Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia

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Caribou (*Rangifer tarandus caribou*), wolves (*Canis lupus*), and moose (*Alces alces*) were radio-collared and monitored in two areas of southeastern British Columbia to determine predator–prey interactions. Throughout the year, wolves and moose used similar areas and habitats, and moose were the primary prey of wolves. In winter most caribou used high-elevation habitats and were spatially separated from wolves and moose living in valley bottoms. In summer, caribou, wolves, and moose at Quesnel Lake used similar areas and habitats, whereas in Wells Gray Park most caribou migrated to rugged, mountainous areas, which kept them spatially separated from wolves and moose. The Quesnel Lake caribou population had a high adult mortality rate (29%/year), wolf predation being the major cause. Calf survival to October was low (2.5/100 adult females) when wolves were present and uncontrolled in the area, but was significantly greater (39/100 adult females) when wolves were reduced or absent. The Quesnel Lake caribou population was found to be declining by about 25%/year, and wolf predation appeared to be the major limiting factor. Caribou in Wells Gray Park had a low adult mortality rate (8%/year) and comparatively high calf survival to October (37/100 adult females). The Wells Gray caribou population was found to be slowly increasing, apparently because its migratory behavior kept it separated from wolves and moose throughout the year, resulting in low wolf predation on the caribou.

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Des Caribous (*Rangifer tarandus caribou*), des Loups gris (*Canis lupus*) et des Orignaux (*Alces alces*) ont été munis d'un collier émetteur et suivis dans deux zones du sud-est de la Colombie-Britannique dans le but d'évaluer les interactions prédateur–proie. Durant toute l'année, les loups et les orignaux utilisaient les mêmes zones et habitats et les orignaux constituaient la principale proie des loups. En hiver, la plupart des caribous utilisaient des habitats en haute altitude et étaient physiquement séparés des loups et des orignaux habitant le fond des vallées. En été, caribous, loups et orignaux du lac Quesnel utilisaient des zones et habitats semblables, alors que dans le parc Wells Gray, la plupart des caribous migraient vers des zones accidentées, plus montagneuses, qui les séparaient des loups et des orignaux. Chez la population de caribous du lac Quesnel, le taux de mortalité des adultes était élevé (29%/an) et la prédation par les loups en était la principale cause. La survie des petits jusqu'en octobre était faible (2,5/100 femelles adultes) lorsque la population de loups n'était pas contrôlée dans la zone, et significativement plus élevée (39/100 femelles adultes) en l'absence des loups ou lorsque le nombre de loups était réduit. La population de caribous du lac Quesnel diminuait d'environ 25%/an et la prédation par les loups semblait être le principal facteur limitant. Chez la population du parc Wells Gray, le taux de mortalité des adultes était faible (8%/an) et la survie des petits jusqu'en octobre était relativement élevée (37/100 femelles adultes). La population de caribous du parc augmentait progressivement, semble-t-il parce que leur comportement migrateur les gardait séparés des loups et des orignaux durant toute l'année, ce qui avait pour effet de réduire la prédation de caribous par les loups.

[Traduit par la rédaction]

Introduction

"Thicker and thicker they came, until the whole pass was a mass of moving mole-grey forms from which a forest of branched antlers sprouted, clashing and clicking together as they pressed onward. . . . For two hours and a half we watched them passing us. It was impossible to count them; we could only guess at their hundreds" (Glynn-Ward 1926). That account of the caribou (*Rangifer tarandus caribou*) migration in what is now Wells Gray Provincial Park in southeastern British Columbia indicates that caribou were very abundant in the early 1900s, but since that time there has been a major population decline. Currently there are only about 250 caribou in the 5200-km^2 park, and one rarely sees more than 25 at one time.

Woodland caribou populations experienced major declines throughout southeastern British Columbia during the 1900s, and disappeared from many parts of their historic range (Bergerud 1978; Stevenson and Hatler 1985). Similar declines occurred over much of the range of woodland caribou in North America (Bergerud 1974).

Caribou declines in British Columbia have often been attributed to habitat destruction by fires or logging, which reduced the availability of lichens, the primary winter food of the caribou (Edwards 1954; Bloomfield 1980). However, Bergerud (1974) proposed that wolf (*Canis lupus*) predation and overharvesting by hunters were the major causes. Bergerud (1974) and Bergerud and Elliot (1986) suggested that caribou declines were related to the colonization of British Columbia by moose (*Alces alces*) in the early 1900s, which supported increased wolf numbers and resulted in increased wolf predation on caribou.

The purpose of this paper is to evaluate the following hypotheses: (*i*) wolf predation is the major cause of currently declining caribou populations in southeastern British Columbia; (*ii*) wolf populations are sustained primarily by moose; (*iii*) wolf predation on caribou is greater in areas where caribou live in close proximity to moose.

Study area

The study area included the Quesnel Lake area and Wells Gray Provincial Park (52°N, 120°W) in southeastern British Columbia (Fig. 1). Most of the Quesnel Lake area and the western and southern

