numbering perhaps 150,000 adults and yearlings in 1976 (S. Luttich, personal communication)
2. The barren-ground population found from the Mackenzie River to Hudson Bay, ranging over about 1.6 million square kilometers (610,000 square miles), calving at at least seven locations and now numbering at least 547,000 animals (Thomas 1969, Parker 1972a, Calef 1977) (see Figure 20); and
3. The Alaskan population (west of the Mackenzie River), ranging over 1 million square kilometers (400,000 square miles) and calving at 15 or more locations and numbering about 600,000 animals between 1964–1970 (Hemming 1971), but reduced to 238,000 animals by 1977 (Davis 1977).

Since about 1964, 7 of the 11 major caribou herds in Alaska have declined by approximately 362,000 animals, or 60 percent (Table 7). These herds were monitored, and why management failed is an extremely important question.

I believe the Alaskan herds declined because of heavy hunting of adults in the absence of satisfactory survival of young. The most significant cause of calf mortality was predation by wolves and possibly grizzly bears. Of the seven herds that declined, six were heavily hunted (10–20 percent annual harvest) while the seventh, the Mount McKinley herd, was only lightly hunted. The decline of the McKinley herd is probably explained by egress to the Mulchatna herd (Haber 1977). This egress would explain the increase of the Mulchatna herd, the only important herd to have increased in recent times except for the Alaska Peninsula herd (Figure 20). The Nelchina herd was the most intensively studied of the herds that declined. Figure 21 shows the increase of this herd from 1955–1962, after the wolves had been reduced, and the subsequent decline of the herd from 1963–1972. Note in Figure 21

Table 7. Population estimates of caribou since 1960 (herd numbers correspond with Figure 20).

Herd number	Herd	Year counted	Census estimated	Method of census	Reference source
1	Queen Elizabeth	1961	26,000	winter aerial transect	Tener 1963
1	Queen Elizabeth[a]	1974	2,700		Miller et al. 1977
2	Banks Island	1972	12,000	winter aerial transects	Urquhart, Unpublished
3	Western Arctic	1970	195,000[b]	aerial photo extrapolation	Hemming 1971
3	Western Arctic	1976	40,000[b]	aerial photo extrapolation	Davis 1977
4	Porcupine[e]	1972	110,000	aerial photo extrapolation	Calef 1974
4	Porcupine[e]	1976	110,000		D. McKnight[c]
5	Beaver	1963	3,000		Hemming 1971
6	Mt. McKinley	1966	8,000	ground count at migration	Haber 1976
6	Mt. McKinley	1976	1,000	aerial census	Haber 1977
7	Delta	1963	5,000		Hemming 1971
7	Delta	1973	2,000		D. McKnight[c]
8	Fortymile	1969	20,000		LeResche 1975
8	Fortymile	1975	4,000	aerial photo extrapolation	Davis 1977
9	Chisana	1963	3,000		Hemming 1971
9	Chisana	1976?	1,000		Davis 1977
10	Mentasta	1965	5,000		Hemming 1971
10	Mentasta	1977	2,700	aerial photo extrapolation	Davis 1977
11	Nelchina	1962	71,000	random quadrats winter	Siniff and Skoog 1964
11	Nelchina	1977	14,000	aerial photo extrapolation	Davis 1977
12	Mulchatna	1963	5,000		Hemming 1971
12	Mulchatna	1976	9,000	aerial photo extrapolation	Davis 1977
13	Kenai	1976	250	direct count from air	Davis 1977
14	Alaska Peninsula	1968	14,000		Hemming 1971
14	Alaska Peninsula	1977	16,700	aerial photo extrapolation	Davis 1977
15	Adak Island	1976	275	direct count from air	Davis 1977
16	Spatsizi	1976	2,000	direct count rutting groups	Hazelwood[c]
17	Bluenose[e]	1967	19,000	air photo and transect count	Thomas 1969
17	Bluenose[e]	1975	90,000	transect count	Calef 1977
18	Bathurst[e]	1967	144,000	air photo and transect count	Thomas 1969
18	Bathurst[e]	1974	174,000	transect count	Calef 1977
19	Beverly[e]	1967	159,000	air photo and transect count	Thomas 1969
19	Beverly[e]	1974	124,000	aerial transects	Calef 1977
20	Kaminuriak[e]	1968	68,000	transects, blocks, photo	Parker 1972a
20	Kaminuriak[e]	1976	45,000	aerial transects	Calef 1977
21	Coats Island	1975	2,000		Parker 1975
22	Baffin Island[e]	1963–1973	10,000–30,000	transects, general observation	Rippen, Unpublished MacPherson, Unpublished
23	Ungava	1976	150,000	count of females on calving grounds	S. Luttich[c]
24	Mealy Mt.	1963	800	winter aerial transects	Bergerud 1967

Table 7.

