THE INFLUENCE OF WOLVES ON THE ECOLOGY OF MOUNTAIN CARIBOU

by

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

(Department of Animal Science)

We accept this thesis as conforming

to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

May 1998

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ABSTRACT

The wolf (*Canis lupus*)/mountain caribou (*Rangifer tarandus caribou*) spatial separation model (Seip 1992a) was examined in highland and mountainous areas of east central and southeastern British Columbia to determine the influence of wolves on mountain caribou ecology. Three key elements investigated were: the importance of wolf predation as a mountain caribou mortality factor, the elevational relationships of mountain caribou, wolves, and moose (*Alces alces*), and the seasonal dietary importance of moose to wolves.

Mountain caribou mortality data from the Columbia Mountains and Quesnel Lake supported the hypothesis that wolf predation is greater in highland than in mountainous areas. Wolf predation was the main mortality factor of caribou in the highlands around Quesnel Lake, but was a minor factor in the other three study areas. Wolf predation at Quesnel Lake occurred primarily during summer/fall at low elevations.

Mountain caribou, wolf and moose radio-telemetry data suggested that wolves in both highland and mountainous areas are more closely associated elevationally with moose than caribou throughout the year. Caribou in highland areas appeared as adept as those in rugged mountains at spacing elevationally away from wolves during all seasons. Significant elevational overlap between wolves and caribou occurred only in the rugged Columbia Mountains, and then, only during summer/fall.

Wolf scats from the Columbia Mountains indicated that mountain caribou were of lesser dietary importance than moose to wolves throughout the year. Moose, particularly in winter, were the main diet item of wolves. Beaver was an important dietary item of wolves during summer/fall.

Elevational separation appears inadequate in explaining the variation in wolf predation on mountain caribou in the highland and mountainous study areas. Differences in wolf densities and

the relative densities of moose and caribou may be the main factors influencing the susceptibility of mountain caribou to wolf predation. It is recommended that studies be conducted in both topography types across a wide range of caribou and moose densities to better explain the influence of wolves on mountain caribou ecology. In addition, it will be necessary to compare the geographic distribution of mountain caribou and wolves to assess if geographic rather than elevational separation occurs. Determining how timber harvesting impacts the numerical and spatial responses of wolves, mountain caribou and moose is also recommended.

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ACKNOWLEDGEMENTS

"We are made to exaggerate the importance of what work we do;
and yet how much is not done by us!" (Thoreau 1854)

From the outset of my search for knowledge and understanding of wolves, mountain caribou and science in general, many individuals graciously helped me move toward attaining this goal. As always, I recognize my path was directed by God and that He sustained me faithfully throughout this adventure. I thank my wife, Sue, for providing patient support and steadfast encouragement throughout all the various phases of this thesis, in particular when I was absent from home and out tracking wolves in the Columbia Mountains. I greatly appreciate my family members and friends for cheering me onward and providing necessary moments of levity.

B. N. McLellan, my research supervisor guided me throughout this research, and most notably provided sage advice, fund-raising support, good coffee and occasionally a floor to crash on. D. Shackleton, my academic supervisor, tried diligently to keep me focused whenever I was within arms length of "the hut". My other committee members: D. Seip, M. Pitt, and T. Sullivan, assisted freely, whenever asked.

R. Ramcharita deserves a special note of thanks for volunteering countless hours in my initial efforts to radio-collar wolves. In addition to almost always keeping the snowmobile tanked up, he shared many ideas which undoubtedly increased the quality of this research. J. Flaa assisted in the field, and together with M. Super and D. Mair spent many hours airborne, locating radio-collared caribou and wolves in the Columbia Mountains. J. Townley helped in backtracking wolves during the winter, while the assistance of D. Lewis, J. Krebs, K. Atkinson and A. Lay also eased my work in the field.

G. Galzi, S. Wilson and S. Leung offered advice and assistance with various database queries. I. Clemens assisted with computer programming and data analysis. K. Allison created a map of the study areas.

Individuals that generously provided data for analysis were: B.N. McLellan and J. Flaa, K. Simpson and G. Woods (Columbia Mountains caribou data); D. Seip (Quesnel Lake caribou/wolf/moose data; Wells Gray caribou/wolf data); J. Young and P. Dielman (Quesnel Highlands caribou/wolf data); K. Simpson (Columbia Mountains moose data); and J. Woods (Banff National Park ungulate weight data).

Financial support for this study was provided by the B.C. Ministry of Forests, Mount Revelstoke and Glacier National Parks, Columbia Basin Fish and Wildlife Compensation Program, Canadian Wildlife Service - University Research Support Fund, The Friends of Mount Revelstoke and Glacier, Revelstoke Community Forest Corporation, Canadian Wildlife Federation - Orville Erickson Memorial Scholarship, University of British Columbia - James Robert Thompson Fellowship, E. Allison, E. and W. Bauman and P. Spaetzel.

Although they will never read this, I am grateful for the wolves, caribou and moose that through direct and indirect observation, allowed me a brief glimpse into their lives and provided many enjoyable moments afield.

Ultimately, I realize that together with the help of many fine individuals, my burdens were lightened, progress was made, and I was truly allowed to enjoy "one of the best times of my life" (B.N. McLellan, personal communication).

CHAPTER 1

GENERAL INTRODUCTION

Mountain caribou (*Rangifer tarandus caribou*) are on the blue or vulnerable list of species in British Columbia (Harper et al. 1994). Their low numbers (Simpson et al. 1997), low rate of reproduction (Bergerud 1978) and reliance on old growth forests for food and shelter which conflicts with timber harvesting needs (Simpson et al. 1996) collectively resulted in this designation.

The distribution and abundance of mountain caribou began to decrease across southern British Columbia in the early 1900s (Munro 1947). Explanations for the decline have included habitat degradation, overhunting and predation (Bergerud 1974; Bloomfield 1980; Edwards 1954; Munro 1947), but wolf (*Canis lupus*) predation has recently been suggested as the most significant limiting factor across southern British Columbia (Bergerud 1988a, 1996; Seip 1991, 1992a; Seip and Cichowski 1996). Bergerud and Elliot (1986) and Seip (1992a) suggested that wolf populations within mountain caribou range are sustained primarily by moose (*Alces alces*), but in areas of gentle topography, wolves were also a significant predator of mountain caribou. Ultimately, it was concluded that mountain caribou in more rolling, highland areas experience more wolf predation than caribou in rugged mountainous areas due to their inadequate degree of spatial separation with wolves and moose (Seip 1992a).