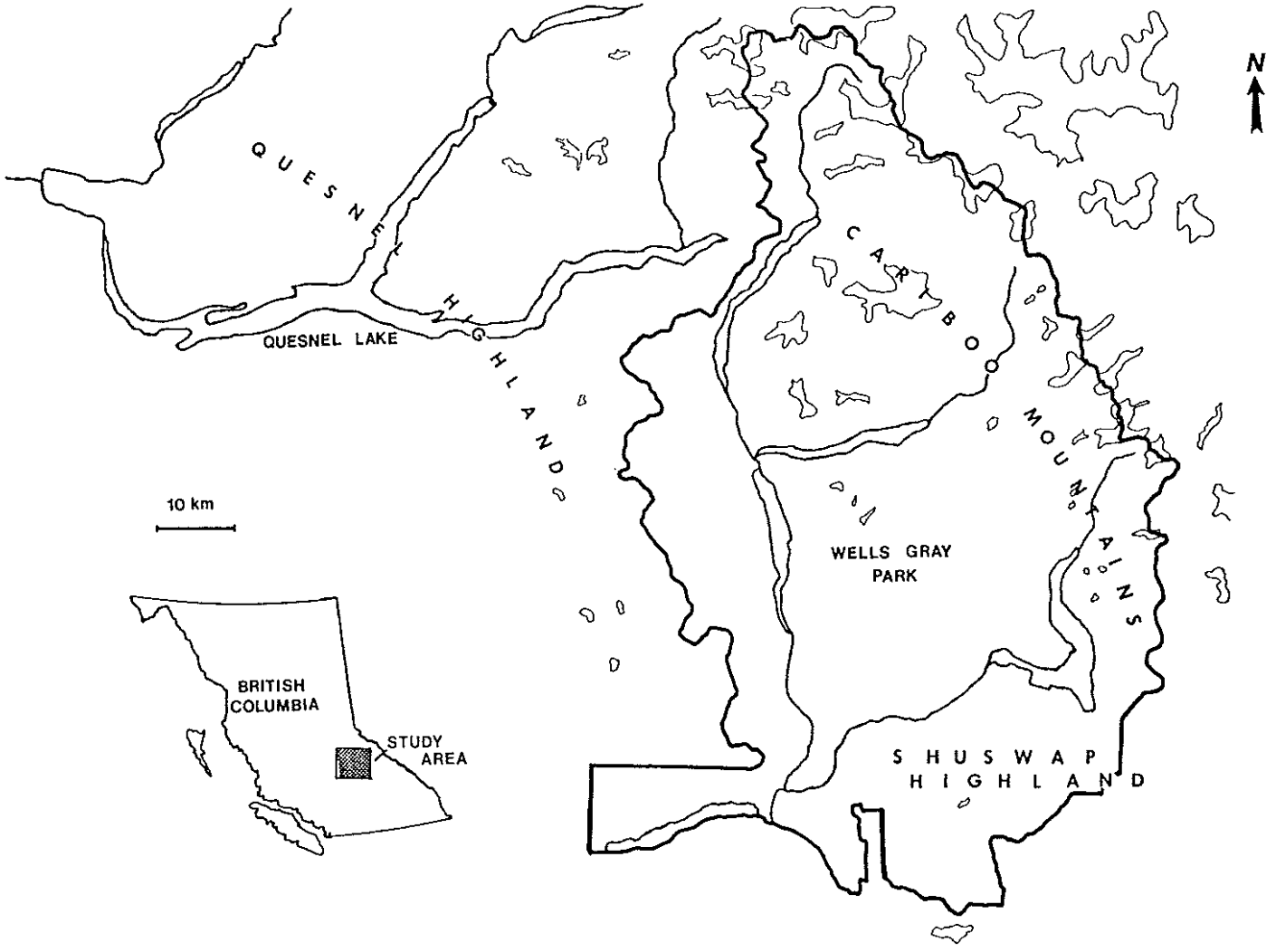

FIG. 1. Map of the study area. The 2200-m contour interval indicates areas of rugged topography.

sections of Wells Gray Park are highland topography (Quesnel Highlands, Shuswap Highland), with sloping plateaus and rounded mountains between 1500 and 2100 m, dissected by rivers and lakes at 800–1200 m. The interior, northern, and eastern sections of Wells Gray Park and the northeastern section of the Quesnel Lake area are steep, rugged mountainous areas (Cariboo Mountains), with many peaks exceeding 2500 m. Annual precipitation is high, with wet summers (400 mm rain) and winter snow depths exceeding 2 m at upper elevations.

The Interior Cedar Hemlock (ICH) biogeoclimatic zone occurs at low elevations up to 1200–1350 m (Lea 1986). Forests in this zone are dominated by western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*), with a moss understory and sparse shrub layer. The Engelmann Spruce Subalpine Fir zone occurs above the ICH zone, up to about 1800 m, and is dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*), with upper elevations supporting an open parkland forest of subalpine fir. Above the tree line the alpine tundra zone supports a variety of sedges, grasses, and forbs, although much of the area is barren rock and glaciers. Shrubland habitats occur within the study area in both wetlands and areas that have been burned or logged.

Ungulate species include caribou, moose, mule deer (*Odocoileus hemionus*), and mountain goats (*Oreamnos americana*). Major predators include wolves, grizzlies (*Ursus arctos*), black bears (*Ursus americana*), and wolverine (*Gulo gulo*).

Methods

Each year from March 1984 to March 1989, 16–19 radio-collared adult female caribou were monitored in the Quesnel Lake area. From March 1986 to March 1989, 24–26 adult female caribou were monitored in Wells Gray Park. Nine radio-collared moose (1 male, 8 females) were monitored in Wells Gray Park from March 1987 to March 1989, and 4–7 adult female moose were monitored each year in the Quesnel Lake area from 1985 to 1989. Two to 4 radio-collared wolves were monitored each year in the Quesnel Lake area from 1984 to 1987, and 2 radio-collared wolves were monitored in Wells Gray Park in 1987.

Caribou were captured in March by net-gunning from a helicopter. Additional caribou were captured each March to replace animals that had died during the previous year. Blood samples collected from the front leg vein were centrifuged and the separated plasma was stored frozen. The plasma progesterone concentration was determined by radioimmunoassay (British Columbia Biomedical Laboratories, Burnaby) to determine pregnancy (Rehbinder et al. 1981). Each caribou was fitted with a radio collar containing a motion-sensitive mortality sensor. Coloured ear tags were attached to aid visual identification.

Moose were captured in winter by using the immobilizing drug Carfentanyl administered by Cap-Chur darts shot from a helicopter. Wolves were captured in the Quesnel Lake area in summer in leghold traps placed around scats and wolf lure. Wolves were captured in Wells Gray Park during winter in neck snares placed around baits.