25	Avalon Pen	1967	720	direct aerial count, autumn	Bergerud 1971a
26	Interior	1966	7,700	winter aerial transects	Bergerud 1971a
27	Slate Islands	1976	200+	walking transects, Lincoln Index	Bergerud[d]
28	Ontario	1959–1964	13,000	winter aerial transects	Simkin 1965
29	Nipigon Islands	1975	75	walking transects, pellet count	Bergerud[d]
30	Selkirk Mts.	1974	20–30	ground observation	Freddy 1974
	Melville Peninsula[e]	1976	45,000	aerial transects	Calef 1977
	Wager Peninsula[e]	1976	12,000	aerial transects	Calef 1977
	Lorriland Refuge[f]	1976	17,000	aerial transects	Calef 1977
	Baffin Island	1974	20,000	aerial transects	Calef 1977
	Kaudy Plateau	1977	1,700	direct aerial count	Bergerud[d]
	Itcha Mts.	1977	250	direct aerial count	H. Mitchell[c]
	Wells Gray	1970	350	snow field census	R. Ritcey[c]
	Waco	1972	8,000	aerial transect	I. Juniper[c]

[a]Does not include all the islands identified by Tener (1961).

[b]Excludes calves.

[c]Personal communication.

[d]Personal files.

[e]See Figure 22.

[f]There also are large numbers of woodland caribou in the Mackenzie Mountains at the Yukon and the Northwest Territories, perhaps 10,000–20,000 (Calef, personal communication).

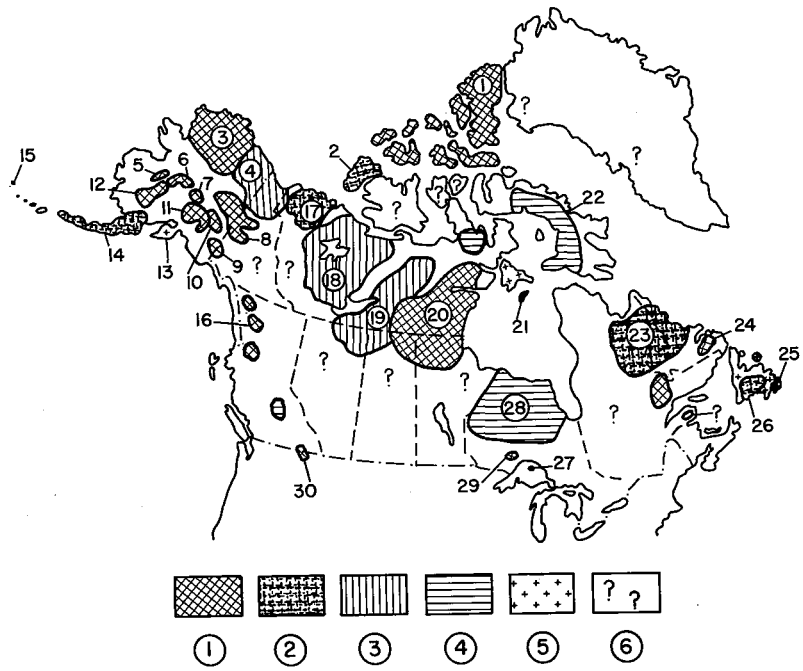


Figure 20. Location of some of the major caribou herds in North America and status since the 1960s. Numbers identify herds listed in Table 7. Population estimates may be known by local biologists for "?" areas but are not to the author: 1. decreased; 2. increased; 3. stable; 4. unknown; 5. introduced; 6. no population trend known.

