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Population ecology of two woodland caribou herds in the southern Yukon

Richard Farnell[1], Norman Barichello[2], Katherina Egli[1] & Gerry Kuzyk[1]

[1]Department of Renewable Resources, Box 2703, Whitehorse, Yukon, Canada, Y1A 2C6.
[2]Nature Services North, Site 20, Comp. 76, RR1, Whitehorse, Yukon, Y1A 4Z6.

Abstract: Since the mid 1980's, the Aishihik herd of woodland caribou (*Rangifer tarandus caribou*) declined from approximately 1500 to 583 animals. During the same period a nearby herd, the Wolf Lake Herd increased from approximately 664 to 1249 animals. This paper compares aspects of the ecology of these two herds to determine how these relationships conform to a general model of caribou population ecology described by Seip (1992). Comparisons include caribou demographic characteristics and distribution patterns, predator densities, abundance of alternate prey, human hunting and snow depth on caribou winter range. Ecological differences between herds were apparent in the ratio of prime bulls to cows, the abundance of moose (*Alces alces*), the occurrence of coyotes (*Canis latrans*), late winter snow conditions, and access to hunting. We hypothesize that the Wolf Lake herd was able to grow because wolves (*Canis lupus*) preyed mainly on the relatively abundant moose population. A highly clumped winter caribou distribution may have further reduced the impact of wolf predation on the Wolf Lake herd. In contrast, the decline of the Aishihik herd was accompanied by a relative scarcity of moose, few prime aged caribou bulls probably due to a more liberal trophy harvest, and wider late-winter dispersion that offered wolves greater access to caribou. The decline may have been exaggerated by the peak in the snowshoe hare (*Lepus americanus*) cycle which may have temporarily improved wolf pup survival. We suspect that moose are normally the primary prey of wolves in the Yukon and that a decline in moose eventually results in their being too scarce to offer an economical prey choice, prompting a prey switch to caribou. Results of our analyses conform incompletely to Seip's (1992) model for woodland caribou population ecology, particularly because the Wolf Lake herd prospered where moose were relatively abundant.

Key words: Wolves, harvest, predator-prey relationships, antipredator strategies, population dynamics

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Introduction

Bergerud (1992) and Seip (1992) presented a general model to explain caribou population ecology. They proposed that, (1) food competition regulates caribou at high densities, through reduced calf production and winter starvation, when predation or human harvest are low; (2) predation can be a major limiting factor of caribou when predators are abundant, and can regulate caribou density if, (a) antipredator strategies are ineffective, or (b) there are densities of alternate prey that can sustain high predator numbers; (3) habitat changes can impair caribou anti-predator strategies and consequently lead to reduced caribou densities; and, (4) human harvest can reduce caribou populations below natural levels.

In the last 10 years, caribou herds in the southern Yukon have been at relatively low densities, in habitats that have remained largely stable. Two herds in different bio-geol-climatic zones (Oswald & Senyk, 1977) reveal different demographic patterns. One, the Wolf Lake herd, located in the south-central Yukon in a typical boreal environment, increased from 1987 to 1993 despite limited management intervention. The other, the Aishihik caribou herd, in the Ruby Range of the Coastal Mountains in the southwest Yukon, declined from 1981 to 1992, and is currently the subject of an intensive rehabilitation program involving aerial reduction of wolves. In this paper we examine the population ecology of these herds and discuss how they conform to the models presented by Bergerud (1992) and Seip (1992).

Data was collected independently for management purposes, and not part of a design to compare the dynamics of these two herds. Therefore the data does not allow for annual comparisons. Data from the Wolf Lake herd are from years 1987, and 1993, while data from the Aishihik herd are from years 1981, 1991, and 1992.

Study area

The Aishihik caribou herd occupies an area of about 7400 km^2 in the southwest Yukon northwest of Whitehorse and north of Haines Junction (Fig. 1). Most of the range lies within the Ruby Range Ecological Region (Oswald & Senyk, 1977) in the rain shadow of the St. Elias Mountains where conditions are arid and windy. Late winter snow accumulation averaged 47.7 cm and annual average winds exceeded 9.2 km/hr, from 1976-1993 at a local snow station at 1160 m above sea level (asl) (Wahl. *et al.*, 1987). Approximately 20% of the Aishihik caribou range is considered alpine. Forests of white spruce (*Picea glauca*) and poplar (*Populus balsamea*) occur in the valleys and on the lower slopes. The area supports some of the highest densities of Dall sheep (*Ovis dalli stonei*) in the Yukon (Barichello *et al.*, 1989), and prior to 1981, relatively high densities of moose (*anecdotal information*). Wolverine (Gulo gulo) are relatively common (Bana, 1986) and coyotes were periodically common, synchronized to the snowshoe hare cycle (Theberge & Wedeles, 1989. Bears (*Ursus* spp.), primarily grizzlies (*U. arctos*) are at densities that are believed to be uniform across much of the southern Yukon (Yukon Government (YTG), unpublished data).