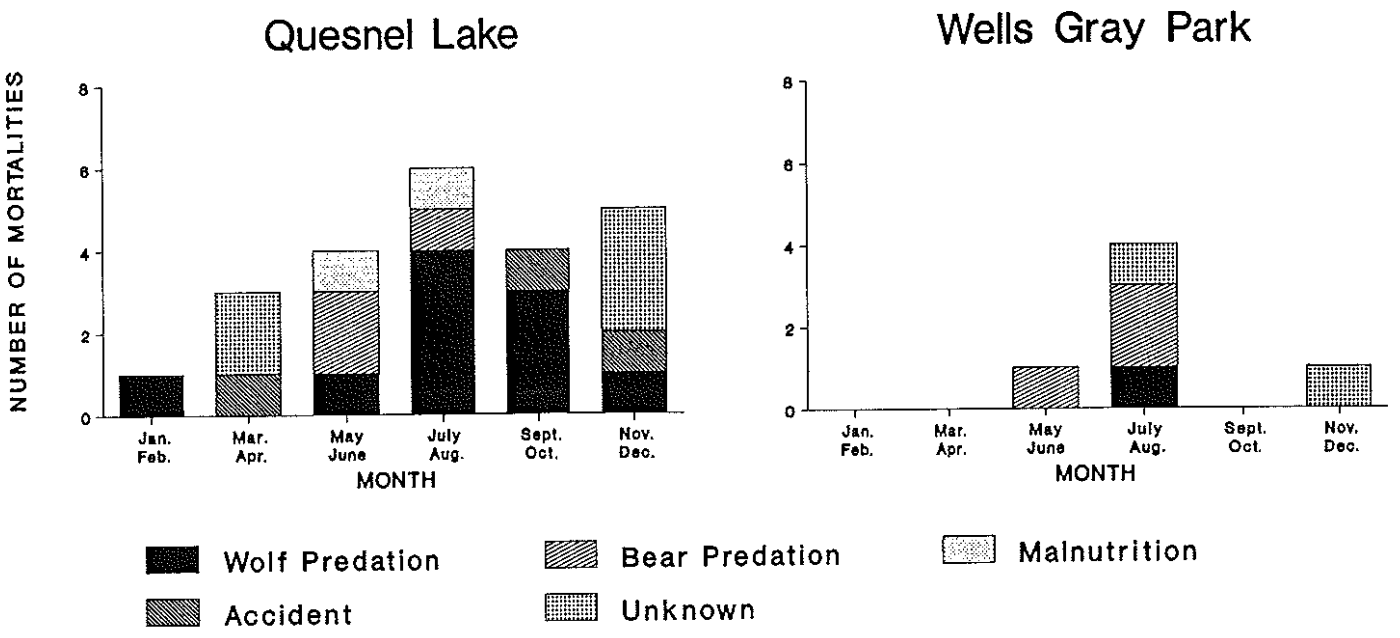

FIG. 2. Timing and causes of mortality of radio-collared adult female caribou, based on 79 caribou-years of monitoring at Quesnel Lake and 76 caribou-years in Wells Gray Park.

Radio-collared animals were located 2–4 times each month by telemetry from an airplane. Location, elevation, and habitat type were recorded for each location. Collared caribou that died (indicated by a mortality signal from the radio collar) were necropsied to determine the cause of death. Position of the carcass, predator sign, and bone marrow fat content were used to determine cause of death.

Caribou calf counts were conducted from a helicopter in late June, August, and October in each year of monitoring. Each radio-collared caribou was observed to determine if it had a calf. In addition, uncollared caribou cows and calves associated with a radio-collared caribou were recorded. The calf/cow ratios for all cows seen were lower than those for radio-collared cows alone because yearling females, and possibly some misidentified young males, were included in the count of all cows seen. Calf/cow ratios and adult mortality rates were compared using 2 × 2 contingency tables (Sokal and Rohlf 1981).

The caribou populations were censused from a helicopter in late March, when most of the caribou were in open subalpine habitats. The census area was searched by flying along the tree line watching for tracks. When tracks were found, the area was searched until the caribou were located, and the numbers of adults, calves, and radio-collared individuals were recorded. The census route was directed by the pilot, who did not have prior knowledge of where radio-collared caribou were located, which precluded a biased search. A sightability correction factor (the proportion of radio-collared animals seen during the census) was used to correct the total count for animals that were not seen.

Wolf scats were collected opportunistically throughout the year and analysed to determine food habits. The percentage of hair from different prey species present in the scats was corrected, based on the body size of the different prey species (Floyd et al. 1978), to determine food habits.

To evaluate the effect of reduced wolf numbers on caribou survival, 4 adult female wolves were shot on the east side of Quesnel Lake in the winter of 1987, and 7 wolves were shot in the Quesnel Lake area in the winter of 1988.

Results

Parameters and limiting factors of caribou populations

Adult mortality

The adult mortality rate was much higher in the Quesnel Lake area than in Wells Gray Park ($G = 14$, 1 df, $p < 0.05$). At Quesnel Lake, 23 radio-collared caribou died during 79 caribou-years of monitoring, an annual mortality rate of 29 ± 5% (SD). In Wells Gray Park, 6 radio-collared caribou died during 76 caribou-years of monitoring, an annual adult mortality rate of 8 ± 3% (SD).

At Quesnel Lake, of 18 adult deaths for which it was possible to determine the cause, 10 (55%) were due to wolf predation, 3 (17%) to bear (*U. arctos* or *U. americanus*) predation, 3 (17%) to accident, and 2 (11%) to malnutrition (Fig. 2). The three accidental deaths included a dislocated hip, an avalanche, and a fall into a canyon. The two cases of malnutrition were inferred from depleted bone marrow fat. Of the 4 adult mortalities in Wells Gray Park for which the cause could be determined, 3 were due to bear predation and the other to wolf predation.

Deaths due to wolf predation occurred during summer and early winter, whereas bear predation occurred during spring and early summer. The two deaths due to malnutrition occurred during summer. The average elevation at which caribou were killed by predators was 1291 ± 363 m (SD).

Pregnancy rate

Plasma progesterone concentrations indicated that 45 of 48 (94%) adult females were pregnant when captured. The 2 female yearlings (21 months old) and 1 female calf (9 months old) that were captured were not pregnant. Plasma progesterone concentrations for pregnant animals ranged from 3.5 to 11.3 ng/mL compared with 0.1–0.2 ng/mL for nonpregnant animals. All 4 adult female caribou that were necropsied in winter were pregnant.

Calf production

There was no difference in calf production by radio-collared females between Quesnel Lake and Wells Gray Park ($G = 0$, 1 df, $p > 0.05$). In late June, following the calving period, 50% (36/72) of the radio-collared adult females in the Quesnel Lake area were accompanied by calves (Fig. 3). There was substantial variation in June calf counts among years, ranging from 33 to 65% of radio-collared cows with calves. About

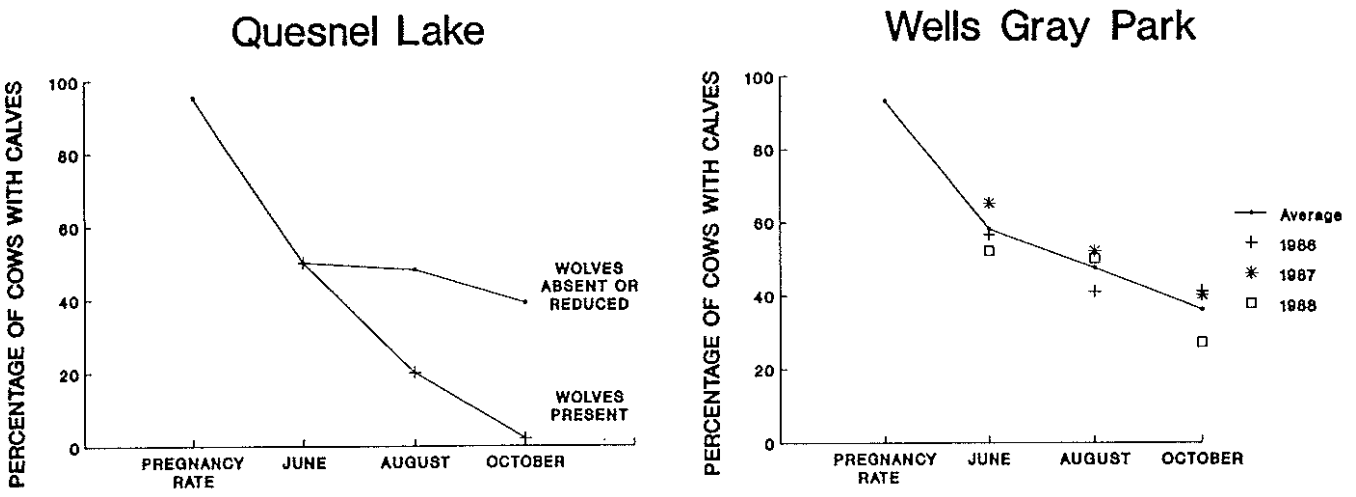

FIG. 3. Percentage of radio-collared adult female caribou with surviving calves.