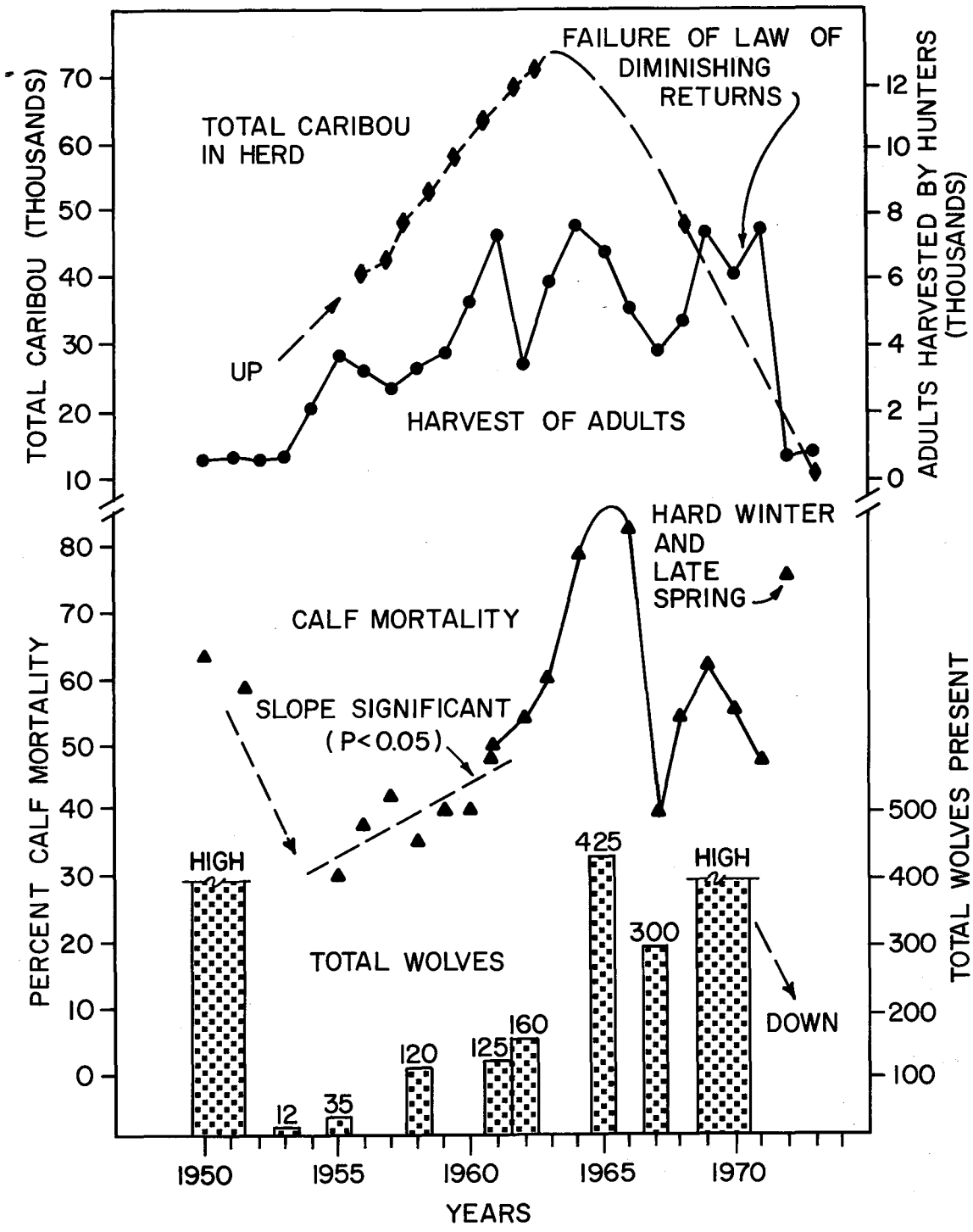


Figure 21. Population changes of the Nelchina herd 1950–1972, including harvest of adults, survival of calves and abundance of wolves (after Rausch 1967, 1969, Skoog 1968, Bos 1975). Calf mortality (1961–1969) is calculated from the percentage of two-year old females in the harvest of the total females two years of age and older, and is believed to underestimate calf mortality by 10–15 percent.

that as wolf numbers increased, survival of the calves decreased. When wolf numbers declined from illegal hunting in 1966, calf survival showed a marked improvement. After 1968, wolves again increased and calf survival was reduced. These data suggest that predation played a dominant role in calf survival in this herd. Calves also may have died from starvation in the winter of 1970–1971 and/or from wind chill in 1972 (Bos 1975). In the other herds, annual calf survival to 12 months of age was known to be poor, often only 15 percent in at least four of the five other herds during their declines. Wolf numbers also were high in the areas of these herds. In summary, these herds had population parameters similar to other herds in North America that declined when hunting was heavy and predator numbers high.

The Porcupine herd did not decline like the seven other herds, yet calf survival was poor; an average of only 19 percent of the calves survived annually in the years 1972–1977 (calculated on the basis that 75 percent of the females gave birth). The one difference between the dynamics of the Porcupine herd and the other herds that declined was that the Porcupine was only lightly hunted—a harvest of less than 5 percent annually. This contrast with the other herds strengthens the view that the other herds declined because of a combination of heavy adult losses from hunting plus a high mortality of calves; adult losses were not replaced.

The decline of the Alaskan caribou population appears to have resulted from overhunting in the absence of adequate recruitment. The same factors were responsible for declines in the Northwest Territories from 1949–1955 (Banfield 1954, Parker 1972) (Figure 22), and in Newfoundland from 1915–1930 (Bergerud 1971a).

