

Population Ecology of Caribou in British Columbia

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Abstract: The abundance and geographic range of woodland caribou (*Rangifer tarandus caribou*) decreased in many areas of British Columbia during the 1900's. Recent studies have found that predation during the summer is the major cause of mortality and current population declines. Increased moose (*Alces alces*) populations may be related to past and current caribou declines by sustaining greater numbers of wolves (*Canis lupus*). Mortality rates were greater in areas where caribou calved in forested habitats, in close proximity to predators and moose. Caribou populations which had calving sites in alpine areas, islands, and rugged mountains experienced lower mortality and were generally stable or increasing. A predator-induced population decline in one area appeared to stabilize at low caribou densities, suggesting that the wolf predation rate may be density dependent.

Key words: Population dynamics, predator-prey relationships, *Rangifer tarandus*

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Caribou ecotypes in British Columbia

All caribou in British Columbia (B.C.) belong to the woodland subspecies (*Rangifer tarandus caribou*), but they can be further divided into two different ecotypes, the mountain ecotype and the northern ecotype (Stevenson & Hatler, 1985). Mountain caribou live in southeastern B.C. (Fig. 1) and spend most of the year at high elevations in subalpine forest and alpine habitats. Deep snow prevents them from cratering for terrestrial forage in winter so they rely primarily on arboreal lichens for winter food. Northern caribou live in the northern and west-central areas of the province. They generally inhabit mountainous areas in summer, and use low elevation pine forests or windswept alpine areas during winter. The low snow depths in those habitats during the winter allow them to crater for terrestrial lichens.

Population declines during the 1900's

The current population of caribou in British Columbia is estimated at 14,000 - 17,000 animals (BCMOE in press). Although there are no reliable estimates of historic populations, the current population is generally believed to be substantially reduced from historic numbers (Bergerud, 1978). Caribou have been eliminated from about 15% of their historic range, especially in the southeastern and central parts of the province (Fig. 1), and some

currently occupied habitats have experienced population declines (Edwards, 1956; Bergerud, 1978; Stevenson & Hatler, 1985; Seip, 1992a).

Overhunting was probably responsible for population declines in many areas during the 1900's. Hunting seasons were extremely liberal until the early 1970's, with an open season for cows that lasted 86 days in 1971 (Stevenson & Hatler, 1985). The annual reported harvest in the early 1970's averaged about 1500 caribou (BCMOE, 1979), which may have been about 10% of the provincial population. Moreover, the hunting pressure was concentrated on more accessible caribou herds so the harvest impacts were much greater in those areas. Hunting became much more restricted in the late 1970's with harvesting limited to trophy bulls and annual reported harvests averaging about 600 caribou (BCMOE, in press). Consequently, since the mid 1970's, legal harvest has not been a major limiting factor of caribou populations.

Caribou population declines in the 1900's have also been related to increased wolf (*Canis lupus*) numbers that were sustained by increasing moose (*Alces alces*) populations (Bergerud & Elliot, 1986). Peterson (1955) reported that during the early 1900's, moose greatly expanded their distribution in B.C., spreading throughout the province from the northeastern corner. Spalding (1990) believed that moose populations were not totally absent from