To determine the influence of wolves on the ecology of mountain caribou, I investigated three elements of the spatial separation model (Seip 1992a): the importance of wolf predation as a mountain caribou mortality factor, the elevational relationships of caribou, wolves and moose, and the seasonal dietary importance of moose to wolves.

Chapter 1 includes this introduction to the research and a description of the four study areas. In Chapter 2, I use mountain caribou mortality data collected during five previous studies (B.N.

McLellan and J. Flaa, unpublished data; Seip 1990, 1992b; Simpson and Woods 1987; J.A. Young and P. Dielman, unpublished data) to compare the rates, causes, seasons and elevations of mountain caribou mortality among four study areas, and in particular, the impact of wolf predation on animals in highland and mountainous areas. In Chapter 3, I use radio-telemetry data (B.N. McLellan, J. Flaa, and B. Allison, unpublished data; Seip 1990, 1992b; K. Simpson, unpublished data; J.A. Young, unpublished data) from the four study areas to examine the elevational relationships of mountain caribou, wolves and moose in both highland and mountainous areas. In Chapter 4, I estimate the seasonal dietary importance of moose to wolves in the Columbia Mountains using wolf scats I collected from that area. The final chapter summarizes my findings and provides some management recommendations.

STUDY AREAS

The four study areas are located in east central and southeastern British Columbia. These areas are: the Columbia Mountains north of Revelstoke (51°30'N, 118°15'W), Wells Gray Provincial Park (52°15'N, 120°W), the Quesnel Lake area (52°45'N, 120°45'W) and the Quesnel Highlands (52°45'N, 121°W) near Horsefly (Fig. 1). The Quesnel Highlands study area encompasses the Quesnel Lake study area, but since the data examined come from two different time periods, and the areas are of considerably different size, they are referred to as separate studies.

Although there are some moderate slopes and plateaus, the topography of the Columbia Mountains and the majority of Wells Gray Provincial Park is typical of rugged terrain. Valleys are narrow and steep with mountains rising to massive rock outcrops and glaciers. Elevations range from 575 to 3200 m in the Columbia Mountains and 630 to 2850 m in Wells Gray Provincial Park. An estimated 375 caribou inhabit the Columbia Mountains study area (McLellan

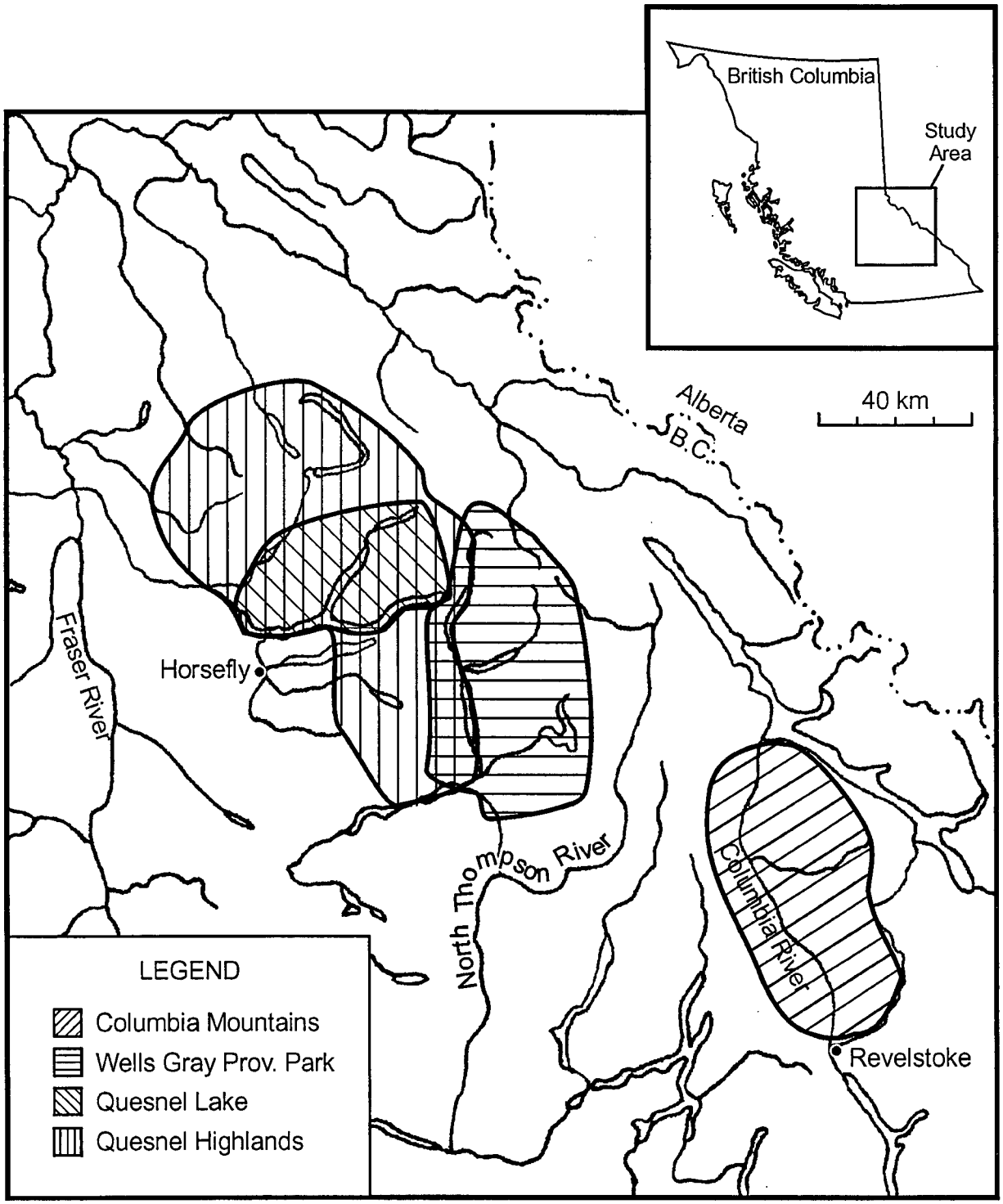

Fig. 1. Location of study areas: Columbia Mountains, Wells Gray Provincial Park, Quesnel Lake, and Quesnel Highlands, British Columbia.

et al. 1994b), while 275 and 302 were estimated within and adjacent to Wells Gray Provincial Park in 1987 and 1989 respectively (Seip 1990).