I believe that three points of view held by some wildlife biologists in Alaska contributed to the management failure experienced there. They were: (1) that large herds would not be overharvested; (2) underestimation of the extent of calf

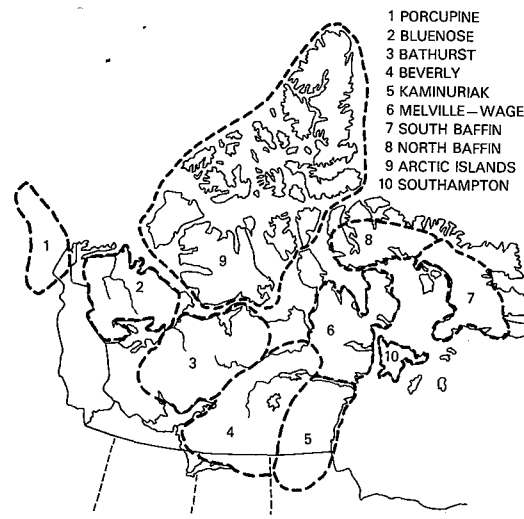


Figure 22. Major caribou ranges in the Northwest Territories (G. Calef, personal communication).

mortality when predator numbers were high; and (3) that food supplies set carrying capacity for caribou populations which, consequently, had to be hunted heavily to prevent the animals from overgrazing habitat and declining in number. There is recent evidence of considerable shifts relating to the first and second views, but the food supply-carrying capacity notion still persists. As a result, some Alaska herds continued to be harvested heavily, with the intent of preventing ranges from becoming overgrazed.

Mathematically, in a herd of 100 animals, approximately 61 will be females. If the herd has had poor prior recruitment of calves, many of the females will be older animals and sexually mature. These females (80 percent pregnant) should produce 49 calves. But, if only 15 percent of these calves live to one year, only seven animals are added to the herd. Seven calves are just about sufficient to equal the annual natural mortality of adult caribou living in areas with few predators. Thus, there is no surplus for hunters and any hunting will reduce future populations.

In addition, population declines are difficult to halt. The law of diminishing returns works neither for men nor wolves (Figure

21), at least initially. Hunters can still find caribou because of the open terrain and their conspicuous habits. Wolf numbers are adjusted only slowly to reduced caribou herds (called predator lag); thus the same number of wolves hunt a smaller supply of game for a time.

If herds are to be harvested heavily, it is essential to determine the percentage of calves in the herd each March–April. Counts made during autumn may not provide an accurate assessment of recruitment if wolf predation is extensive on the winter range. The loss of just one calf crop can be extremely serious. Several herds that declined in Alaska were not monitored as to calf survival for several consecutive years. When they were checked, it was too late; the herds already were reduced substantially.

MANAGEMENT

Estimating population parameters

Caribou, because they usually live in open habitats, are relatively easy to census. Various herds have been estimated by:

1. Aerial transect counts in winter (Bergerud 1963);
2. Aerial census of quadrats selected at random from stratified density strata in winter or on the calving grounds (Siniff and Skoog 1964, Parker 1972a);
3. Tag-resighting methods (Lincoln Index) (Parker 1972b);
4. Aerial photographic techniques (Parker 1972a); and
5. Actual counts of animals or tracks where they intersected roads or rivers.

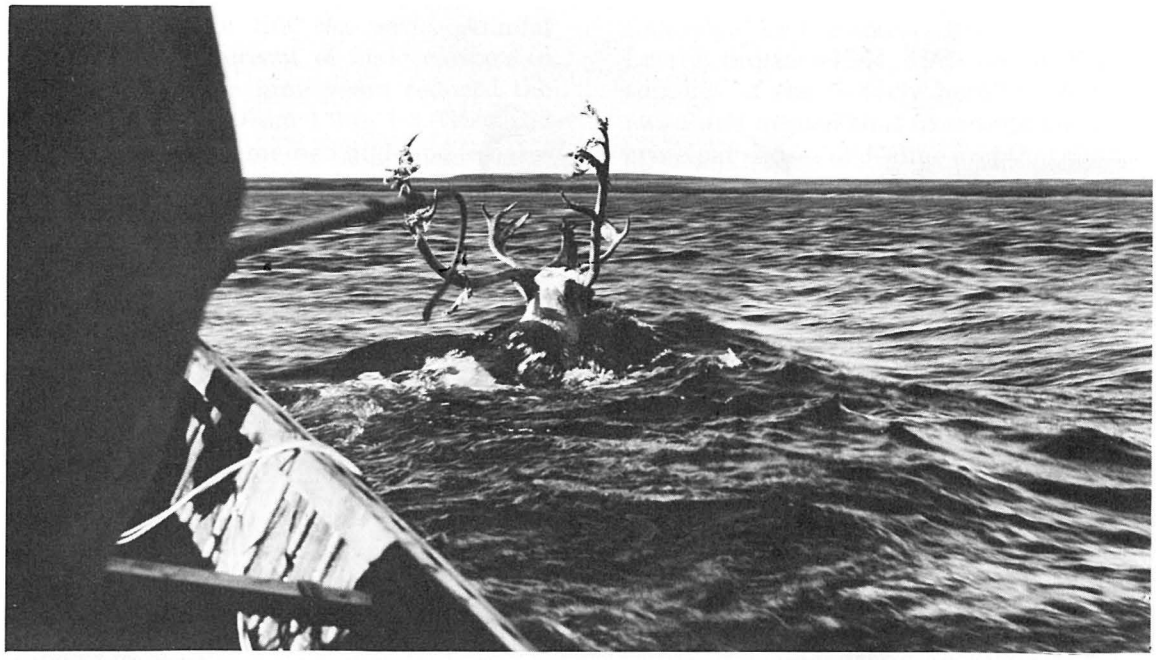
At present, the most common technique is to photograph females in July when nearly all of them gather in huge postcalving aggregations. Males, calves and yearlings then are prorated to the July female count based on classification counts of the herds during the autumn rut when all age-sex classes are represented proportionally. Census results should not be accepted unless two independent methods show agreement. The most comprehensive treatment of census procedures is Parker's (1972a) census of the Kaminuriak herd in 1968.