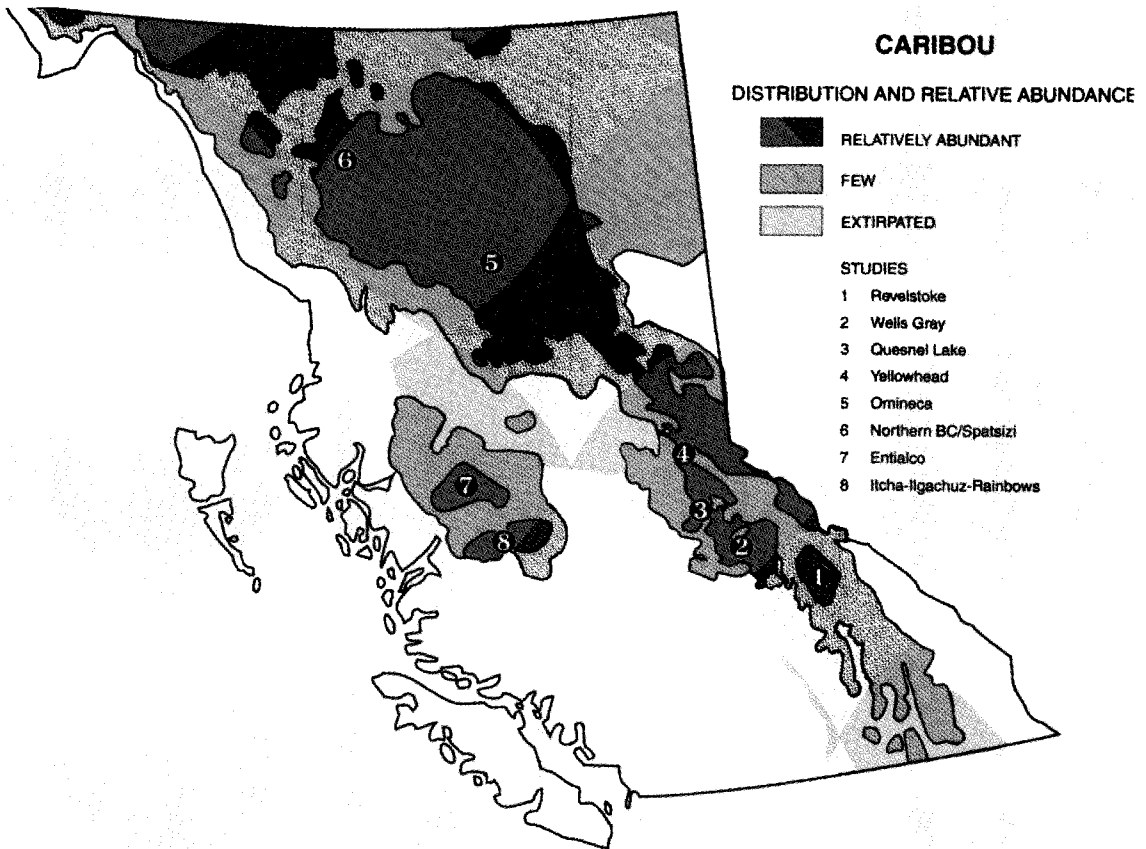


Fig. 1. Current and historic distribution of caribou in British Columbia (Bergerud, 1978, BCMOE, 1979), and the location of recent caribou research projects.

central B.C., but that sparse and scattered populations greatly increased in number during the 1900's. In either case, moose populations greatly increased throughout the province during the 1900's. Bergerud & Elliot (1986) and Seip (1992a) suggested that the increased moose population supported increased wolf numbers and resulted in increased wolf predation on caribou. The first reports of major declines in caribou numbers in some areas like Wells Gray Park coincided with the arrival of moose (Edwards, 1956). That process was probably slowed or reversed by provincial wolf control programs during the 1950's, but resumed when wolf control was terminated in the 1960's (Archibald, 1989). Seip (1992a) reported that the Quesnel Lake caribou herd was declining due to wolf predation during the mid-1980's, and the wolf population was being sustained primarily by moose.

In summary, the general pattern throughout most of this century appears to be a population decline and range reduction of caribou in B.C.. Overhunting in accessible areas, and increased wolf predation resulting from increased moose populations, were likely the major factors contributing to

those declines. In addition, some historic habitats have been abandoned due to habitat destruction or disturbance (Stevenson & Hatler, 1985).

Current population status

Several recent research projects (Table 1) have greatly increased our understanding of caribou population ecology in the province. Radio-telemetry studies have provided data on basic ecology, calf recruitment and adult survival. The reliability of population estimates has been improved by an increase in census effort, and by using marked animals to calculate the proportion of the population counted during censuses.

Pregnancy rate

Several studies have determined the pregnancy rate of adult female caribou by measuring plasma progesterone levels in winter. These studies reported that about 94% of adult females (≥ 2 years) were pregnant (Table 2). Bergerud & Elliot (1986) reported 84% of adult female caribou (≥ 2 years) in northern B.C. were pregnant, based on the presence of distended udders during the calving period. The

lower value based on distended udder counts probably occurs because those counts would include non-parous 2 year olds that would have been classed as yearlings (1.5 years old) the previous winter when progesterone levels are sampled.

Neonatal survival

During post-calving surveys in late June, only 50 - 64% of radio-collared, adult females were accompanied by calves (Table 3). Post-calving counts for all cows, both collared and uncollared, generally recorded fewer calves (Table 3), presumably because those counts included some yearling cows that did not breed, and possibly some misidentified young males. Apparently it was common for about 40% of adult females that were pregnant to lose their calves by the end of the calving period.