The Quesnel Lake and Quesnel Highlands study areas contain some rugged mountains but generally consist of highlands with rounded, vegetated mountains and moderate slopes (Holland 1976). Large rock outcrops are rare and glaciers are absent. Elevations range from 728 m to almost 2600 m. The Quesnel Lake study area was estimated to have 220 mountain caribou in 1986, but dropped to 94 in 1989 and 95 in 1997 (Seip 1992b; J.A. Young, unpublished data). In 1997, 358 mountain caribou (J.A. Young, unpublished data) were estimated to reside in the Quesnel Highlands area. A portion of the Quesnel Highlands study area is rugged with mountains reaching 2800 m.

The majority of the valley bottoms within the four study areas are in the Interior-Cedar-Hemlock (ICH) biogeoclimatic zone which occurs up to 1250 - 1350 m. Forests in the ICH zone are dominated by closed canopies of western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) (Ketcheson et al. 1991). Low elevations in the northern and western portions of the Quesnel Highlands contained the Sub-Boreal Spruce (SBS) zone and are dominated by hybrid white spruce (*Picea engelmannii* x *glauca*) and subalpine fir (*Abies lasiocarpa*) (Meidinger et al. 1991). Mid slopes in the four study areas are occupied by the Engelmann Spruce-Subalpine Fir (ESSF) biogeoclimatic zone, which extends to 1800 - 2000 m. Lower portions of the ESSF are dominated by closed canopy forests of hybrid white spruce and subalpine fir (Coupe et al. 1991) while subalpine fir increases in abundance at higher elevations and near timberline, grows in small clumps, forming the more open subalpine parkland (Coupe et al. 1991). The Alpine Tundra (AT) zone occurs at the highest elevations in the four study areas.

Snowpacks in the mountainous portions of the study area are high and average 1.3 m in valley bottoms and 2.8 m at snow stations between 1620 and 1920 m (B.C. Ministry of Environment

1985). Snowfall accumulations in the Quesnel Highlands are lower than those of the mountains and average 1.0 m in valley bottoms and 1.9 m at stations between 1570 and 1900 m during the late winter (B.C. Ministry of Environment 1985).

Ungulates in all four study areas include: woodland caribou, moose, mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and mountain goats (*Oreamnos americanus*). Wolves, grizzly bears (*Ursus arctos*), black bears (*U. americanus*), and wolverines (*Gulo gulo*) are the main predators within the study areas.

CHAPTER 2

WOLVES: THEIR ROLE IN MOUNTAIN CARIBOU MORTALITY

INTRODUCTION

Since the latter part of the nineteenth century, woodland caribou populations have declined across a large portion of their historic North American range (Anderson 1938). In southern British Columbia, the mountain ecotype began decreasing around 1900 and disappeared from some areas (Munro 1947). Currently there are about 2500 mountain caribou and almost all are found in British Columbia (Simpson et al. 1997). Mountain caribou feed largely on arboreal lichen during the winter (Antifeau 1987, Edwards and Ritcey 1960, Rominger and Oldemeyer 1990, Servheen and Lyon 1989; Simpson et al. 1997; Terry 1994), and because these lichens are most abundant on old trees, caribou management conflicts directly with forest harvesting. Maintaining present mountain caribou populations and their requisite habitats is a major conservation challenge in British Columbia (Simpson et al. 1997, Stevenson and Hatler 1985).

Several hypotheses have been proposed to explain the decline of mountain caribou. Overharvesting by native (Munro 1947) and recreational hunters due to liberal hunting regulations, combined with improved access, was suspected (Bergerud 1974; Bloomfield 1980; Seip and Cichowski 1996). Habitat degradation due to fires (Edwards 1954) and timber harvesting was thought to reduce caribou winter food, decrease shelter and disrupt travel corridors (Bloomfield 1980). In portions of southern British Columbia, cougar (*Puma concolor*) predation was believed to have caused the extirpation of caribou in one area (Munro 1947), while predation by an increasing wolf population during the 1930s and 1940s was suggested in other areas (Bergerud 1974; Munro 1947). Although more pluralistic hypotheses have been proposed to explain the widespread decline in mountain caribou (Bloomfield 1980; Stevenson and Hatler

1985), wolf predation is currently emphasized as the primary factor involved (Bergerud 1974, 1988a, 1996; Seip 1991, 1992a; Seip and Cichowski 1996).

Bergerud and Elliot (1986) reported that in areas where wolves are abundant, caribou populations decline, and Seip (1992a) proposed that mountain caribou in highland areas with less ability to space away from wolves and moose, experience more wolf predation particularly in summer, than caribou in rugged mountains. The objectives of this chapter are to: 1) compare rates, causes, seasons and elevations of mountain caribou mortality among four study areas, 2) compare wolf and caribou densities among those study areas, and 3) test whether wolf predation on caribou is greater in highland areas than in mountainous areas.

METHODS

Capture and monitoring

The mountain caribou mortality data from the four study areas (Columbia Mountains; Wells Gray Provincial Park; Quesnel Lake; Quesnel Highlands) were collected during five previous studies (B.N. McLellan and J. Flaa, unpublished data; Seip 1990, 1992b; Simpson and Woods 1987; J.A. Young and P. Dielman, unpublished data). Most mountain caribou in the four study areas were captured by net-gunning from a helicopter in subalpine habitats during late winter (McLellan et al. 1994a; Seip 1990, 1992b; Young et al. 1996). Other caribou were captured by darting with immobilization drugs during the 1981-85 Columbia Mountains study (Simpson and Woods 1987) and at the start of the 1984-89 Quesnel Lake study (Seip 1992b). All caribou were fitted with mortality-motion sensitive radio collars. Radio-collared animals were relocated from aircraft two to four times per month and location and elevation were recorded for each relocation.