For animals that live in forested habitats, I have used the King strip census in May and June. A tally of carcasses from winter mortality was conducted concurrently. Also, diagrams of male antlers of forest-dwelling races have been drawn to identify individuals for a total count of males (Bergerud 1973). The other components of the herd can be added based on autumn composition counts.

Animals can be aged as calves, yearlings and adults by comparing body size and antler growth. The short face of young animals contrasts well with the longer horse-face of adults. Until 12 months old, calves can be distinguished from adults during aerial surveys, and during ground observation until the animals are 17 months old. Collected animals should be aged by noting wear on the mandibular teeth or by cross-sectioning incisors and counting annulations in the cementum (Skoog 1968, Miller 1974).

The sexes usually can be distinguished by the larger size of males (thick neck, white mane and large antlers in the autumn) and the Roman nose of males in contrast to the straight profile of females. The best method is to ignore all other characteristics and observe the animals from the rear for the presence or absence of the vulva (Bergerud 1961). The sex of animals killed by hunters can be checked by measuring the length of the lower mandible or the diastema length of the mandible (Miller 1974).

The pregnancy rate of caribou can be estimated by field counts (air or ground) of antlered females in May. Nonpregnant females shed their antlers in March or April, whereas pregnant females shed their antlers at the time of calving (Skoog 1968, Bergerud 1976). This technique requires that the observer know the percentage of females in the population that have the antler characteristics, which can be determined by counts in



This photograph, and the next two, illustrate the sequence of events during caribou-tagging operations at Duck Lake, Manitoba. Here, a bull caribou (antlers shedding velvet) is approached. Extended shepherd's crook will be used to pull the animal safely to the canoe for marking.

A live caribou is held momentarily while metal tag and yellow streamer are attached to the ear.

A tagged caribou swims toward shore moments after its release. It and other barren-ground caribou were tagged to provide information on intermingling among herds, eastward and westward movements, and rate of travel. Photos by E. F. Bossenmaier; courtesy of the Manitoba Wildlife Branch.

autumn. It also is possible to tell whether a female has given birth by the presence or absence of a large milk udder immediately postcalving (Bergerud 1964). If a female is seen with a large udder and no calf, it can be concluded that her calf died, since calves invariably follow their dams in populations that calve in open habitats. Microtechniques are now well-advanced for determining past pregnancies of a female based on counts of corpora lutea of pregnancy in the ovaries (Dauphine 1976).

Harvest objectives

The data seem clear; men and predators compete for a common resource. If wolf and/or grizzly bear numbers are high—one predator per 65–130 square kilometers (25–50 square miles) hunting moose and caribou, or one predator per 259–311 square kilometers (100–120 square miles) hunting mostly caribou—only 10–20 percent of caribou calves may survive to 12 months of age. Also, the natural mortality of adult caribou when predators are present is possibly 7–10 percent or more. In these situations, there can be practically no human harvest; the balance is too fine. If a harvest is required for subsistence hunters, wolf populations in those areas must be reduced. In the absence of wolves, possibly 15–20 percent of a caribou herd can be cropped in years when there is no extensive wind chill mortality of calves.

Managers charged with supervising recreational hunting probably can permit a harvest of 10–15 percent of the males even in the presence of moderate wolf numbers; for example, one wolf per 518 square kilometers (200 square miles). The harvest probably can be only 5 percent if both sexes are taken (Parker 1972a). Hunting of only

males will alter the sex ratio. Annual harvests of 11 percent of male caribou in Newfoundland for nine years reduced the male-female ratio from 1:2 to 1:3 (Bergerud 1971b). Fertility remained high and females continued to conceive in their first heat period. If the sex ratio is unbalanced to 1:5–9, possibly not all the females will be bred in their first estrus. Calves born 10–12 days later than the majority of calves will be at a survival disadvantage.