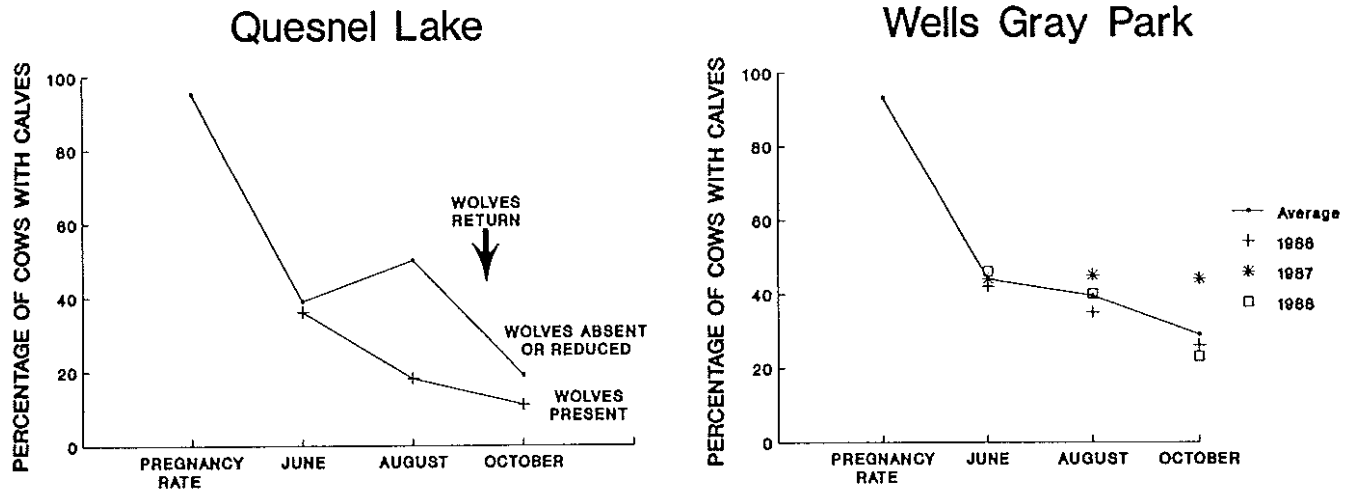

FIG. 4. Percentage of all female caribou seen that had surviving calves.

38% (65/170) of all cows seen during June calf counts in the Quesnel Lake area had surviving calves (Fig. 4).

In Wells Gray Park, 57% (39/69) of radio-collared adult female caribou had surviving calves immediately following the calving period, and 44% (62/140) of all cows seen had surviving calves. There was little variation in June calf counts between years in Wells Gray Park (Figs. 3, 4).

There was no difference ($G = 1.2$, 1 df, $p > 0.05$) in June calf production between caribou whose calf survived the previous summer and those that had lost their calf. For the two areas combined, 62% (20/32) of radio-collared caribou that had a surviving calf in August had another calf the following June, and 48% (24/50) of caribou that did not have a calf in August had a calf the following June.

Calf survival

In the Quesnel Lake area, calf survival through the summer appeared to be related to wolf abundance. In the summer of 1984, wolves were present on both sides of Quesnel Lake. Three radio-collared wolves belonging to a pack of about 6 ranged over the area on the west side of the lake. Other uncollared wolves were present on the east side of the lake, including wolves with pups at a den site. The percentage of radio-collared caribou with calves decreased rapidly during summer, and by October no radio-collared cows had surviving calves (Table 1). The following March, there were 8.3 calves per 100 adults in the population (Table 2).

In the winter of 1984–1985, the radio-collared wolves and associated pack members from the west side of Quesnel Lake crossed the ice to the east side of the lake. The wolves remained on the east side of the lake throughout the summer of 1985. On the west side of the lake the absence of wolf scats on roads and our unsuccessful efforts to trap additional wolves indicated that wolves were rare or absent during the summer of 1985. No radio-collared caribou were killed by wolves on the west side of the lake during the summer of 1985, which also suggested that wolves were absent. Caribou calf survival was high on the west side of the lake, where wolves appeared to be absent, but on the east side of the lake, where radio-collared wolves and associated pack members were present, no collared cows had surviving calves in October (Table 1). The following March there were 23 calves per 100 adults on the west side of the lake but no calves on the east side of the lake (Table 2).

In the summer of 1986, wolves were again present on both sides of the lake, based on monitoring of radio-collared wolves on the east side and detection of tracks and scats on the west

TABLE 1. Percentages of radio-collared female caribou with calves at Quesnel Lake in October in areas where wolves were present and uncontrolled compared with areas where wolves were reduced or absent

Year	Wolf abundance	No. of females	No. of females with with calves	% with calves
1984	Present	11	0	0
1985	Present	8	0	0
1985	Naturally absent	9	5	56
1986	Present	14	1	7
1987	Present	7	0	0
1987	Reduced	7	2	29
1988	Reduced	7	2	29
Total	Present	40	1	2.5
Total	Reduced or absent	23	9	39
Total	Reduced	14	4	29

side. Calf survival declined rapidly during the summer months, and only 1 of 14 collared cows had a surviving calf in October (Table 1). By March there were 9.9 calves per 100 adults in the population (Table 2).

In March of 1987, 4 female wolves belonging to the pack on the east side of Quesnel Lake were shot as part of a wolf-control experiment. In addition, 1 of the 2 surviving radio-collared wolves moved out of the Quesnel Lake area to the east side of Wells Gray Park soon after the others were shot. The other radio-collared wolf also abandoned the area, but its destination is not known. Given that radio-collared wolves in the pack had ranged over the entire study area east of the lake, and that the maximum number of wolves observed in the pack was 7, it is likely that following wolf removal, there were few or no wolves remaining on the east side of the lake. The following summer, 2 of 7 radio-collared cows had calves survive to October on the east side of the lake, whereas no radio-collared cows (0/7) had surviving calves on the west side, where wolves had not been reduced. In March the number of calves per 100 adults was greater ($G = 4.4$, 1 df, $p < 0.05$) in the wolf-control area than in the area where wolves were not reduced (Table 2).

Seven wolves were removed from the Quesnel Lake area (4 on the east side, 3 on the west) by shooting and trapping in the winter of 1987–1988. Based on the distribution and numbers of wolves present during previous years when wolves were radio-collared, it is likely that between 30 and 50% of the wolves in the area were killed. Some wolves were known to remain in the Quesnel Lake area, because 2 radio-collared adult caribou were killed by wolves during the summer. Calf survival may have been higher in October as a result of the wolf reduction (Table 1), but by March the population contained few calves (Table 2).