A series of wildfires in the 1930's burned much of the forested habitats in valley bottoms, but in recent decades habitats have changed little. Human development in the area, has included a small network of mining roads on the western boundary of the herd's range, and an all season road into the eastern portion of the range to serve hydro electric development on Aishihik Lake. Currently, there is road access into the eastern portion of the range, and boat access along the western boundary of the range.

The Wolf Lake herd occupies an area of about 9600 km^2 in the upper watersheds of the Wolf, Liard, and Nisutlin rivers (Fig. 1), largely within the Pelly Mountain Ecological Region (Oswald & Senyk, 1977). The range is centred around Wolf Lake on the Nisutlin Plateau, which is in a large boreal upland contained by the Cassiar and Pelly mountains. Here, the terrain is broad and rolling, with a forest cover of white spruce interspersed with extensive subalpine meadows. Treeline is at 1350 m and 27% of the range of the caribou herd is classified as alpine.

Considerably more snow falls on the range of the Wolf Lake caribou herd than on the Aishihik range; late winter accumulations averaged 87.5 cm at a snow station at 1110 m asl within the Wolf Lake herd range, from 1987-1992. Winds are also less common in the range of the Wolf Lake herd, averaging 7.9 km/hr at a nearby weather station (Wahl *et al.,* 1987). The distribution of < 300 stone sheep (*Ovis dalli stonei*) (anecdotal information) is restricted to the very eastern edge of the caribou range (Barichello & Carey, 1988). Moose habitat is moderate to good. Bears and wolverine are at average Yukon densities (YTG, unpublished data). Coyotes are rare in the area (anecdotal information; unpublished trapping records).

Habitat has changed little in recent decades with infrequent and small wildfires. Considerable mining exploration and development occurred in the 1970's during which time a number of winter roads penetrated the range. Currently, there is little human activity within the range and virtually no road access.

There are obvious differences in the two woodland caribou ranges. The Aishihik range is more mountainous with a lower treeline, more arid and windy, and with minimal snow limitations to caribou (Russell & Martell, 1984). On the Wolf Lake range there are fewer wind blown slopes and snow depths periodically exceed the depths thought to impede caribou travel (Russell & Martell, 1984). The average annual caribou ranges are similar in size, but there is greater road access into the Aishihik area.

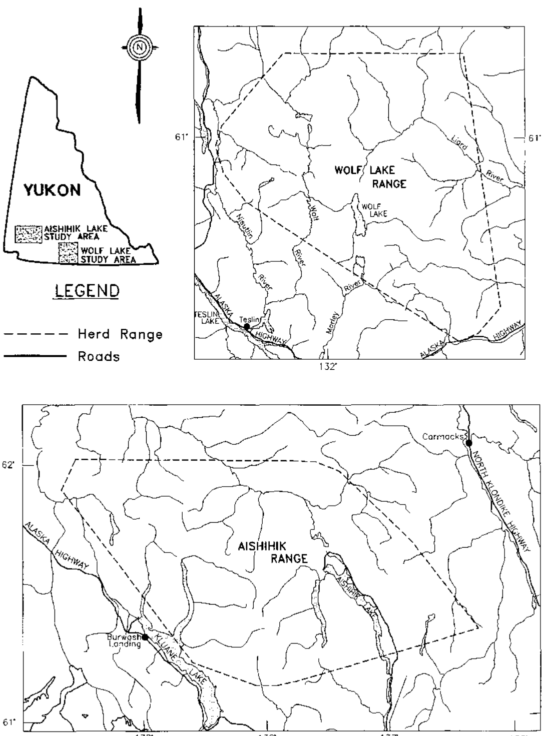

Fig. 1. Ranges of the Wolf Lake and Aishihik caribou herds.

Methods

We define herd as a population of caribou that uses a common winter range that is geographically distinct from the home ranges of other populations. The distribution of both herds was determined on the basis of radio relocations, helicopter sample counts during the post-calving and rut periods, and intensive fixed-wing and helicopter flights during the late winter.