A growing segment of the public wants unharvested ecosystems. They wish to view ungulates and wolves interacting in their natural setting. Even in this setting, I believe that many caribou populations are below desirable densities (*cf.* Walters et al. 1975). A valuable experiment would be to remove whole wolf packs as suggested by Haber (1977). This removal would test Haber's hypothesis that intrapack social restraints suppress reproduction in wolves. In any case, the caribou population should increase, the wolf population would bounce back, and the ecosystem then could proceed on its own course of evolution, but at higher equilibrium densities of predator and prey.

Habitat problems

Range destruction of climax lichens by forest fires has long been considered the nemesis of caribou (Scotter 1964). Leopold and Darling (1953) were the first to formalize this hypothesis. After a four-month tour of Alaska, they postulated that caribou were climax animals requiring climax lichens, and concluded: "Caribou have been . . . very much reduced in central and southern Alaska by burning over the winter range." To the contrary, Skoog (1968) thought fires had little impact on caribou in Alaska. Edwards (1954) published that caribou had declined in British Columbia because of habitat destruction by fires. Cringan (1957) expressed a similar opinion with respect to woodland caribou in Ontario. Hunting, predation and disease were presented as alternative reasons for declines in British Columbia and Ontario (Bergerud 1974b). Lastly, Scotter (1964, 1967) studied forage supplies of the Beverly herd in Saskatchewan and argued that fires were one of the principal causes of decline and that the vast destroyed range would not permit a caribou population increase for several years. However, he later changed his view that fires were harmful and said that effects were equivocal (Rowe and Scotter 1973). In yet another paper, he agreed in conjunction with the several authors that a 5-times increase in area covered by fires would have little influence on caribou numbers and that the range could support a 6.5-times increase in numbers (Bunnell et al. 1975).

About 1967, caribou ecologists began to recognize the beneficial effects of forest fires. Ahti and Hepburn (1967) recommended controlled burning in Ontario of peatlands, bogs and spruce muskegs to increase lichen supplies. Bergerud (1971c) argued that forest fires had increased lichen forage in Newfoundland by opening up forest canopies and destroying stunted alpine conifers. Bergerud (1972) also felt that caribou did not require lichens and often ate other foods in winter. Heinselman (1973) argued for the need to restore fire to its natural role in the forests of northern Minnesota. Johnson and Rowe (1975) studied fire on the winter range of the Beverly herd and reported that lightning accounted for 99.9 percent of the area burned from 1966–1972. They felt that fires probably improved the caribou range by mineralizing nutrients and renewing the growth of sedges, forbs, shrubs and even lichens. They concluded: "If it is accepted that fires are part of the boreal forest ecosystem then it follows that the vegetation has never existed in a climax state . . . over wide areas. The mosaic of vegetation of all ages visible today is probably close to the norm. The carrying capacity of the land may well be similar to what it always has been."

Miller (1976) concluded after a three-year study of caribou range in northern Manitoba that forest fires benefited caribou by maintaining the heterogeneity of habitat types. I have also noted this fire-created hetero-

geneity in Labrador and Ontario. Many heavily utilized lichen-woodland winter ranges owed their existence to repeated burning.

Debates about the values and use of fire on caribou ranges in the boreal forest finally have brought action. In 1976, the Canadian federal government ceased fire-fighting operations in the Northwest Territories in large areas of noncommercial forest (caribou range).

On this question of limiting factors on caribou populations, Leopold and Darling (1953) stated: "We cannot agree with the viewpoint expressed by Green (1950) that because Alaska is large and funds . . . small it necessarily follows that the game program must be directed towards controlling the action of predators, both men and wolves, rather than improving the range. To ignore range limitations for caribou is to ignore the crux of the problem. One fire easily could undo the work of decades in protecting a local population from men and wolves."

Hindsight indicates that Green was right, and that Leopold and Darling were wrong. Consequently, caribou habitat management was misdirected for nearly one-quarter of a century. It has not been demonstrated that an absolute shortage of food has caused caribou declines, but "men and wolves" clearly have been implicated.

Another dated argument is that caribou will overgraze their range and crash. The decline of free-ranging caribou due to an absolute shortage of foods caused by high populations has not been documented. Again, it was Leopold and Darling (1953) who formalized this concern. They hypothesized on the basis of declines of closely herded reindeer in Alaska and deer populations in the United States that overgrazed their ranges and starved in winter. Caribou, however, are not like sedentary reindeer and deer. As caribou numbers increase, their movements become more pronounced, their ranges expand and grazing pressure is distributed over larger and larger areas.