For all years combined, calf survival was greater in October ($G = 12$, 1 df, $p < 0.05$) and March ($G = 8$, 1 df, $p < 0.05$), when wolves were naturally absent or reduced by wolf control (Tables 1, 2). When wolves were present and uncontrolled, only 1 of 40 (2.5%) radio-collared adult female caribou had a calf that survived to October, and there were about 7 calves per 100 adults in the population in March (Fig. 3). When wolves were absent or reduced by wolf control, 9 of 23 (39%) radio-collared adult females had a calf that survived to October, and there were 14.7 calves per 100 adults in the population in March.

TABLE 2. Numbers of calves per 100 adults at Quesnel Lake in March

Year	Wolf abundance	No. of adults	No. of calves	No. of calves per 100 adults
1985	Present	109	9	8.3
1986	Present	65	0	0.0
1986	Naturally absent	96	22	23.0
1987	Present	141	14	9.9
1988	Present	49	2	4.0
1988	Reduced	35	5	14.0
1989	Reduced	94	6	6.0
Total	Present	364	25	6.9
Total	Reduced or naturally absent	225	33	14.7
Total	Reduced	129	11	8.5

TABLE 3. Numbers of calves per 100 adults in the Wells Gray caribou population in March

Year	No. of adults	No. of calves	No. of calves per 100 adults
1987	182	39	21.4
1988	157	24	15.3
1989	226	37	16.4
Average			17.7

When wolves were absent or reduced, a greater percentage of all cows seen had surviving calves in August ($G = 6.2$, 1 df, $p < 0.05$) but not in October ($G = 0.6$, 1 df, $p > 0.05$). In August, 50% (12/24) of all cows seen had surviving calves when wolves were absent or reduced compared with 18% (9/49) when wolves were present and uncontrolled. In October, 19% (6/31) of all cows seen had surviving calves when wolves were absent or reduced compared with 11% (8/72) when wolves were present and uncontrolled. The decline in the number of calves between August and October when wolves were absent or reduced coincided with the movement of new wolves into the area in late summer or early fall, as indicated by radio-collared adult caribou being killed by wolves (Fig. 4).

Evaluation of the effect of wolf control alone (not including the year when wolves were naturally absent) indicated that calf survival to October (Table 1) was greater ($G = 4$, 1 df, $p < 0.05$) in areas where wolves were reduced than in areas where wolves were present and uncontrolled. However, calf recruitment in March (Table 2) was not increased ($G = 2$, 1 df, $p > 0.05$), possibly because wolves usually recolonized the removal areas by early fall.

The percentage of radio-collared cows with calves in June was not related to the presence of wolves ($G = 0.6$, 1 df, $p > 0.05$). When wolves were absent or reduced, 57% (15/26) of radio-collared cows had surviving calves in June compared with 46% (21/46) when wolves were present and uncontrolled.

During the 5-year study period at Quesnel Lake, only 16% (10/63) of radio-collared cows had surviving calves in October (presumably 8.0 female calves per 100 adult females), and there were 9.8 calves per 100 adults (58/589) in March. Therefore, calf recruitment was inadequate to balance the high adult mortality rate.

Calf survival was greater in Wells Gray Park than at Quesnel Lake in October ($G = 5.8$, 1 df, $p < 0.05$) and March ($G =$

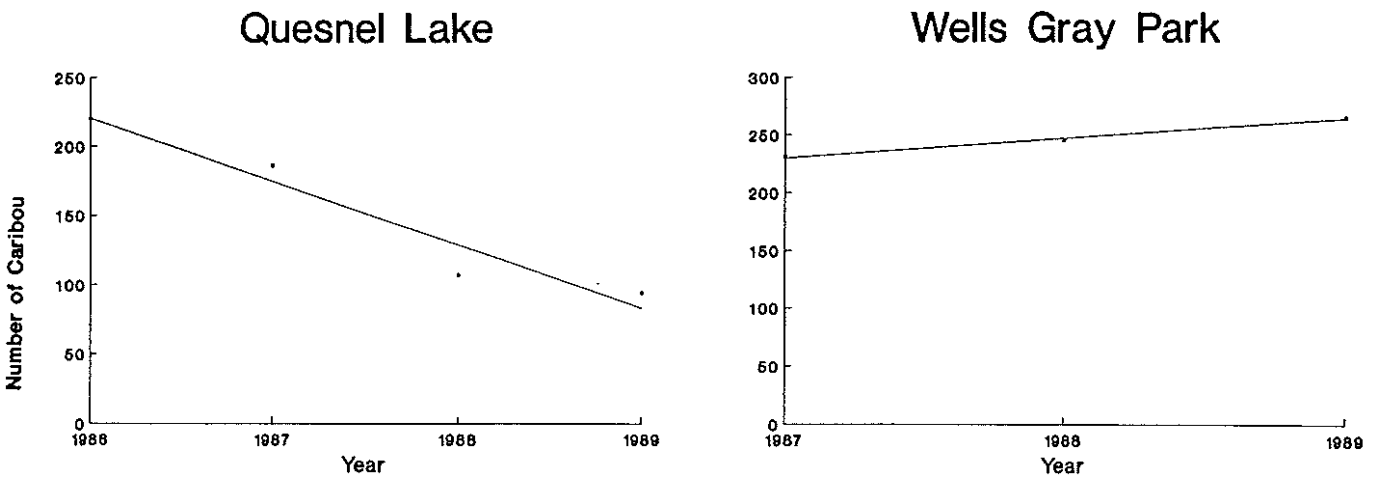

FIG. 5. Estimated caribou population, based on March census counts corrected for sightability.

16, 1 df, $p < 0.05$). In Wells Gray Park, about 36% (23/64) of radio-collared cows and 29% (54/185) of all cows seen had surviving calves in October (Figs. 3, 4). In March there were 17.7 calves per 100 adults in the population (Table 3). Therefore, calf recruitment was greater than the adult mortality rate, so the population was probably slowly increasing.

Although overall calf survival for the park was high, calves of caribou that spent the summer in the southern sections of the park had a lower survival rate ($G = 5.6$, 1 df, $p < 0.05$) than calves of caribou that spent the summer in the interior and northern sections of the park. In October, only 7% (1/14) of radio-collared cows that spent the summer in the southern section of the park had surviving calves compared with 44% (22/50) of the radio-collared cows that spent the summer in the northern or interior sections of the park.