Mortality factors and seasons

When a signal from a motion-sensitive radio collar indicated that a caribou was dead, the site was investigated and if possible, the caribou was necropsied to determine cause of death. Mortality causes were first classified as predation, not predation, and unknown. Cases of predation were then divided into wolf, bear, wolverine or unknown. Non-predation deaths were divided into accident, avalanche, malnutrition or unknown. Criteria used to attribute predation mortalities to wolf, bear or wolverine were: presence of predator, tracks, scats, or hair at the mortality site; extensive blood on carcass, ground or snow; distribution of the carcass, and site conditions (B.N. McLellan and J. Flaa, unpublished data; D.R. Seip, unpublished data; J.A. Young, unpublished data). Malnutrition deaths in all four study areas were determined from bone marrow fat content (B.N. McLellan and J. Flaa, unpublished data; D.R. Seip, unpublished data; K. Simpson, personal communication; J.A. Young, unpublished data), with renal and rump fat measures also used in the Columbia Mountains. Mortalities were classified as unknown when insufficient carcass remnants were available at the mortality site to assign a mortality cause. Mortalities were also classed as not predation but unknown when necropsies on relatively intact carcasses failed to reveal a mortality agent. All caribou mortalities were assumed to be classified to the correct mortality factor.

Date of mortality was assumed to fall half way between the date the caribou was last relocated alive and the date when the mortality signal was first heard (Mayfield 1975). I classified season of mortality as spring (May 1 - May 28), summer/fall (May 29 - Nov 7), early winter (Nov 8 - Dec 7) or late winter (Dec 8 - Apr 30). These seasons denote shifts in elevation and habitat use by mountain caribou and correspond to the conventional seasons of other mountain caribou studies (Antifeau 1987; Simpson and Woods 1987; Terry et al. 1996). Seasonal delineation for

each study area was determined by plotting mean caribou elevation by Julian week (McLellan et al. 1994a). Boundaries between seasons were then identified when the weekly change between mean caribou elevation was greatest, indicating a major elevational shift. Seasonal boundaries were then averaged among study areas to attain the four standardized seasons.

Mountain caribou and wolf density estimates

The 95% adaptive kernel method (Seaman and Powell 1991) was used to estimate the annual distribution of each caribou population and wolf pack from the relocations of radio-collared animals. Density estimates for each population were obtained by dividing the mean annual distribution by the estimated number of individuals in each caribou population or wolf pack. The mean of all wolf pack density estimates in each study area was used for inter-study comparisons. Estimates of caribou population size in each study area were obtained from censuses conducted during late winter as described by McLellan et al. (1994b), Seip (1990, 1992b) and J.A. Young (personal communication). Estimates of winter wolf pack sizes (Fuller and Snow 1988) were obtained during relocation flights, while the number of packs in each study area were estimated from incidental observations and wolf radio-telemetry data (B.N. McLellan, J. Flaa, and B. Allison, unpublished data; Seip 1990, 1992b; J.A. Young, unpublished data).

Statistical analyses

Annual mortality rates were estimated by dividing the total number of caribou mortalities by the total number of caribou years (one caribou monitored for one year is a caribou-year), based on methods described by White and Garrott (1990) for survival data. Multiple male and female caribou were radio-collared in the Columbia Mountains so tests for differences in male and

female caribou mortality rates were made. If no difference between rates was found, the mortality data of both sexes were pooled. Chi-square tests of independence (Siegel and Castellan 1988) were used to test for differences in mortality rates among genders and areas. If different rates were found among areas, the contingency table was partitioned into subtables following the methods of Siegel and Castellan (1988) to determine the cause of the difference. Fisher's exact test (Siegel and Castellan 1988) was used to test whether wolf predation on caribou is higher in highland areas than in mountainous areas using mortality from study areas with adequate sample sizes. Levels of significance for all tests were set at $p < 0.05$.

RESULTS

Mortality rates

In total, 155 mountain caribou (132 adult females; 11 adult males; 9 juvenile females; 3 juvenile males) from the four study areas were radio-collared and monitored for a total of 410 caribou-years between 1981 and 1996 (Table 1). Different annual mortality rates were found among the four study areas ($\chi^2 = 15.56$, df = 3, $p = 0.002$). Partitioning the contingency table showed no difference between rates in Wells Gray Provincial Park, the Columbia Mountains and the Quesnel Highlands ($\chi^2 = 0.18$, df = 1, $p = 0.75$), but the mortality rate of caribou at Quesnel Lake was higher than the other study areas ($\chi^2 = 14.56$, df = 1, $p < 0.001$).

Table 1. Level of mountain caribou monitoring and annual mortality rate (%)± (sd) within study areas.

Study Area	No. of caribou-years of monitoring	No. (age - sex) of radio-collared animals					Annual mortality rate
		Ad F	Ad M	Juv F	Juv M	Total	
Columbia Mountains 1981-85 & 1992-96	162	41	9	7	3	60	12.3 ± 2.6 [a]
Wells Gray Prov. Park 1986-89	75	27	1	2	-	30	8.0 ± 3.1
Quesnel Lake 1984-89	81	31	1	-	-	32	28.4 ± 5.0
Quesnel Highlands 1993-96	92	33	-	-	-	33	13.0 ± 3.5

[a] Combined mortality rate of male and female caribou, as their mortality rates were not significantly different ($\chi^2 = 0.02$, df = 1, $p = 0.90$).

Causes, seasons and elevations of mountain caribou mortalities

Mountain caribou in the four study areas died from a variety of factors. The proportion of wolf to non-wolf caribou deaths differed between the highland area, Quesnel Lake and the Columbia Mountains (Fisher's exact test, $p = 0.0002$). Wolf predation was the main mortality factor at Quesnel Lake, accounting for 10 (56%) of the known deaths, but was a minor factor in the other three study areas (Table 2). Bear predation was the most prominent mortality factor in Wells Gray Park, causing three (75%) of the known deaths. Avalanches were the greatest single factor contributing to caribou deaths in the Columbia Mountains, causing six (35%) known mortalities. Mountain caribou in the Quesnel Highlands, though, died from a variety of predation (43%) and non-predation (57%) factors.

The highest seasonal mortality rate occurred during spring, but most mountain caribou died during the summer/fall or late winter (Table 3). Thirteen (56.5%) caribou deaths at Quesnel Lake occurred during the summer/fall, eight of which were due to wolf predation. The summer/fall accounted for five (83.3%) caribou deaths in Wells Gray Park, with bear predation causing three

Table 2. Causes of radio-collared mountain caribou mortalities within study areas.