The causes of that neonatal calf mortality have not been well documented for B.C. caribou. Searches of the Itcha Mountain calving grounds in June located three calves that appeared to be emaciated or stillborne, and two calves that were killed by predators (Cichowski, unpubl. data). Page (1985) radio-collared newborn calves in Spatsizi and found that they died from a variety of causes including predators and accidents. More extensive studies elsewhere have found that neonatal mortality resulted from emaciation, stillbirths, congenital defects, accidents and predation (Adams *et al.*, 1988; Whitten *et al.*, 1992; Roffe, 1993; Adams & Mech, in press).

Calf survival through the summer

Calf survival through the summer, following the period of neonatal mortality, was quite variable and appeared to be related to the level of wolf predation. Although most populations had about 40 calves/100 cows in late June, counts of calves in March were quite variable among areas (Table 4). Most surveys recorded 15-20 calves/100 adults in March, which indicated that about 20 - 40% of the calves alive in late June had subsequently died (assuming that 40% of the adults counted in winter were bulls). Surveys at Entiako, and Quesnel Lake in the mid 1980's, recorded only about 10 calves/100 adults in March which indicated that about 60% of the calves present in late June had died. Most of that mortality occurred during the summer months, prior to October calf counts (Seip, 1992a; Cichowski, unpubl. data).

Wolf predation appeared to be a major cause of caribou calf mortality after the initial neonatal period. Seip (1992a) reported that when wolves were present and uncontrolled at Quesnel Lake during the mid-1980's, calf/cow ratios in October were only 2.5 calves/100 adult females, compared to 39 calves/100

adult females when wolves were absent or reduced by wolf control. Bergerud & Elliot (1986) reported 15.1% calves in the fall for northern B.C. herds when wolf numbers were low compared to 7.5% calves when wolves were more abundant. The major

Table 1. Recent studies of woodland caribou in British Columbia that provide the source of data used in this paper.

Study Area and Period	Reference
Revelstoke (1981-84)	Simpson & Woods, 1987
Wells Gray Park (1986-89)	Seip, 1990, 1992a
Quesnel Lake (1985-89)	Seip, 1992a, 1992b
Quesnel Lake (1992-94)	J. Young, unpubl. data
Yellowhead (1988-91)	G. Watts, unpubl. data
Omineca (1991-94)	M. Wood, unpubl. data
Northern B.C. (1977-82)	Bergerud & Elliot, 1986
Spatsizi (1980-84)	Hatler, 1986
Entiako (1985-88)	D. Cichowski, unpubl. data
Itcha-Ilgachuz-Rainbows (1985-88)	D. Cichowski, unpubl. data

Table 2. Pregnancy rate of adult female caribou (2+ years) based on winter plasma progesterone concentrations.

Area	Sample size	Pregnant (%)
Itcha-Ilgachuz	34	97
Quesnel Lake	21	95
Yellowhead	21	95
Entiako	18	94
Wells Gray	27	93
Omineca	19	90
Average		94

Table 3. Percentage of caribou cows with surviving calves in late June.

Area	Radio-collared Cows with Calves (%)	Total Cows with Calves (%)
Wells Gray	57	44
Entiako	53	43
Itcha-Ilgachuz-Rainbows	64	42
Quesnel Lake (1985-89)	50	38
Northern B.C.	--	38
Average	56	41

importance of wolf predation in limiting calf recruitment has also been demonstrated in the Yukon and Alaska (Gasaway *et al.*, 1983; Farnell & McDonald, 1988; Whitten *et al.*, 1992; Adams & Mech, in press).

Adult survival

The only reliable estimates of adult mortality rates have come from monitoring the survival of radio-collared caribou. Annual adult mortality rates varied from 0-29% among studies in B.C. (Table 5). Most studies found that the major period of mortality occurred between May and October, especially during periods when caribou were migrating between winter and summer ranges. Adult caribou experienced a higher mortality rate at low elevations than at high elevations (Seip, 1992a; Cichowski, unpubl. data; Watts; unpubl. data; Wood, unpubl. data). Several of the studies were unable to determine the primary causes of mortality

because dead caribou were not visited immediately after death. However, when cause of death was determined, wolf and bear (*Ursus* spp.) predation were the primary causes of adult mortalities. Avalanches were a major cause of adult mortality in the Revelstoke studies (Simpson, 1987a; B. McLellan, pers. comm.), an area of steep rugged terrain and very high snowfall and avalanche hazard.