Caribou population size and trends

An average of 83% (79/95) of the radio-collared caribou were seen during March censuses in clear weather. Weather conditions obscured visibility during the 1988 census in Wells Gray Park, limiting access to some areas, and only 66% (14/21) of the radio-collared caribou were seen. All of the total counts were corrected using the 83% sightability factor, except for the 1988 Wells Gray census for which a correction factor of 66% was used. The corrected population estimate for the Quesnel Lake area declined from 220 caribou in 1986 to 94 in 1989 (Fig. 5). This decline represents an exponential growth rate of $r = -0.28$, or a finite rate of increase of 0.754. The density in the 2300-km^2 area declined from about 0.1 to 0.04 caribou/km^2 between 1986 and 1989. Because only about 50% of the study area consisted of preferred winter habitat types (Seip 1992), the density on the winter range was about double the above values, i.e., it declined from 0.2 to 0.08 caribou/km^2.

The corrected population estimate for Wells Gray Park increased from 231 to 265 between 1987 and 1989 ($r = 0.05$, finite rate = 1.04). The density in the 5200-km^2 park was about 0.05 caribou/km^2. The density on preferred winter habitat types was 3–5 times greater, i.e., 0.15–0.25 caribou/km^2.

Wolf densities

Monitoring of radio-collared wolves was not adequate to provide precise estimates of wolf densities. However, the area of the annual home ranges of radio-collared wolves in packs was about 600 km^2. The observed winter pack size was 6–8 wolves. Assuming that the home ranges represented exclusive territories, the estimated population density was about 1 wolf/100 km^2 in areas of highland topography.

Seasonal habitat used by caribou, wolves, and moose

Winter

From November to April, caribou in both the Quesnel Lake area and Wells Gray Park were located primarily at mid and high elevations in subalpine forests or parkland habitats (Figs. 6, 7). In early winter, some caribou used low-elevation cedar–hemlock forests, but as winter progressed they moved to higher elevations. Moose were located almost exclusively at low elevations in riparian shrublands, burns, and adjacent forest types during winter (Figs. 6, 7).

The radio-collared wolves in the Quesnel Lake area remained primarily on low-elevation moose winter ranges during winter (Seip 1992). The two radio-collared wolves in Wells Gray Park belonged to two different packs that ranged over most of the low-elevation areas in the southern section of the park during winter (Seip 1990). There was no sign of other wolves living in the rugged interior and northern sections of the park during winter. Wolf habitat used in winter included primarily low-elevation shrublands and adjacent forests, similar to habitats used by moose (Figs. 6, 7). Consequently, there was almost no overlap between areas, elevations, or habitats used by caribou and those used by wolves and moose in winter. Analysis of wolf scats from the Quesnel Lake area indicated that during winter, moose were the primary prey whereas caribou composed a very small component of the diet (Fig. 8).

Summer

Caribou in the Quesnel Lake area did not exhibit any distinct seasonal migrations and used the same high-elevation, subalpine forest habitats in summer and in winter (Figs. 6, 7). Most moose at Quesnel Lake migrated 10–20 km from valley-bottom winter ranges to summer ranges in mid- and upper-elevation forest habitats in areas where caribou were also located (Figs. 6, 7). Wolves at Quesnel Lake were found primarily at lower elevations in summer, but they also used mid- and upper-elevation forests in areas where both caribou and moose were located. Therefore, the areas and habitats used by Quesnel Lake caribou in summer were also used by

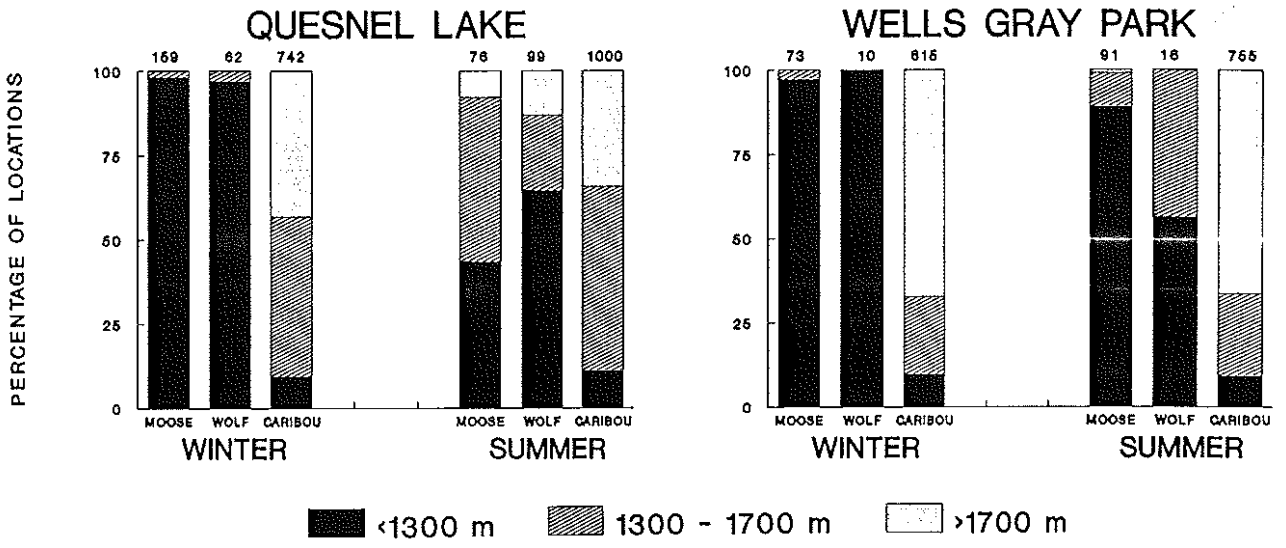

FIG. 6. Percentages of radio-collared caribou, moose, and wolf locations at different elevations. The number above each bar is the number of locations.