Study Area	Predation			Non-predation				Unk.	Total mortalities
	Wolf	Bear	Wolverine	Malnutrition	Avalanche	Accident	Unk.		
Columbia Mountains 1981-85 & 1992-96	-	2	3	1	6	3	2	3	20
Wells Gray Prov. Park 1986-89	1	3	-	-	-	-	-	2	6
Quesnel Lake 1984-89	10	3	-	2	1	2	-	5	23
Quesnel Highlands 1993-96	2	-	1	1	1	2	-	5	12
Total	13	8	4	4	8	7	2	15	61

of these. Ten (50%) deaths occurred during late winter in the Columbia Mountains with avalanches causing five of these and wolverine predation three. In the Quesnel Highlands, four (33.3%) deaths occurred in both summer/fall and late winter, but no clear seasonal mortality factor was observed. Deaths resulting from accidents and malnutrition did not exhibit strong seasonal affinities in any study area.

Table 3. Seasonal causes of radio-collared mountain caribou mortalities across all study areas (Columbia Mountains 1981-85, 1992-96; Wells Gray Provincial Park 1986-89; Quesnel Lake 1984-89; Quesnel Highlands 1993-96). Length of season (days) in brackets.

Season	Predation			Non-predation				Unk.	Total
	Wolf	Bear	Wolverine	Malnutrition	Avalanche	Accident	Unk.		
Spring (28)	-	2	-	1	-	2	-	3	8
Summer/Fall (163)	10	6	-	1	1	2	2	7	29
Early Winter (30)	-	-	-	1	1	1	-	2	5
Late Winter (144)	3	-	4	1	6	2	-	3	19

In study areas where wolf and bear predation occurred, most caribou were killed by these predators at low elevations (Table 4). Wolverine predation, however, occurred at both high and low elevations. Caribou were most likely to be killed by avalanches while at high altitudes, but

mortalities caused by malnutrition and accidents occurred with the greatest frequency at low elevations.

Table 4. Type and frequency of mortalities occurring above or below the median seasonal elevation of radio-collared mountain caribou across all study areas (Columbia Mountains 1981-85, 1992-96; Wells Gray Provincial Park 1986-89; Quesnel Lake 1984-89; Quesnel Highlands 1993-96).

Elevation	Predation			Non-predation				Unk.	Total
	Wolf	Bear	Wolverine	Malnutrition	Avalanche	Accident	Unk.		
Above Median	2	1	2	-	6	2	1	4	18
Below Median	11	7	2	4	1	5	1	7	38

Mountain caribou and wolf densities

Among the four study areas, the highest estimated caribou density (11.4 caribou/100 km^2) occurred in the highlands around Quesnel Lake in 1986 (Table 5), but in 1989, the estimated density fell to 4.9 caribou/100 km^2. This was within the range of caribou densities (3.4 to 5.3 caribou/100 km^2) observed in the other highland (Quesnel Highlands) and mountainous (Columbia Mountains; Wells Gray Provincial Park) study areas.

The two highland study areas (Quesnel Lake; Quesnel Highlands) had the highest estimated wolf densities and observed winter pack sizes, but wolf density was not estimated for Wells Gray Park as the number of wolves/pack was unknown (Table 6). Wells Gray Provincial Park, the Columbia Mountains and the Quesnel Lake study areas each had two known wolf packs, while the Quesnel Highlands study area had four.

Table 5. Mountain caribou density estimates based on mean annual distribution of populations.

Study	Year of population estimate	Number of caribou (95% C.I.)	Mean annual distribution (km^2)	Density (caribou/100 km^2)
Columbia Mountains (1992-96)	1994	375 (337 - 413)	7018	5.3
Wells Gray Prov. Park	1987	275 (220 - 297)	8206	3.4
(1986-89)	1989	302 (258 - 346)	"	3.7
Quesnel Lake	1986	220 (197 - 243)	1931	11.4
(1984-89)	1989	94 (86 - 102)	"	4.9
Quesnel Highlands (1993-96)	1997	358 (294 - 422)	9398	3.8

Table 6. Mean wolf density estimates within pack territories.

Study	Number of known wolf packs/study area	Number of wolves/radio-collared pack (winter)	Mean density (wolves/100 km^2 of pack territory)
Columbia Mountains (1992-96)	2	3-4	0.61
Wells Gray Prov. Park (1986-89)	2	Unknown	Unknown
Quesnel Lake (1984-89)	2	6-8	0.84
Quesnel Highlands (1993-96)	4	5-8	0.81

DISCUSSION

Variation in wolf predation among highland and mountainous study areas

Mortality data from the four study areas showed that mountain caribou at Quesnel Lake had a much higher mortality rate than in the other three study areas, as the caribou density dropped from 11.4 to 4.9 caribou/100 km^2 between 1986 and 1989. The results support the hypothesis that wolf predation is greater in highland areas than in mountainous areas as suggested by Seip (1992a). Wolf predation was the main cause of caribou deaths at Quesnel Lake (Seip 1992a, 1992b) but heavy wolf predation was not reported in any other study area. Non-wolf mortality

factors were more common in rugged mountainous terrain. It appeared that bears were the major predator of caribou in Wells Gray Park (Seip 1990). Avalanches were the single most important mortality factor of caribou in the Columbia Mountains, but both wolverine and bear predation were also notable (B.N. McLellan and J. Flaa, unpublished data; Simpson and Woods 1987). Another study, in the southern Selkirk Mountains, found cougar predation was the cause of most caribou mortalities (Compton et al. 1995).

Seip (1992a) attributed differences in wolf predation on mountain caribou in highland and mountainous areas to differences in the degree of elevational and geographic separation between caribou and wolves. Upon examination, elevational separation (Seip 1992a) does not appear to adequately explain the large variation in wolf predation among the four study areas. Except for summer/fall in the Columbia Mountains, caribou in both highland and mountainous areas were found to maintain elevational and hence geographic separation from wolves (see chapter 3). The separation of mountain caribou and wolves in geographically different areas during summer/fall in the Columbia Mountains although not examined in this thesis, may as reported elsewhere (Bergerud 1985; Bergerud et al. 1990; Cumming et al. 1996; Seip 1990, 1992a) explain why wolf predation on caribou was not observed in this study area.