A number of caribou population charactenstics were determined in some years since 1981 including populabon size, herd composition, and mortality rates.

Population estimates of the Aishihik herd were determined from helicopter searches in fall, 1981, and again in late winter, 1990. These population estimates were absolute counts with no adjustments for sightabililty biases, or survey intensity. For the Wolf Lake herd, a population estimate was determined in March 1987 and in March 1993, using Gasaway *et al.*'s (1987) Stratified Random Quadrat Design, modified for clumped caribou distributions (Farnell & Gauthier, 1988).

Density of caribou was defined as the herd size divided by the average size of its annual range (Bergerud, 1992). A late winter density was also determined from the total estimated population divided by the known area of distribution. Population trend, defined as the exponential rate of increase, was calculated according to the following equation (Bergerud, 1980):

Rate of increase $(r) = (\ln N_{year2} - \ln N_{year1}/(year2 - year1)$, *where N=population size.*

Population composition of sex and broad age groups was determined from sample counts during helicopter searches in mid-October (rut), and March (late-winter). Sex was determined on the basis of antler structure and the presence of a penis sheath or vulval patch. Broad age classes of males (immature and mature bulls) were recorded based on antler development. Calves were distinguished based on body size and antler development (Farnell & Russell, 1984).

Progesterone levels in blood samples were determined from a sample of adult cows in late winter, 50 and 16 cows were tested from the Aishihik herd in 1991 and 1992, and 20 were tested from the Wolf Lake herd in 1993. Calficow ratios from sample counts during helicopter searches in October and March provided a crude index of survival of calves. Adult mortality rate was inferred from calculations of the percent of radio-collared caribou found dead.

We also derived an index of cow dispersion, calculated as the average minimum distance to another radio-collared individual (either sex).

Our evaluation of hunting mortality is incomplete. Also, causes of natural mortality are unknown.

Snow data were collected by Environment Canada and Water Resources, from various stations in the Yukon. We report snow accumulation from one station within each herd range, measured at similar elevations in March when snow is typically deepest (Farnell & McDonald, 1987; Wahl *et al.*, 1987). Data were not available to compare summer range or caribou body condition.

The current distribution and abundance of other resident ungulates (moose, thinhorn sheep and mountain goats (*Oreamnos americanus*)), is roughly known for both regions. In 1991 in a 3662 km^2 area of the Aishihik region moose were systematically censused using the Stratified Random Quadrat Design (Gasaway *et al.*, 1987; Larsen & Ward, 1991). Moose population trends were determined in 1992 based on complete fixed-wing aircraft coverage of a considerably smaller area within Aishihik (YTG, unpublished data). Sheep have been counted over the entire Aishihik caribou range in 1975 and again in 1993, based on complete helicopter searches of all known sheep range in July YTG, unpublished data). These surveys are presumed to represent total population counts because of the conspicuousness of all sheep in the summer and the intensity of the search (Barichello *et al.*, 1987).

Moose within a 4210 km^2 area of the Wolf Lake caribou range were tallied in 1986 (Jingfors & Markel, 1987) using the Stratified Random Quadrat Design (Gasaway *et al.*, 1987), and population trends were determined in 1992 for a 249 km^2 portion of the census area (Smits *et al.*, 1993). In addition, all moose observed during the caribou census of 1987 and 1993 were recorded, and their density calculated in relation to the designated winter range. Moose density in the Wolf Lake area for 1993 was estimated by applying the growth rate observed in the caribou census area from March 1987 to March 1993, to the November 1986 density of moose derived from the systematic search of moose habitat. Most of the sheep range in the range of the Wolf Lake caribou herd was surveyed for sheep in 1991 through intensive helicopter seaches as described above. It was assumed, based on age composition, that this population was growing; this assumption was supported by subjective assessment by trappers in the region. We therefore applied an arbitrary, but conservative annual growth rate of 10% to the 1991 count to yield a 1993 estimate. These counts are believed accurate, however their precision remains untested.

Wolf numbers were derived from intensive aerial surveys. designed to determine wolf abundance (Hayes *et al.*, 1991; Hayes & Baer, 1987), had corrected for lone wolves by adding a factor of 10% (Stephenson, 1978). Grizzly bear population densities were crudely estimated based on historic kill and anecdotal information (B. Smith, pers. comm.).

To assess the relative importance of wolves in these ecological communities we calculated an ungulate biomass/wolf index, according to Fuller (1989) and Keith (1983). This index (biomass of ungulate prey/density of wolves) was based on relative biomass ratios where 1 moose had an equivalent usable biomass to 6 sheep and 3 caribou (Fuller, 1989).