Radio-telemetry studies generally did not find poaching to be an important mortality factor, probably because most of the studies occurred in inaccessible areas and parks. However, there is evidence that poaching can be a locally important cause of adult mortality in areas with road access. Johnson (1985) reported 21 known cases of caribou illegally shot in the endangered Selkirk and Purcell populations between 1967 and 1983. He concluded that with the additional number of illegal kills that go unreported, man-caused deaths could equal recruitment in these populations. Similarly, Seip & Stevenson (1987) reported 13 cases of illegal caribou kills during an eight year period in the North Thompson area. Assuming that many other illegal kills probably went unreported, poaching would have been a major mortality factor for the small caribou population in that area.

Overall, in most areas the primary cause of adult mortality appeared to be predation, especially for caribou occupying lower elevations between May and October. The direct evidence of predation on adults was supported by the indirect evidence that adult caribou mortalities from unknown causes were also most common at lower elevations between May and October. Adult caribou generally experienced good survival during the winter months, except in areas of high avalanche risk. Starvation or malnutrition were not major mortality factors for adults. Illegal hunting was a locally important cause of adult mortality in some areas with easy road access.

Table 4. Number of caribou calves/100 adults in late winter.

Area	Calves/100 adults
Revelstoke	20.5
Itcha-Ilgachuz-Rainbows	20.0
Omineca	19.4
Yellowhead	18.6
Quesnel Lake (1992-93)	18.0
Wells Gray	17.7
Northern B.C.	11 - 15
Entiako	10.3
Quesnel Lake (1985-89)	9.8

Table 5. Rate, timing, and major cause of mortality for radio collared adult female caribou.

Area	Annual adult female mortality rate (%)	Season and major cause
Quesnel Lake (1992-94)	0	-
Yellowhead	5	Summer, unknown
Wells Gray	8	Summer, predation
Spatsizi	13	Winter, unknown
Itcha-Ilgachuz-Rainbows	15	Summer, predation
Omineca	19	Summer, unknown
Revelstoke	19	Winter, avalanches
Entiako	24	Summer, predation
Quesnel Lake (1985-89)	29	Summer, predation
Average	15	

Population trend

The population trend of caribou in different areas of the province was variable. Some populations had low adult mortality rates, high calf recruitment, and were probably increasing (Table 6). Other populations had high adult mortality, low recruitment, and were likely decreasing. The Quesnel Lake population was declining in the mid-1980's, but stabilized during the early 1990's.

Populations that had low calf recruitment usually also had high adult mortality ($r = -0.67$, $p < 0.1$), suggesting that both parameters were limited by a common cause in most populations, i.e. predation in summer (Table 6). In general, winter calf recruit-

Table 6. Annual adult female mortality, calf recruitment, finite growth rate, and probable population trend of caribou herds in British Columbia.

Area	Adult female mortality (%)	Calf recruitment (% calves)	Growth Rate (λ) ¹
Yellowhead	5	15.7	1.13 (+)
Quesnel Lake (1992-94)	10	15.9	1.07 (+)
Wells Gray	8	15.0	1.08 (+)
Itcha-Ilgachuz-Rainbows	15	16.7	1.08 (+)
Omineca	19	16.3	0.97 (stable)
Revelstoke	19	17.0	0.98 (stable)
Entiako	23	9.3	0.85 (-)
Quesnel Lake (1985-89)	29	8.9	0.78 (-)

¹ $\lambda = (1-M)(1-R)$ where M = adult mortality rate and R = calf recruitment rate (Bergerud & Elliott, 1986).

ment greater than 15% calves appeared to be indicative of populations that also had sufficiently high adult survival to be stable or slowly increasing. Populations with only about 10% calves in winter also had low adult survival and were probably declining. Similarly, Bergerud (1988, 1992) reported that calf recruitment was correlated with adult survival and if calves constituted less than 15 - 16% of the winter population, the herd was likely decreasing.

Anti-predator strategies and the density of caribou populations

The density of caribou populations in B.C. appears to be related to their ability to become spatially separated from predators during the summer months. The abundance of wolves is largely determined by the availability of other prey species, such as moose (Seip, 1992a). Moose and wolves are more abundant in low elevation forested habitats than in alpine habitats during summer (Seip, 1992a). Also, grizzly bears (*U. arctos*) use lower elevation forested habitats more than alpine areas (Simpson, 1987a). Consequently, caribou which migrate to alpine habitats during the summer reduce their exposure to predators (Bergerud *et al.*, 1984; Seip, 1992a).