Two other factors may account for the variation in wolf predation on mountain caribou among the highland and mountainous study areas. Firstly, wolf density differences (Bergerud and Elliot 1986) may explain why few caribou were killed by wolves in the mountainous study areas (Columbia Mountains; Wells Gray Provincial Park), while caribou at Quesnel Lake frequently died from wolf predation. Bergerud and Elliot (1986) reported that caribou populations decline in areas where wolf densities exceed 0.65/100 km^2. Wolf density within pack territory in the

Columbia Mountains (0.61/100 km^2) did not reach this critical level and it appears unlikely that wolves in Wells Gray Provincial Park exceeded it either. Wolves in the highlands around Quesnel Lake, however, with more wolves per pack, and smaller territories than wolves in the Columbia Mountains, had densities (0.84/100 km^2) above the critical threshold. This may have lead to more wolf predation on Quesnel Lake caribou. If wolf abundance is ultimately determined by the availability of prey biomass (Boertje and Stephenson 1992; Dale et al. 1994; Hayes 1995; Messier 1985, 1994; Packard and Mech 1980), and alternate ungulate prey remain sparse in the wet, rugged mountains of mountain caribou range (Terry et al. 1996), caribou in those areas should continue to be less susceptible to wolf predation.

Secondly, the relative densities of moose and caribou (Cumming et al. 1996; Seip and Cichowski 1996) may also be a factor influencing the susceptibility of mountain caribou to wolf predation. Optimal foraging theory (Krebs and McCleery 1984) predicts that wolves should hunt in the most optimal areas available to them, selecting the most energetically profitable prey (MacArthur and Pianka 1966). Assuming wolves in the four study areas hunted optimally, one can infer from the indirect evidence (wolf scat contents and/or elevations used by wolves) that at the prey densities wolves encountered, moose were considered the more profitable prey. If the density of moose decreased and/or caribou density increased significantly, wolves would be expected to switch predation efforts (functional response) from moose to caribou (Farnell et al. 1996). This behaviour would continue until once again it became more profitable to prey on moose (Messier 1995). Perhaps this explains why caribou numbers plunged at Quesnel Lake between 1986 and 1989 (Seip 1992a), but have since stabilized (J.A. Young, personal communication), even though wolf density remained high. The relatively high caribou density (11.4/100 km^2) in 1986 may have been sufficient to alter wolves from preying largely on moose

to also prey on caribou as this density is above the equilibrium density of 3.0-4.0 mountain caribou/100 km^2 as suggested by Seip and Cichowski (1996).

Seasons and elevations of mountain caribou mortality factors

It has been reported that mountain caribou are most vulnerable to wolf, bear, and cougar predation during summer (Compton et al. 1995; Seip 1990; Seip 1992b) especially at lower elevations (Seip 1992a). Mortality data from the Quesnel Highlands and Columbia Mountains studies support these findings. Unlike other carnivores, wolverines killed radio-collared caribou only during the late winter at both valley bottom and subalpine elevations (B.N. McLellan and J. Flaa, unpublished data; J.A. Young, unpublished data). Mountain caribou may be most susceptible to predation by this relatively small carnivore in late winter because the caribou have depleted most of their fat reserves and may be in poor condition. Malnutrition deaths did not exhibit this biological pattern in the four areas examined, but this is likely due to a relatively small number of mountain caribou mortalities.

CHAPTER 3

ELEVATIONAL RELATIONSHIPS OF MOUNTAIN CARIBOU, WOLVES AND MOOSE

INTRODUCTION

Wolves that prey primarily on moose, but sometimes switch to woodland caribou, have been implicated as a major cause of both past and present declines in mountain caribou populations (Bergerud 1974, 1988a, 1996; Seip 1991, 1992b, Seip and Cichowski 1996). It was suggested that woodland caribou could only exist on ranges shared with high densities of moose or deer and wolves if a habitat feature allowed caribou to avoid wolves and their alternate ungulate prey (Bergerud 1974).

Elevation appears to provide caribou with a unique means to space away from wolves and their alternate ungulate prey. In northern B.C., the northern ecotype of woodland caribou used rugged mountainous terrain and intra-specific dispersion to provide spatial separation from wolves and moose (Bergerud et al. 1984; Bergerud and Page 1987). In the Quesnel Lake area of east central B.C., wolves were sustained primarily by moose (Seip 1992b), but during the summer, their distribution overlapped with mountain caribou and they appeared to kill enough caribou to cause a rapid decline (Seip 1992a). Meanwhile, caribou that were spatially separated from moose and wolves in the nearby rugged mountains of Wells Gray Provincial Park experienced little wolf predation (Seip 1990). Seip (1992a) proposed that caribou living in highland habitats were more available and thus more prone to wolf predation than caribou in more mountainous terrain where they were separated from wolves. The spatial separation model (Seip 1992a) of which elevation is a component, may apply throughout mountain caribou range. The objective of this chapter is to test the following hypotheses: 1) wolves show more elevational overlap with moose than with mountain caribou, and 2) mountain caribou in highland

areas show less elevational separation from wolves than those living in rugged mountains.

METHODS

Capture and elevational monitoring of mountain caribou, wolves and moose

Radio telemetry data on mountain caribou and wolves from two study areas (Columbia Mountains 1992-96; Quesnel Highlands 1993-96), and moose radio-telemetry data from one study area (Columbia Mountains 1984-85), were used to evaluate the two hypotheses. Seip (1992a) did not statistically test the mountain caribou and wolf radio-telemetry data (Wells Gray Provincial Park 1986-89; Quesnel Lake 1984-89) nor the moose radio-telemetry data (Quesnel Lake 1984-89) so these data were also examined. Captured animals were fitted with radio collars and relocated from aircraft two to four times each month. Ground telemetry was also used to locate wolves in winter during the 1992-96 Columbia Mountains study. The location and elevation were recorded for each relocation.

Statistical Analyses

Elevation of radio locations were often asymmetrically distributed, thus two-tailed robust rank-order tests (Siegel and Castellan 1988) were used to test whether wolves and caribou, and wolves and moose used different elevations during each season in the highland and mountainous study areas. Frequency of use analyses were not used due to inadequate sample sizes in each study area during some seasons. Seasonal intermedian distances of wolves and caribou, and wolves and moose in highland and mountainous areas were also compared as another measure of the hypotheses. Seasons were based on elevational movements of caribou (McLellan et al. 1994a) and were classified as spring, summer/fall, early winter and late winter (see chapter 2). The level of significance for all statistical tests was set at $p < 0.05$.