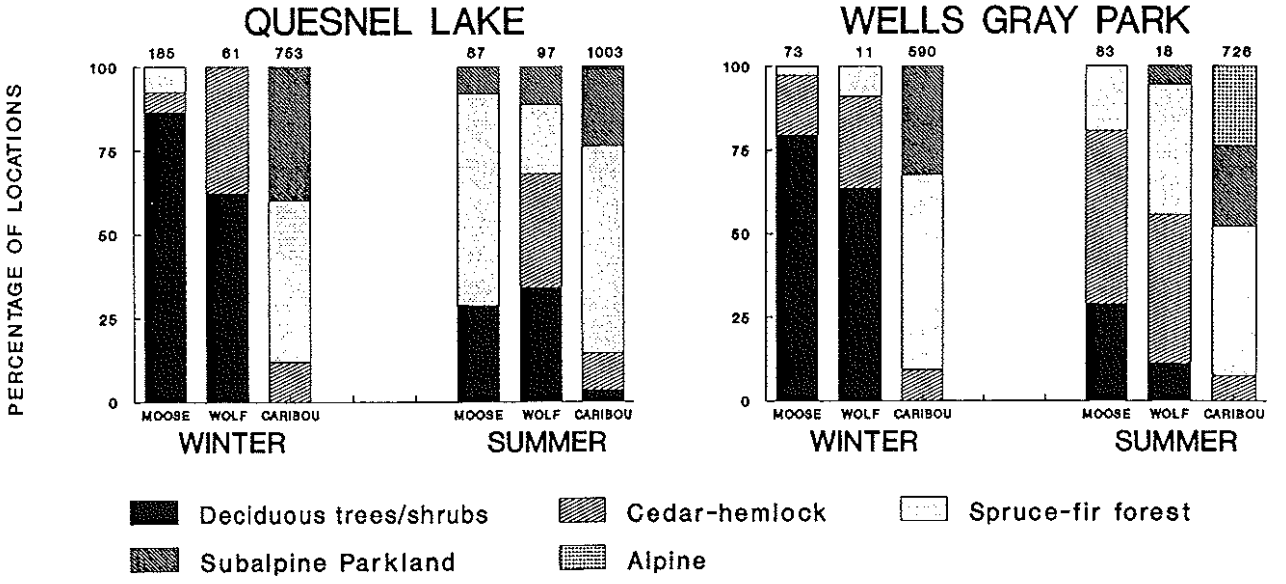

FIG. 7. Percentages of radio-collared caribou, moose, and wolf locations in different habitat types. The number above each bar is the number of locations.

moose and wolves. Moose were the primary prey of wolves during the summer, but caribou were also eaten (Fig. 8).

Most caribou in Wells Gray Park migrated 20–60 km from winter ranges in the southern and western highland sections of the park to summer ranges in rugged mountains in the central and northern sections of the park (Seip 1990). However, some caribou remained in southern highland areas in summer. This migration resulted in Wells Gray caribou using higher elevations and more alpine habitat in summer than Quesnel Lake caribou did (Figs. 6, 7). Most moose in Wells Gray migrated 10–20 km to summer ranges in low and mid-elevation forest–wetland complexes. There appeared to be little use by moose of the rugged mountainous areas that the caribou used in summer (Fig. 9). Therefore, there was little overlap in ranges, elevations, or habitat types used by moose and caribou in Wells Gray Park in summer (Figs. 6, 7, 9). Although data for radio-collared wolves in Wells Gray were sparse, it appeared that the two wolf packs living in the park remained primarily in the southern part of the park on summer ranges used by moose (Fig. 9). Wolves were not found in the mountainous areas and upper-elevation habitats where most of the summer caribou locations occurred (Figs. 6, 7, 9).

Discussion

The results support the hypotheses. Wolf predation appeared to be the primary cause of declining caribou numbers in the Quesnel Lake area. Wolves were sustained primarily by moose throughout the year, but became a major predator on caribou during summer, when caribou, wolves, and moose occupied similar areas and habitats. The low level of wolf predation and the increasing caribou population in Wells Gray Park corresponded to the minimal contact that the caribou had with moose and wolves throughout the year. The migration of most Wells Gray Park caribou to rugged, mountainous summer ranges spatially separated them from moose and wolves.

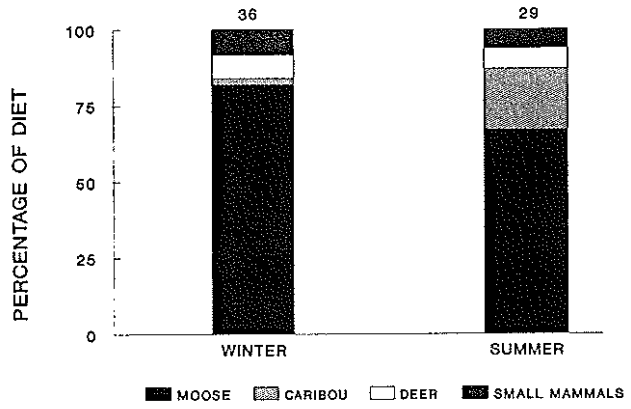

FIG. 8. Seasonal food habitats of wolves, based on scat analyses. The number above each bar is the number of scats.

The adult mortality rate at Quesnel Lake was very high and wolf predation was the major cause of death. In contrast, adult caribou in Wells Gray Park had a low mortality rate and wolf predation was minimal. Bear predation was a significant cause of adult mortality in both study areas and occurred primarily in spring and early summer, when both bears and caribou used slides and riparian areas for feeding.

Food availability did not appear to be an important limiting factor. No caribou died of malnutrition during the winter months. The two cases of death due to malnutrition occurred in summer when high-quality food was abundant, suggesting that those individuals may have been diseased or old and unable to feed. The high pregnancy rate was also indicative of a population without severe nutritional limitations (Thomas 1982; Skogland 1985). Caribou whose calf survived the summer were as likely to produce a viable calf the following year as those whose calf died, indicating that the nutritional costs of lactation were not limiting subsequent calf production.

Calculations of arboreal lichen availability indicated that available food resources in winter greatly exceeded the requirements of the caribou (Seip 1992). Also, the density of caribou on winter ranges ($0.08-0.2/km^2$) was far below the 4–8 woodland caribou/km^2 that Bergerud (1983) reported for a population regulated by arboreal lichen availability on the Slate Islands in Ontario.

Although most adult female caribou were pregnant, about half of the calves apparently died during the calving period. Wolf predation did not appear to be a major cause of early calf mortality, because mortality levels were similar in the two study areas, despite the differences between areas in the level of wolf predation on adults, and the apparent lack of contact between wolves and caribou in Wells Gray Park. Also, the proportion of calves in June at Quesnel Lake was not related to wolf abundance. Similar low proportions of caribou calves in June have been reported in southern British Columbia, where wolves were rare or absent (Scott and Servheen 1985). The major causes of mortality during the calving period are not known, but it is likely that the newborn calves are vulnerable to a wide range of mortality factors including other predators, accidents, birthing problems, and weakness at birth (Page 1985; Adams et al. 1988).

After the calving period, calf survival at Quesnel Lake was quite variable and appeared to depend primarily on the abundance of wolves. When wolves were absent or reduced, almost all calves that were alive in June survived the summer months. When wolves were present and uncontrolled, almost no calves

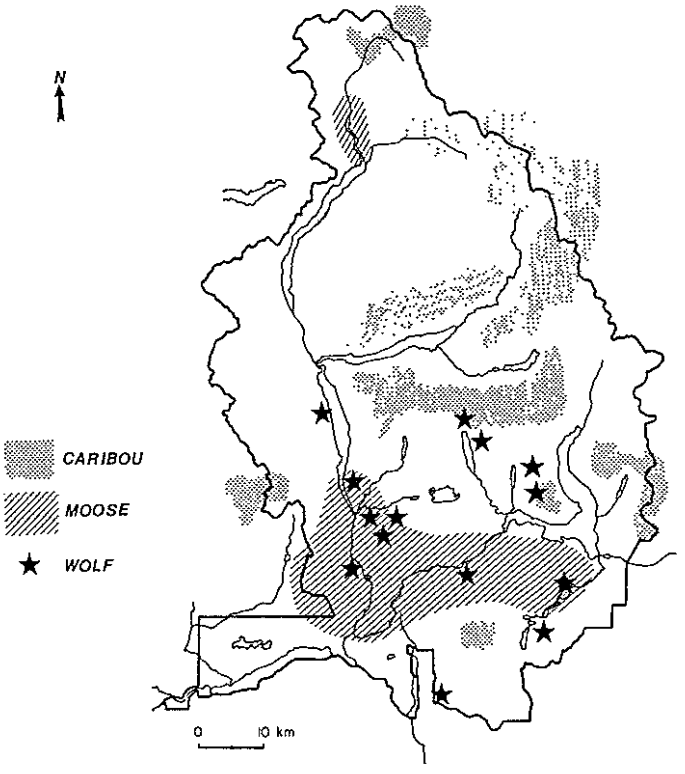

FIG. 9. Summer ranges of radio-collared caribou, moose, and wolves in Wells Gray Provincial Park.