In west-central B.C., radio-collared adult female caribou that calved on large alpine plateaus in the Itcha, Ilgachuz and Rainbow mountains had high calf survival through June (Table 7). In the adjacent Tweedsmuir-Entiako area, radio-collared caribou

Table 7. Percent of radio-collared, adult female caribou with surviving calves during late June in different habitat types in west-central British Columbia.

Area/habitat	Adult females (n)	With surviving calves (%)
<i>Tweedsmuir-Entiako</i> (1985-93) in forest	53	24.5
alpine/subalpine	51	70.6
on islands	5	80.0
<i>Itcha-Ilgachuz-Rainbows</i> (1985-88) alpine-subalpine	56	62.5

that calved in low elevation forested areas had very low calf survival, whereas caribou that calved in alpine and subalpine habitats had higher calf survival, similar to the Itcha-Ilgachuz-Rainbows (Table 6). Two caribou that calved on islands, one of them over 3 successive years, also had high calf survival. Cumming & Beange (1987) also reported that caribou in Ontario calve on islands to avoid predators.

In southeastern B.C., Seip (1992a) reported that caribou in Wells Gray Park and Quesnel Lake were spatially separated from wolves and moose throughout the winter because the caribou used subalpine forests while moose and wolves were located primarily in the valley bottoms. Wolves were sustained primarily by moose during the winter months and rarely killed caribou. In summer, caribou, wolves and moose at Quesnel Lake used similar subalpine forest habitats, whereas in Wells Gray Park, most caribou migrated to rugged alpine areas which kept them spatially separated from wolves and moose. Migration to alpine habitats in Wells Gray Park resulted in low wolf predation on caribou during the summer and a slowly increasing population. In contrast, wolf predation was a major mortality factor for caribou adults and calves during the summer at Quesnel Lake and the herd was declining. The primary difference in wolf predation between these two areas appeared to be related to the degree of spatial separation between caribou and wolves during the summer. Other caribou populations in B.C. that migrate to rugged, alpine habitats during the summer, such as Yellowhead and Omineca, also appear to be stable or increasing (Table 6).

Seip (1992a) concluded that wolves might extirpate the Quesnel Lake caribou because the wolves were sustained primarily by moose and would not decline in numbers in response to declining caribou abundance. However, since the mid-1980's, caribou

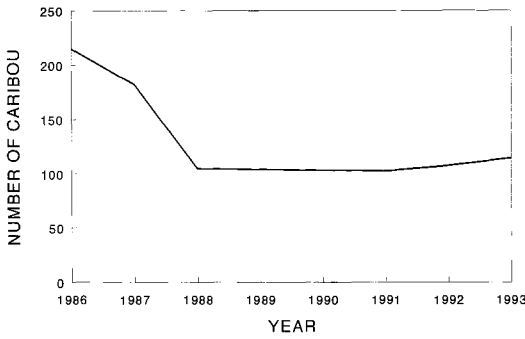


Fig. 2. Population trend of woodland caribou in the Quesnel Lake area, based on March counts corrected for sightability.

recruitment has increased, adult mortality has decreased and the population has stabilized (Table 6, Fig. 2). Radio-monitoring has indicated that wolves are still at a similar abundance in the area but the killing rate on caribou had apparently declined (J. Young, pers. comm.). Perhaps the remaining caribou were individuals that traditionally used secure calving sites that go undetected by wolves. The stabilization of this caribou herd suggested the predation rate was density-dependent. However, the reduced predation rate appeared to be primarily due to a reduced functional response of wolves rather than any decrease in wolf numbers.

The Quesnel Lake caribou stabilized at a density of about 0.04 caribou/km² over the entire annual range. Densities on winter ranges were higher (0.2/km²), but the density over the annual range best represents the density at which caribou were available to wolves through the year. Other B.C. caribou herds that space out in subalpine forests and alpine peaks in summer also occurred at a density of about 0.04/km² over the annual range (Table 8). In contrast, caribou herds that aggregated on large alpine plateaus in summer, i.e. the Itcha-Ilgachuz-Rainbows herd and the Spatsizi herd, occurred at a density of about 0.1-0.2/km² over the annual range. That density is similar to caribou herds in Yukon and Alaska (0.15-0.3/km²) that aggregate on alpine plateaus during summer (Farnell & McDonald, 1988, 1990; Adams & Mech in press).