We derived an additional index of caribou/wolf to represent the exposure of the two herds to wolves on the late winter range. We assumed that wolf densities were mediated principally through territoriality (Mech, 1977; Keith, 1983; Fuller, 1989), and therefore that densities of wolves were relatively uniform despite seasonal changes in caribou distribution.

To identify if a general threshold existed where a shift in wolf prey occurred, we derived indices of moose biomass to caribou biomass (kg of moose/kg of caribou), and moose and sheep biomass to caribou biomass, using the relative biomass ratios described above (Fuller, 1989).

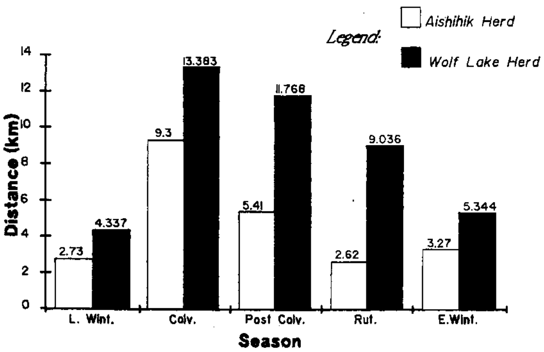

Fig. 2. Average distances between radio-collared caribou against season, for the Aishihik and Wolf Lake caribou herds.

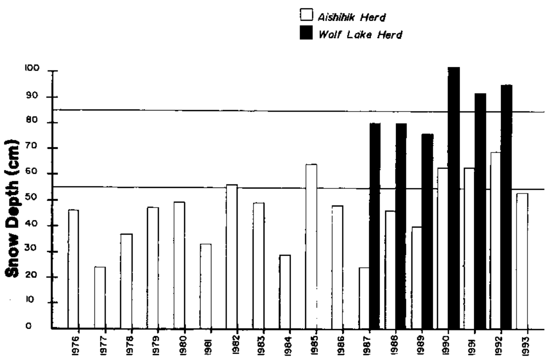

Fig. 3. Snow depths on 1 March on the Aishihik and Wolf Lake caribou winter ranges. The horizontal reference lines at snow depths of 55 and 85 cm represent the depths at which feeding and mobility, respectively, are adversely affected (Russell & Martell, 1984).

Results

Aishihik herd

Caribou in the Aishihik herd were initially radio-collared in 1990; 17 and 16 radio collars were active in 1991 and 1992, yielding approximately 85 fixes/year.

The Aishihik caribou herd declined from at least 1,500 animals in 1981 to 785 animals in 1991, and 583 individuals in 1992. This decline coincided with a shift in the bull:cow ratio toward fewer bulls, and a decline in the October calf:cow ratio (Table 1, lines 6 and 11). In 1991 and 1992 the estimated proportion of mature bulls (large antlers) to cows was < 0.1. Pregnancy rates were high (>95%) and the estimated sex ratio of calves in the fall was 68 males/100 females in 1992. In addition to what appears to be high calf mortality from birth to October, the mortality rate of radio-collared adults (mostly cows) was as high as 20% (1-5 of 20 collared caribou died) in 1991, and 48% (13 of 27 collared caribou died) in 1992.

In both 1991 and 1992, cows were more highly dispersed at calving, than during other seasons (Fig. 2). Although caribou in late winter had a clumped distribution in 1991, at 523 animals/1000 km^2 (Table 1, line 4), the herd was dispersed over an estimated 1500 km^2 (Fig. 1).

Late winter snow accumulation was higher than average after 1989 (Fig. 3), but still below 69 cm, and therefore considered insufficient to impair foraging and travel (Russell & Martell, 1984).

Human hunting of the Aishihik herd is poorly documented. The licenced harvest was believed to represent about 4% of the herd from 1979 to 1983, and the 1990 harvest was calculated at 4% of the 1991 population estimate (Table 1, lines 13 & 14)(Carey *et al.*, in prep). The reported native harvest was low (Quock, 1992). Poaching and wounding losses were not estimated. The extent to which hunting contributed to the initial decline of caribou, from 1981 to 1991, is unknown.

Grizzly bears within the range of the Aishihik caribou herd were at densities typical for the southern Yukon, of 16/1000 km^2 (Larsen & Markel, 1989) (Table 1, line 16). We have no evidence of grizzly bear predation on caribou.