RESULTS

Seasonal use of elevations by mountain caribou, wolves and moose

In spring, caribou in the highland (Quesnel Lake; Quesnel Highlands) and mountainous (Columbia Mountains; Wells Gray Provincial Park) study areas used lower elevations than during late winter, however, they remained separate from wolves which occupied still lower elevations (all $p < 0.001$) (Figures 2,3,4 and 5). In contrast, no difference was observed in the elevations used by wolves and moose in the Columbia Mountains ($\hat{U}$ [19,10] = 1.69, $p = 0.091$) or in the highlands around Quesnel Lake ($\hat{U}$ [6,14] = 0.608, $p = 0.543$) during spring (Figs. 2 and 4).

During summer/fall, wolves in all study areas increased their use of higher elevations (Figs. 2,3,4 and 5), particularly in the rugged Columbia Mountains where elevations used by wolves and caribou did not differ ($\hat{U}$ [38,1314] = 1.46, $p = 0.143$), nor did those used by wolves and moose ($\hat{U}$ [38,230] = 0.396, $p = 0.692$) (Fig. 2). Wolves and caribou during summer/fall in Wells Gray Provincial Park, and in both highland areas (Quesnel Lake; Quesnel Highlands) remained elevationally separate (all $p < 0.001$), although wolves at Quesnel Lake showed some use of high elevations during June (Fig. 4). In the Quesnel Lake area, moose and wolves used different elevations in the summer/fall ($\hat{U}$ [92,64] = -2.34, $p = 0.019$) with moose using higher elevations (Fig. 4).

During early winter, wolves and caribou in highland and mountainous areas again used lower elevations, but still little altitudinal overlap occurred (Figs. 2,3,4 and 5) ($p < 0.01$ in all areas). Alternately, wolves and moose were found at similar low elevations in both the Columbia Mountains ($\hat{U}$ [15,6] = 0.134, $p = 0.893$) (Fig. 2) and the Quesnel Lake study areas ($\hat{U}$ [15,15]

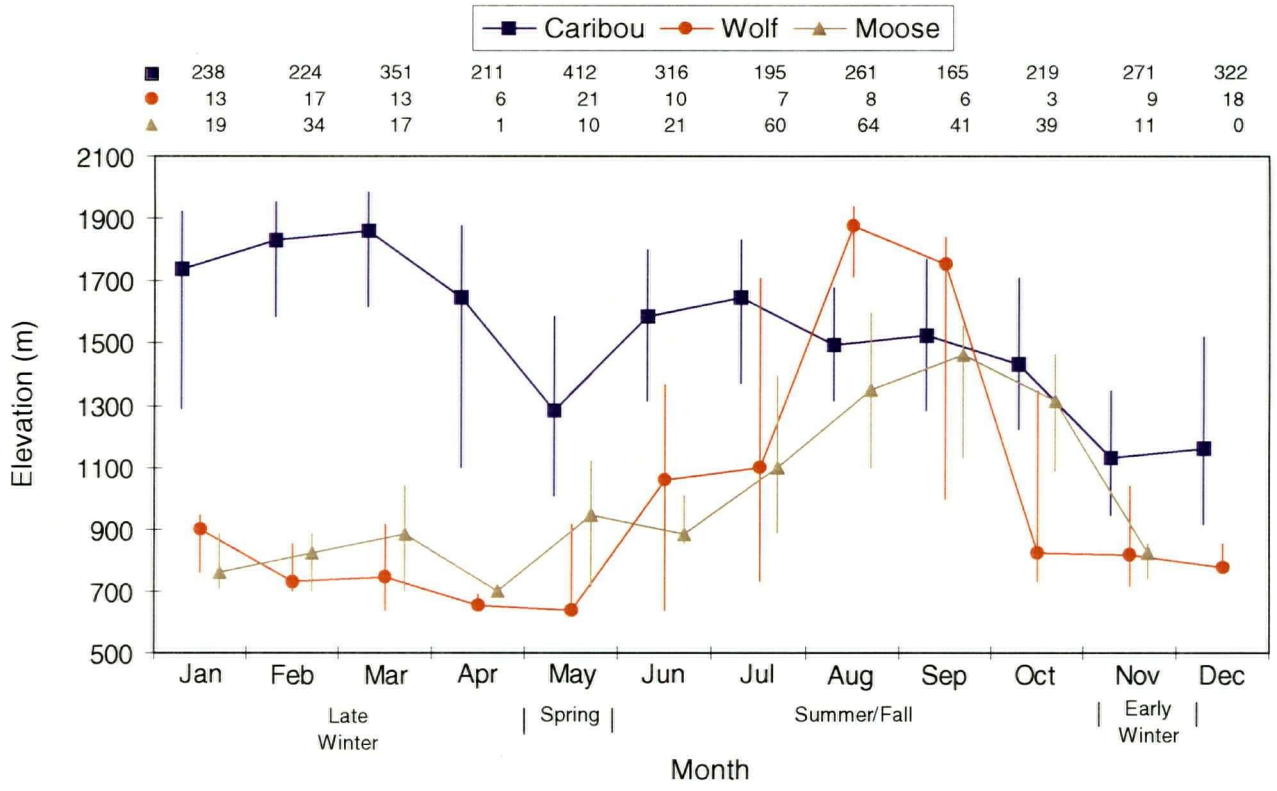

Fig. 2. Columbia Mountains radio-collared mountain caribou, wolf and moose median monthly elevations and interquartile ranges (1992-96 caribou and wolf; 1984-85 moose).