Prior to the increase in moose abundance in B.C. during the 1900's, it is likely that higher densities of caribou were able to co-exist with wolves. However, when moose numbers increased, caribou that lived in close proximity to moose habitat were eliminated or greatly reduced, and the caribou remaining today represent animals that were more effective at spacing away from moose and wolves in summer. For example, in Wells Gray Park, most of

the caribou that traditionally spent the summer in close proximity to moose habitat have disappeared and the current stable population represents caribou that migrate away from moose habitat in the summer (Seip, 1992a). Current stable caribou populations should be able to maintain their densities, as long as their predator avoidance strategy is not further disrupted by natural or human factors.

These results support the general model proposed by Seip (1991), that the abundance of caribou is primarily determined by the effectiveness of their anti-predator strategy. Caribou which aggregate on alpine plateaus for calving and summer range are fairly effective at avoiding predators and attain the highest caribou densities in B.C. Caribou that space out in subalpine forests during summer experience greater exposure to predation and are reduced to lower densities (Seip, 1992a). Caribou which live in boreal forests in northeastern B.C. have the fewest options to become spatially separated from predators and consequently occur at even lower densities (1 caribou/25-250 km²; BCMOE, in press), similar to other areas of the boreal forest across Canada (Edmonds, 1991; Cumming & Beange, 1993).

Although numerous other limiting factors such as weather conditions and diet quality may cause significant year to year variation in caribou population growth, often by influencing vulnerability to predation, it appears that the effectiveness of predator avoidance strategies is the dominant factor that determines the natural population density of caribou populations in British Columbia.

Table 8. Densities of caribou on their total annual range for herds that space out in alpine/subalpine forests in summer, compared to those that aggregate on alpine plateaus.

Area	Annual Range (km ²)	Number of Caribou	Density (caribou/km ²)
<i>Space out in subalpine/alpine</i>			
Yellowhead	15,000	600	0.04
Quesnel Lake	2300	95	0.04
Wells Gray	5200	265	0.05
Entiako	16,000	500	0.03
<i>Aggregate on alpine plateaus</i>			
Itcha-Ilgachuz	10,000	1500	0.15
Spatsizi	10,000	2145	0.21

Implications for caribou management

Caribou populations have a limited capacity to sustain harvest. It appears that in the past, overhunting was responsible for reducing caribou populations. Legal hunting is not currently a major limiting factor, however, illegal hunting remains a major problem in some areas with road access. One of the major threats to caribou populations is increasing road development and access into areas of caribou habitat.

In some areas, caribou are vulnerable to being killed by avalanches during the winter. Caribou generally prefer more gentle terrain in winter (Terry *et al.*, this volume), but excessive disturbance by snowmobiles can displace caribou into steeper, more avalanche prone terrain (Simpson, 1987b; Seip, pers. obs.). Therefore, snowmobiles and other disturbances that displace caribou from preferred winter ranges may increase their risk of accidental mortality.

Wolf predation is a major limiting factor of caribou populations, and wolf control is an effective technique to increase caribou survival (Gasaway *et al.*, 1983; Bergerud & Elliot, 1986; Farnell & McDonald, 1988). However, public opposition makes it unlikely that wolf control will be widely used in British Columbia in the future. Therefore, we must provide habitat conditions that allow caribou to avoid wolves.

Habitat management practices for caribou have traditionally concentrated on providing lichens for winter foraging. Although caribou winter habitat must provide adequate food resources, it is also important how that habitat is distributed on the landscape. The primary habitat requirement of caribou is to have areas where they can effectively avoid predators. Forest harvesting practices that produce a patchwork of different forest age classes, linked with a network of roads, may contain enough lichens to support a caribou herd, but probably will not provide an environment where caribou can effectively avoid predators and poachers. A patchwork of early seral and mature forests puts caribou into close proximity to predators by enhancing habitat for other prey species that prefer early seral forests. Concentrating caribou into small areas of suitable habitat also makes them easier for predators to locate. The development of roads provides access for poachers and predators. Consequently, caribou habitat management practices should provide a perpetual supply of large, contiguous areas of suitable summer and winter habitat, with little or no vehicle access and disturbance, so that caribou can space out at low densities and avoid predators and poachers.

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