In March 1991, wolves in the Aishihik area were at densities similar to that of other regions of the Yukon, at 11.5/1000 km^2, but by February 1992, had declined to 8.1/1000 km^2. This decline coincided with a decline in average pack size from 6.0 to 4.1 (YTG, unpubl. data). This adjustment reflects the very low ungulate biomass/wolf density ratio of 73 in 1991 and a caribou/wolf ratio of only 7.8. In late winter 1990-91, despite the concentration of caribou, there were only 45 caribou/wolf on the late winter range.

Alternate ungulate prey were relatively scarce in the Aishihik range in 1991 and 1992. Moose were at a low density, and sheep, although relatively abundant, provided comparably low available biomass. The biomass ratio of moose and sheep to caribou was only 3.7 and 3.2 in the Aishihik area in 1991 and 1992, while moose biomass alone was only 2.7 and 2.3 times more than caribou (Table 1, line 22 & 23).

Wolf Lake herd

In the Wolf Lake herd 14 and 29 active collars were located 67 and 151 times in 1987 and 1993, respectively.

The Wolf Lake caribou herd was at a relatively low density in 1987; 664 ±133 caribou were estimated in late winter, yielding a density of only 69/1000 km^2 (Table 1, line 3). This low density coincided with few (29) bulls/100 cows (Table 1, line 6). However, the calf:cow ratio in March 1987 was 28/100 cows (Table 1, line 11), mature bulls were common (53% of all bulls had large antlers), and adult mortality was estimated to be less than 10% (Table 1, line 12). From 1987 to 1993 the Wolf Lake herd grew to 1249 ±150 caribou (average annual rate of 10.5%). Bulls were more strongly represented (48 bulls/100 cows; Table 1, line 6) and there was a higher proportion of younger bulls (63% of bulls were considercd young bulls) in the Wolf Lake herd in 1993, as compared to 1987. This apparent demographic shift toward younger bulls was consistent with population growth which was likely achieved through high levels of recruitment and low adult mortality. Although the March 1993 measure of recruitment was relatively low (13 calves/100 cows), this was consistent with a general pattern in the Yukon that year toward low calf/cow ratios, presumably induced by a record late spring (Department of Indian and Northern Development, weather bulletin). In late winter 1993, the pregnancy rate was 95% (Table 1, line 9), and 40% of all calves (10 months old) were males.

Radio-collared Wolf Lake cows were highly dispersed at calving in 1992 and 1993, with a nea-

Table 1. Population ecology data for the Aishihik and Wolf Lake caribou herds, Yukon Territory.

	Aishihik herd			Wolf Lake herd	
Month	Oct	March	Oct	March	March
Year	1981	1991	1992	1987	1993
1.Mean annual range size (km^2)	-	7345	7345	9663	9663
2.Estimated population size (n)	1500	785	583	664	1249
3.Caribou/1000 km^2	204	90	80	69	129
4.Caribou/1000 km^2 (March)	-	523	-	658	891
5.Population change (r)	-	-0.06	-0.30	-	0.11
6.Bulls/100 cows	81	19	35	29	48
7.Mature bulls/100 bulls	-	29	29	53	37
8.Mature bulls/100 cows	-	6	10	15	18
9.Pregnancy (%)	-	96	97	-	95
10.Male:female calf (Oct)	-	-	0.7	-	0.6
11.Calves/100 cows (Oct)	-	20	7	28	13
12. Adult death rate (%)	-	7-20	48	10	4
13. Harvest (non-native)	60	31	0	5	19
14. Harvest (native)	-	2	0	-	2
15. Wolves/1000 km^2	-	11	8	10	9
16. Grizzly/1000 km^2	-	16	16	15	15
17. Moose/1000 km^2	107	82	60	130	321
18. Sheep/1000 km^2	165	165	149	21	26
19. Ungulate biomass/wolf (kg)	-	73	83	94	251
20. Alt. prey/caribou (kg)	2.0	3.7	3.2	5.8	7.6
21. Moose/caribou (kg)	1.6	2.7	2.3	5.7	7.5
22. No. caribou/wolf (Mar)	-	45	-	66	101

rest radio-collared neighbour 13.4 km away, on average (Fig. 2).

In contrast caribou were clumped in late winter 1987 and 1993, with densities of 658 and 891 caribou/1000 km^2, respectively (Table 1, line 4). Snow accumulation in late winter, 1987 to 1992, exceeded the snow threshold believed to hinder movements of solitary caribou (Fig. 3), and may have induced a clumped late winter distribution. It is noteworthy that growth in the Wolf Lake herd was apparent from 1987 to 1993, despite the fact that snow reached depths thought to hinder caribou foraging and travel (Russell & Martell, 1984).