As to the question of full range occupancy, Skoog (1968) thought it almost axiomatic that no caribou herd has ever occupied all of its potential range. Snow cover prevented caribou from utilizing but a fraction (2–10 percent) of their range (Skoog 1968, Miller 1976). As a result, some areas may be denuded of lichens while a few feet away lichens are lush. This happens regardless of caribou density. Range overutilization, in a botanical sense, in areas of reduced snow cover should be considered the norm for caribou range (Bergerud 1974d).

Caribou ecologists have attempted to measure range carrying capacity since the start of management efforts. Estimates of maximum sustained densities have ranged from one reindeer per 8.1 hectares (20 acres) to one caribou per 109 square kilometers (42 square miles). Presently, I am investigating a population on the Slate Islands, Lake Superior, Ontario, where there is about one caribou per 14 hectares (35 acres). Similar high densities have existed there since at least the 1940s. There are no terrestrial lichens available, and the only substantial arboreal lichens are above a 1.5-meter (5-foot) browse line; in fact, there is hardly any food at all in the winter. Ahti (unpublished), a lichenologist, estimated in 1958 the carrying capacity of that section of Ontario at one animal per 109 square kilometers (42 square miles). The actual sustained density is 768 times the estimated carrying capacity. I do not know of any studies of the range of free-ranging caribou that have resulted in (1) increased numbers, (2) improved animal quality, or (3) a predicted decline where it could be shown that birth or death rates were altered due to an absolute shortage of food.

There is no answer to the perennial question of how many caribou a given range can support. Range has not yet been shown to limit numbers. In 1963–1965, the Nelchina herd reached the highest density of any major caribou herd in recent times (1.5–1.9 caribou per square kilometer: 4–5 per square mile). However, after several years of study when the population was peaking, Skoog (1968) felt that there were no problems of food shortage, then or in the future.

He said: "In reality, caribou populations in Alaska seem to have maintained densities much lower than the maximum dictated by food alone." He was speaking of both the past and present.

Caribou populations reach various unpredictable population levels. This is the Andrewartha and Birch (1954) theory of population regulation. Predator-prey oscillations appear to be a major factor in the rise and fall of caribou populations (Bergerud 1971a, 1974).

The flora cannot be measured to determine maximum stocking, but caribou can be collected to measure their health and sizes and, thus, the quality of their range. For example, reindeer introduced to a virgin, high quality range on St. Matthew Island, Alaska showed increased body-growth rates and ultimate body size compared to the genetic stock from which they originated (Klein 1968). Part of their superior performance may relate to the lack of harassing insects on the ocean island, but since average size declined at high stocking levels, nutrition also must have been involved.

Wildlife managers might be well-advised to collect animals in May and June to assess the annual impact of winter nutrition, and again in September for statistics on oversummering conditions. Collected animals would provide a wealth of data. Some examples are: (1) nutritional quality of forage (Klein 1962), (2) fat deposits (Dauphine 1976), (3) growth rates, (4) disease and parasitism, and (5) blood parameters (LeResche et al. 1974). Population data available from such collections would include age structure, pregnancy rates and reproductive history.

Another habitat problem is that of unstocked ranges. For a long time, managers did not feel that it was feasible to restock caribou because of the belief that caribou were wilderness animals that required climax lichen stands far removed from civilization. This not being so, opportunities exist for reestablishing old herds and establishing new ones, even if the flora is not as it was. Two potentially serious limitations are disease if deer are present and excessive wolf or lynx predation. Releases should succeed on islands without wolves, lynx or deer. When wolves are present, island archipelagoes should be considered. Here the releases of caribou could "island hop" to escape wolves.

From 1961–1964, the Newfoundland government introduced caribou to 18 sites. Success varied but, to date, animals have been harvested legally from four of these sites. A major problem was keeping the animals on the habitats where they were introduced (Bergerud 1974c).

Excellent results were achieved from the release of 23 calves on Adak Island in the Aleutians in 1958 and 1959. Harvests have been as high as 30 percent of the population (in 1973), a record for sustained yield. Another record was that one of the harvested males weighed 318 kilograms (700 pounds), the largest caribou recorded. Islands without predators offer substantial opportunities for population growth, maximum survival and high yields.

Other management problems

There are a multitude of possible or imagined problems associated with increased human use of the North. These include illegal hunting, construction of barriers to movement, abandonment of ranges, human harassment and disturbed predator-prey interactions. The susceptibility of caribou to overhunting is becoming well recognized. There is no solution except more intensive management, including better law enforcement and less poaching.