survived the summer. Wolf control significantly increased calf survival during the summer months, but wolves recolonized the area by fall, and calf survival decreased soon after wolves returned. The major importance of wolf predation as a mortality factor for caribou calves, and increased calf survival resulting from wolf control, have been demonstrated in numerous other studies (Gasaway et al. 1983; Bergerud and Elliot 1986; Adams et al. 1988; Farnell and McDonald 1988).

In Wells Gray Park, a large proportion of the calves that were alive in June survived through the summer and were present in the March population. Calf survival rates in Wells Gray Park were similar to those at Quesnel Lake when wolves were reduced or absent. The high calf survival in Wells Gray Park indicates that wolf predation was low on calves as well as on adults.

High wolf predation on caribou at Quesnel Lake resulted in a declining population, whereas low wolf predation in Wells Gray Park resulted in a slowly increasing population. Wolf predation at Quesnel Lake remained high despite a decline of over 50% in the caribou population, indicating that mortality due to wolf predation was not density-dependent within that range of population densities. Because the wolf population was sustained primarily by moose, wolf numbers could be maintained despite declining caribou numbers. Therefore, wolves could potentially extirpate the caribou population.

Differences in wolf predation between the two areas appeared to be related to the amount of contact that caribou had with moose and wolves. Throughout the year, wolves and moose used similar areas and habitats. In both study areas, caribou had little contact with wolves and moose during winter. Caribou were located primarily at high elevations in subalpine forests, whereas moose and wolves were found primarily in valley-bottom forests and shrublands. Wolves fed almost exclusively

on moose during winter. Wolf predation on caribou was uncommon and limited to those caribou that used low-elevation forests during November and December.

In May, most moose at Quesnel Lake migrated to summer ranges in high-elevation spruce–fir forests and used areas and habitats where caribou were also located. Wolves also regularly used high-elevation habitat types in areas where caribou and moose were located, although radiotelemetry locations indicated that den sites were in low-elevation forests. Although moose continued to be the primary prey of wolves in summer, caribou were also killed when caribou, wolves, and moose occupied similar areas, elevations, and habitats.

In Wells Gray Park, moose migrated to summer ranges but generally used lower elevation habitats than moose at Quesnel Lake. Wolves were located primarily in areas and habitats used by moose. Most caribou in Wells Gray Park migrated 20–60 km from winter ranges in highland topography to summer ranges in rugged mountains (Seip 1990). Caribou in Wells Gray Park used higher elevations and more alpine habitat in summer than did caribou at Quesnel Lake. The average elevation at which caribou in Wells Gray Park and Quesnel Lake were killed by predators (1291 m) was lower than the average elevation used by caribou in summer (Fig. 6), indicating that caribou at low elevations were more vulnerable to predation. The migration of Wells Gray caribou to rugged mountains in summer resulted in their using areas, elevations, and habitats different from those used by moose and wolves. Consequently, caribou were largely separated from moose and wolves in summer as well as winter. This spatial and habitat separation apparently resulted in low wolf predation on adults and calves. Bergerud et al. (1983) and Bergerud and Page (1987) discussed the role of dispersion in mountains as an antipredator tactic of caribou in other areas.

Caribou that spent the summer in the southern parts of Wells Gray Park, closer to areas used by moose and wolves, had lower calf survival than those caribou that spent the summer in the rugged interior and northern sections of the park. In the past, it appears that many more caribou spent the summer in highland areas in the south of Wells Gray Park. Ritcey and Jury (1984)[1] reported that summer census results between 1970 and 1984 indicated a major reduction (from 141 to 3 caribou seen) in caribou numbers in the southern highland areas of the park, whereas declines in the central and northern areas of the park were much less severe (from 116 to 41 caribou seen). These results support the idea that caribou migrating to rugged mountains in summer experience less wolf predation than caribou that remain in areas used by moose and wolves. Many of the caribou populations that have disappeared since the 1920s may have been nonmigratory populations that spent the summer in highland areas, whereas caribou that had a migratory tradition were less vulnerable to predation and survived.

Why are wolves eliminating caribou from areas where wolves and caribou previously coexisted? The most likely reason appears to be that the predator–prey system has been modified by the recent addition of moose as an alternative prey (Bergerud and Elliot 1986). Hatter (1950) reported that moose were absent from central British Columbia until the early 1900s. Spalding (1990) disputes the idea that moose were totally absent, but he does conclude that populations were sparse and scattered prior to the 1900s, possibly due to severe winters throughout the 1800s. In either case, there was either a colonization or a major population increase of moose in the Wells Gray Park area around 1925–1930. The first reports of major declines in caribou numbers coincided with the arrival or increase of moose in the area (Edwards 1956).

Before the increase in moose abundance occurred, wolf populations in areas of caribou habitat in southeastern British Columbia were probably very low due to a lack of available prey in winter. Use of high elevations by caribou and mountain goats in winter makes them largely invulnerable to wolves. Mule deer migrate out of these high-snowfall areas in winter. Colonization by or an increase in number of moose since the 1920s has made prey available at low elevations that sustains wolves during the winter months. Increased wolf populations appear to be the primary cause of subsequent declines in caribou populations. That process was probably delayed by provincial wolf-control programs in the 1950s but resumed when wolf control was terminated in the 1960s.

In summary, it appeared that wolf predation was the major cause of a decline in caribou numbers in the Quesnel Lake area. The high level of wolf predation was probably related to colonization by or increase in moose populations in about 1925–1930. The presence of moose sustained increased wolf populations, which resulted in increased wolf predation on caribou. Caribou that lived in highland areas during summer were in close contact with moose and wolves and experienced high wolf predation. Caribou that migrated to rugged mountains became spatially separated from moose and wolves and had higher survival rates. If present trends continue, the remaining caribou populations that spend the summer in highland areas will be eliminated, and only those caribou that migrate to rugged, mountainous habitat for the summer will survive. If this consequence is considered unacceptable, reducing wolf and (or) moose populations in highland areas may allow caribou to survive.

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