Human hunting on Wolf Lake caribou was slight with < 2% annual reported harvest in 1987 and 1993. Low harvest-levels undoubtedly reflect the relatively poor access into the range of the herd.

Grizzly bears are believed to have been at a relatively low density (15/1000 km^2), despite limited harvest (YTG, unpubl. data). Wolves were counted in the Wolf Lake area in 1986 and again in late winter 1994, they were estimated at densities of 10.3 (Hayes & Bowers, 1987) and 8.8/1000 km^2 (YTG, unpubl. data), and in packs averaging 5.8 and 6.3 wolves, respectively. Ungulate biomass per wolf, per 1000 km^2 grew from 94 to 251 kg, coinciding with estimated annual population growth rates for caribou, moose and sheep, of 10.5% (n=6 years), 12.2% (n=7 years), and 10.7% (n=2 years), respectively. In late winter there were an estimated 66 and 101 caribou/wolf on late winter range in 1987 and 1993 (Table 1, line 2).

Moose appeared readily available to wolves in the Wolf Lake area in both 1987 and 1993; for every kg of caribou there were an estimated 5.7 kg and 7.5 kg, respectively, of moose available (Table 1, line 21). Sheep contributed little to the available ungulate biomass.

Snowshoe hare numbers were believed to have peaked in the southern Yukon in 1991, and presumably were at relatively high densities from 1989-91. Subsequently they crashed across the southern Yukon (M. O'Donaghue, pers. comm.). It has been suggested that the availability of snowshoe hare may facilitate wolf pup survival during the summer when large mammals are scarce (Keith, 1983; Hayes, 1992). This buffer may delay the numerical wolf response to declining prey and amplify the eventual response.

Discussion

Demographic similarities between the two herds

The Aishihik and Wolf Lake caribou herds conformed to the typical patterns of distribution of woodland caribou, being highly dispersed at calving and clumped during late winter (Fig. 2). Dispersal at calving is thought to be a strategy whereby cows choose scattered, remote, and inconspicuous sites to minimize the risk of predation (Bergerud, 1980; Bergerud *et al.*, 1984; Bergerud & Elliot, 1986). Clumping in late winter may be an outcome of snow conditions that force caribou into limited areas where they can effectively crater for forage (Bergerud, 1978). Russell & Martel (1984) suggested that there were two snow thresholds for caribou, one between 60 and 70 cm, above which individuals had difficulty securing food and travelling, and the other threshold between 80 and 90 cm, above which the mobility of groups was handicapped. In the Yukon the greatest snow depths are generally recorded in March (Wahl *et al.*,1987), coinciding with clumping of caribou (Farnell & McDonald, 1987).

The Aishihik and Wolf Lake herds also displayed similar demographic characteristics that would be expected of relatively small woodland caribou herds. The sex ratio favoured females, presumably as a result of differential mortality between sexes. This phenomenon, however, may have been linked with herd size. When the Aishihik and Wolf Lake herds were below 800 animals sex ratios were skewed with less than 30 bulls per 100 cows. For the Aishihik herd, sport hunting may have compounded an already unbalanced sex ratio. However, the Wolf Lake herd with minimal hunting losses had a similarily skewed sex ratio of 29 bulls per 100 cows in 1987 when the herd numbered less than 700. Bergerud & Elliot (1986) suggested that when recruitment was low there was a strong bias toward female recruits, and that there was greater predation on bulls than cows, acting together to skew small declining herds in favour of females. Similarily, in the Yukon, most small herds with low recruitment are highly skewed toward females (Farnell & McDonald, 1989; YTG, unpubl. data).

Both the Aishihik and Wolf Lake herds also had high pregnancy rates in the years tested (94%), yet both of these woodland herds had variable fall-winter calf cow ratios, ranging from 7 to 28 calves per 100 cows. We speculate that the low calf:cow ratios from both herds in the winter of 1992-93 are related to above average snow packs and the late arrival of spring in 1992. Bergerud & Elliot (1986) found that calf survival was generally high in years of early snow melts, and hypothesized that relatively high losses of calves in deep snow years was due to the increased vulnerability of calves in deep snow.

Demographic differences between the two herds.