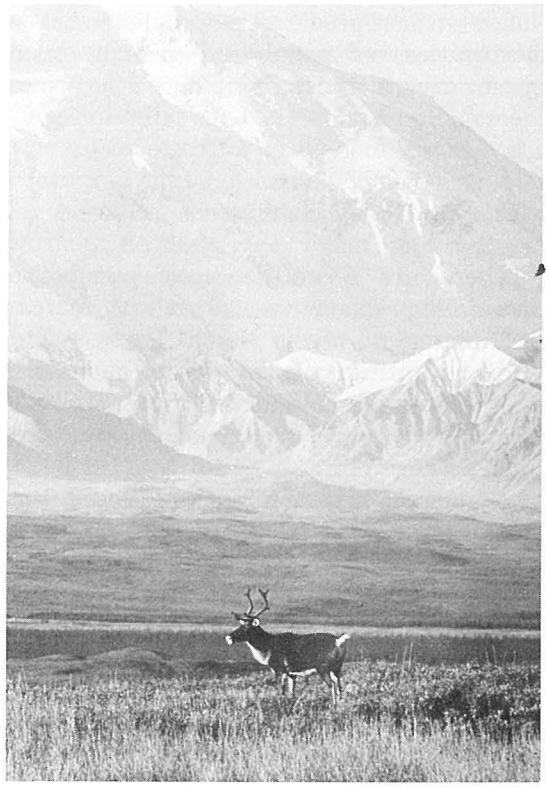
Large caribou herds need vast space to make suitable range adjustments to winter food shortages, insect attacks and predators. Experiments have been conducted to determine if caribou can navigate pipelines and roads which recently have been constructed. Results have been inconclusive, in part because of faulty experimental design

and logistic limitations. It has been noted that caribou sometimes stand under elevated pipelines and in the shade of adjacent buildings to escape insect attack. It is likely that caribou will habituate to these artificialities; they have shown no fear of human construction in the past. If we could step back in time and travel with Lewis and Clark across the vast shortgrass prairie, would we have predicted that pronghorn would adapt to super highways, trains and even barbed wire? Caribou probably are more adaptable than pronghorn.

Furthermore, there is not any good evidence in the literature showing that caribou abandon their ranges as a result of disturbance, with the possible exception of calving areas. To the contrary, a small herd in Ontario winters each year on an active airstrip because of good lichen stands favored by open forest canopies on the runway approaches. Skoog (1968) indicated that there was not sufficient evidence to suggest that Alaskan caribou deserted ranges adjacent to roads in areas where hunting occurred. However, many ranges have been vacated simply due to the attrition of caribou populations. Clearly, if all animals of a population or herd are eliminated, a valuable tradition of uses of the landscape also is eliminated. But if caribou populations are allowed to increase, former ranges may be occupied again.

Also, I think the adverse effect of human harassment of herds has been overstated. Such harassment cannot be condoned, and caribou ecologists may be among the worst offenders. However, the additive effect of such harrassment to the natural stresses of the extrinsic environment are not measurable. In summer, caribou are harassed by insects to the extent that feeding ceases, entire herds stampede and weights remain static. The animals have the ability to cope with this sort of stress. The same applies to the winter season when caribou can lose up to 25 percent of their fall weights and, at times, exist in wretched physical condition. Harassment is serious when young calves are present; herds stampede and the young can be trampled or separated and abandoned by their dams. Human activity should be avoided near calving grounds.

Another more subtle, adverse effect of man is modifying the interaction between predators and caribou. Banfield (1974b) reported that caribou travel down seismic lines, and that wolves may be having increased hunting success by ambushing along these routes. In a new national park in Canada, a road and trail through a key caribou range are now being planned. If these routes are completed and traveled in the winter by snowshoers or snowmobilers, wolves will travel on the routes of compacted snow and enter this winter range more frequently. Wolves need to be studied in greater detail in order to predict how man will adversely affect the complex predator-prey relationships in changing ecosystems used by caribou.



A lone caribou of the Mount McKinley Herd in lush vegetation near the base of Mount McKinley, Alaska. Photo by William E. Ruth.

THE FUTURE

In general, there is reason to be very hopeful for the future of caribou. They are highly adapted to their environment and also adaptable. *Rangifer* is the only ungulate that can use the lichen pastures of the North. Densities of two caribou per square kilometer (5.2 per square mile) or higher might be achieved. The ultimate question for caribou is the same as that once posed for bison—can the land be theirs to wander?

BIG GAME

OF NORTH AMERICA

ECOLOGY AND MANAGEMENT

A Wildlife Management Institute Book

Compiled and edited by
John L. Schmidt and Douglas L. Gilbert

Illustrated by
Charles W. Schwartz

Technical Editors
Richard E. McCabe and Laurence R. Jahn

Published by STACKPOLE BOOKS