There were notable demographic differences between the Aishihik and Wolf Lake herds. The Aishihik herd declined from 1981 to 1991 (average annual rate of -6.5%), and continued to decline at a rate of 30%, to 583 individuals, in 1992. This decline was associated with a further skewing of the sex ratio, the disproportionate loss of large bulls and increasing levels of adult natural mortality. And yet, the Wolf Lake herd over a similar period grew from 664 caribou in 1987 to 1249 in 1993; an average annual growth rate of 10.5%. This growth was associated with a low adult mortality rate and an increase in the proportion of bulls, in particular young bulls. Bergerud & Elliot (1986) suggested that populations with high recruitment and therefore good representation of young cohorts would have a more balanced sex ratio because young males typically enjoy higher survival than do older males.

Ecological implications

There were no obvious mechanisms to explain the different demographic trends between herds. During the study period, changes in habitat or distribution were not apparent. The Wolf Lake herd was generally subject to relatively deep snows, undoubtedly compromising its activity patterns and distribution, in contrast to the Aishihik herd whose activities were minimally impaired by snow conditions. Yet it was the Wolf Lake herd that increased. Greater precipitation in the Wolf Lake area may have yielded better summer range conditions and consequently better caribou body condition; unfortunately range quality or body condition were not measured.

The influence of hunting of caribou in the southern Yukon is unknown, as harvest data was inadequately reported. It is noteworthy that large-antlered bulls were consistently more common in the Wolf Lake area, possibly reflecting greater sport hunting in the Aishihik area. However, these comparisons are weak as our data does not allow within-year comparisons.

The importance of large bulls to the demography of *Rangifer* is poorly understood. It is possible that, in populations with a relatively small number of bulls and few prime bulls, breeding takes place over a longer period (Kojola, 1991; Baskin, 1970). Consequently, proportionally more late, less viable calves would be produced with low birth weights (Reimers *et al.,* 1983) and higher vulnerability to predation (Bergerud, 1980). The cost of delayed parturition may also effect the fall weight of the dam, and therefore her ability to conceive and survive during the upcoming winter (Eloranta & Nieminen, 1986; White, 1983; Reimers, 1983). In addition, the active participation of young bulls in the rut may predispose them to greater post-rut mortality (Leader-Williams, 1980).

Although pregnancy rates have remained high in both Aishihik and Wolf Lake herds, we have no data on the timing of birthing or its variability, or on birth weights.

Cows may also be predisposed to higher levels of predation because bulls are relatively scarce in the population, possibly explaining the high mortality rates of cows observed in the Aishihik herd. Hunting of bull caribou in small herds with disparate sex ratios and low recruitment is unlikely to be sustainable. Whether the selective harvest of trophy bulls will exacerbate a population decline is only speculative but warrants further study.

Densities of wolves were similar in Aishihik and Wolf Lake areas and similar to densities throughout the southern Yukon. In both areas, densities of wolves ranged from 8.1 to 11.5/1000 km^2, from 1987 to 1993. Likewise, grizzlies were believed to be at similar, relatively low densities, and their effect on the caribou populations in the southern Yukon are unknown. Caribou in Denali were reported to suffer relatively high neonatal losses from grizzlies (Adams *et al.*, 1988; 1989), with the highest losses in a year following a winter of deep snow that persisted through calving, and in a year where snowfall was high during calving. Although we cannot rule out the significance of grizzly predation as an important factor in the population biology of southern Yukon caribou, it does not explain the difference in demographic trends between the Aishihik and Wolf Lake herds.

Coyotes are common in the Alshihik area and absent in the Wolf Lake area, but their relationship with caribou or other large ungulates is unknown. In eastern Canada, coyotes have replaced wolves in some areas as a major predator on white-tailed deer (Messier *et al.*, 1986), and in Manitoba coyotes are both a predator and a scavenger on large ungulates (Paquet, 1992). In southeastern Alaska, there is concern that high densities of coyotes have become significant predators on Dall sheep and perhaps caribou calves (C. Gardner, pers. comm.). Coyotes in the Kluane region are believed to be synchronized with the snowshoe hare cycle (Theberge & Wedeles, 1989; M. O'Donaghue, pers. comm.). The recent collapse of the snowshoe hare population is believed to have resulted in high rates of dispersal of a relatively high density of coyotes in the Kluane region, but there is no evidence of coyote predation on caribou calves. Due to the potential impact of calf loss to coyotes, we suggest further investigation of this factor. There were some significant differences between Aishihik and Wolf Lake in the amount of alternate prey. The ungulate biomass/wolf ratio index (Fuller, 1989), and the amount of alternate prey, in relation to caribou, was substantially less in the Aishihik area in 1991, as compared to the Wolf Lake area in 1987. The biomass of moose in relation to caribou was almost twice as much in Wolf Lake as it was in Aishihik. While the relative availability of alternate prey declined in the Aishihik area from 1991 to 1992, it increased dramatically in the Wolf Lake area from 1987 to 1993.

We know that moose are an important part of wolf diet in the southern Yukon (Hayes *et al.*, 1991), and hypothesize that prey switches to caribou are prompted by significant declines in moose, such that moose become a relatively uneconomical prey.

In the Aishihik area, the caribou decline may have been further amplified by the population explosion of snowshoe hares from 1989-91 which may have temporarily sustained high productivity of wolves, despite the decline in moose.

We cannot explain the lack of an apparent numerical response by wolves to expanding populations of moose, caribou, and sheep in the Wolf Lake area. Wolf densities throughout the Yukon are similar despite apparent differences in prey biomass. In the Finlayson area, the number of ungulates increased significantly, yet the wolf population has plateaued at an estimated density of 11/1000 km^2, similar to those densities reported prior to the wolf cull (Farnell & Hayes, in prep.).

Dispersal of cows prior to calving, to high elevation, remote, predator free habitats, has been discussed as a predator avoidance strategy (Bergerud, 1980). In addition there may be some anti-predator advantage to clumping during the winter. The population regulation of wolves is mediated by territorial behaviour (Mech, 1977; Peterson *et al.*,1984; Fuller, 1989). Presumably, a confined winter distribution will expose caribou to fewer wolves (more caribou/wolf) (Cummings *et al.*, this volume). In the Wolf Lake area caribou were found at higher densities in late winter in 1987 and 1993, as compared to caribou in the Aishihik area in 199.1 (64 and 87 caribou for every wolf, compared to 46 caribou/wolf).

Late winter clumping behaviour of caribou, although perhaps reducing their contact with wolves, in extreme instances could induce over-grazing and trampling losses, consequently reducing reproductive success and/or lower calf birth weights. However, on the Wolf Lake winter range caribou stocking rates have been low in the last few decades.

Results of this study conform incompletely to Bergerud's (1992) and Seip's (1992) model. We agree that predator avoidance behaviour, including dispersed calving, winter aggregations, seasonal migrations, and the presence of alternate prey are important factors in shaping the population ecology of woodland caribou at low densities when hunting is not excessive. However, the apparent mechanisms in the Yukon are different to that proposed by Seip (1992). Moose are thought to be a preferred prey of wolves in areas where caribou and moose coexist. We predict that when moose decline to a level whereby they are scarce in relation to caribou, wolves will shift their predation to caribou. This requires further testing, either experimentally, or by monitoring naturally fluctuating populations.

Our observations, therefore, are inconsistent with the notion discussed by Seip (1992), that wolf populations grow with increasing numbers of moose thereby decreasing the ratio of caribou to wolves and leading to disproportionate losses to caribou. Clearly, if this were true, the Aishihik herd should have increased and the Wolf Lake herd declined.

The relationships between caribou, wolves, and snowshoe hares, and the implications of highly skewed adult caribou sex ratios are poorly understood, but perhaps significant in the population ecology of Yukon woodland caribou.

Conclusions

Low adult mortality, favourable calf production, and limited human hunting contributed to the growth of the Wolf Lake herd. This population growth may have been tied to the relative availability of moose as an alternate, and probably primary prey, to wolves, combined with the limited impact of human hunting. The highly clumped winter distribution may have further reduced the impact of wolves on caribou. The failure of the wolf population to increase with increasing numbers of prey is unknown.

The Aishihik herd decline was driven by high adult mortality and low recruitment. Here, moose were scarce during the caribou decline, and wolf predation on caribou was believed to be high as there were few prey alternatives. A snowshoe hare explosion (which probably resulted in increased wolf pup survival), the relatively wide dispersion of caribou in the winter, and the direct mortality from hunting may have further amplified the decline. The effect of habitat quality is also unknown and perhaps important.

The influence of hunting is poorly understood from our data. Although highly speculative, an excessive harvest of trophy bulls from a herd with high natural adult mortality and low recruitment may further skew the sex ratio and the age structure, debilitating the population through higher natural mortality rates of cows and young bulls, and depressed calf production. These relationships, between hunting and caribou population demography, between coyotes and caribou, and between wolves and snowshoe hare are poorly understood in the Yukon, and warrant further study.

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