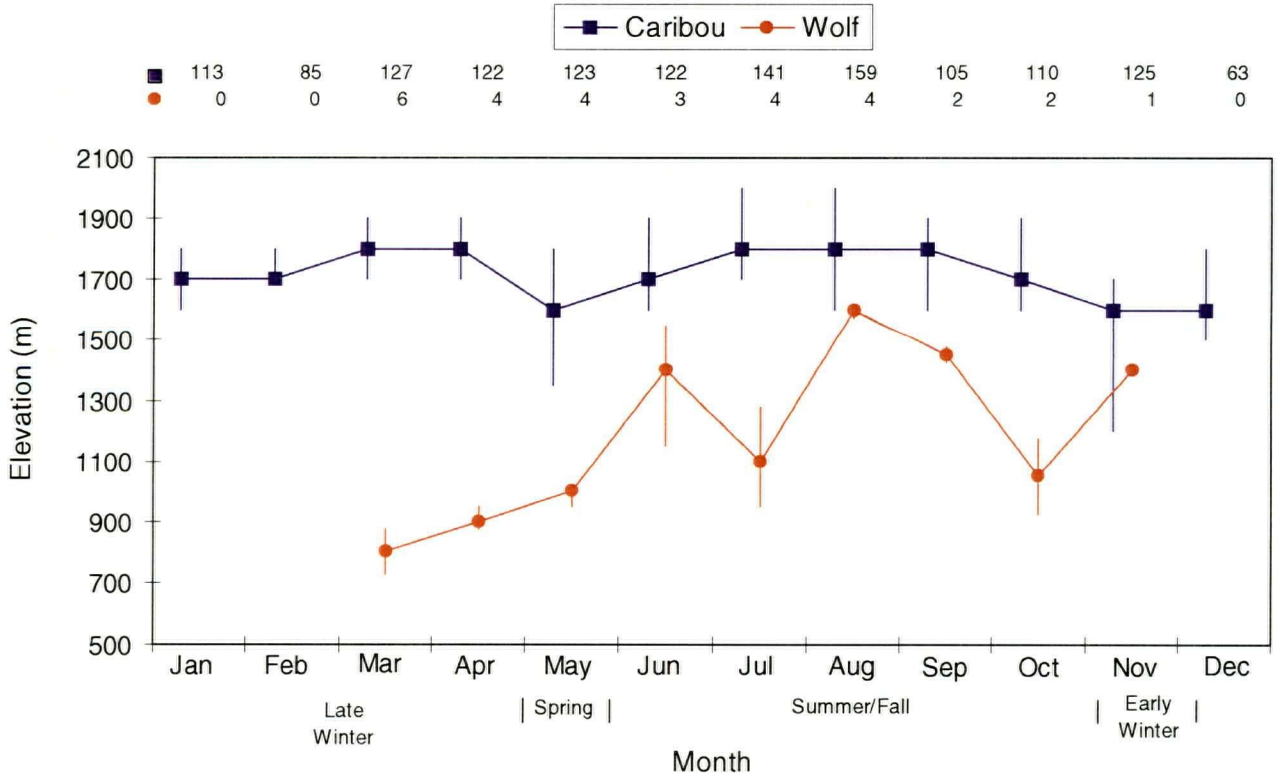

Fig. 3. Wells Gray Provincial Park radio-collared mountain caribou and wolf median monthly elevations and interquartile ranges (1986-89).

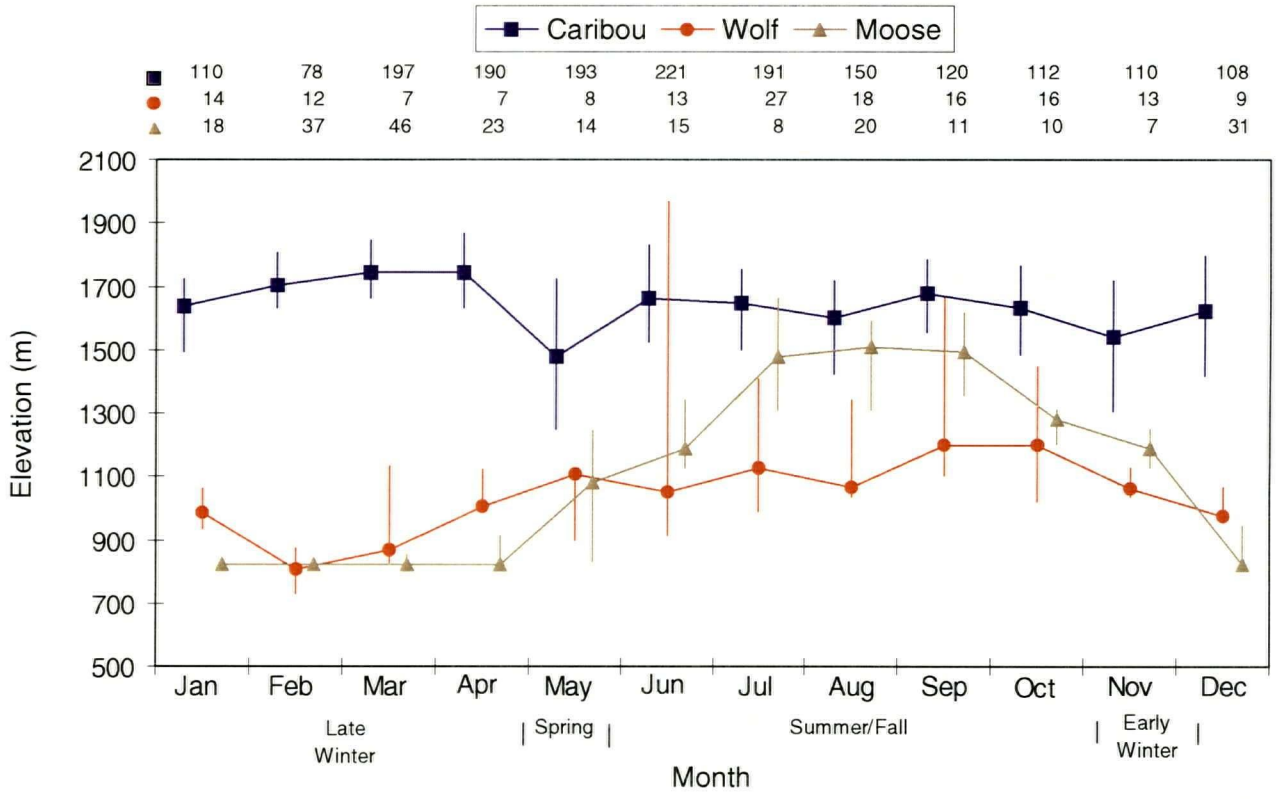

Fig. 4. Quesnel Lake radio-collared mountain caribou, wolf and moose median monthly elevations and interquartile ranges (1984-89).

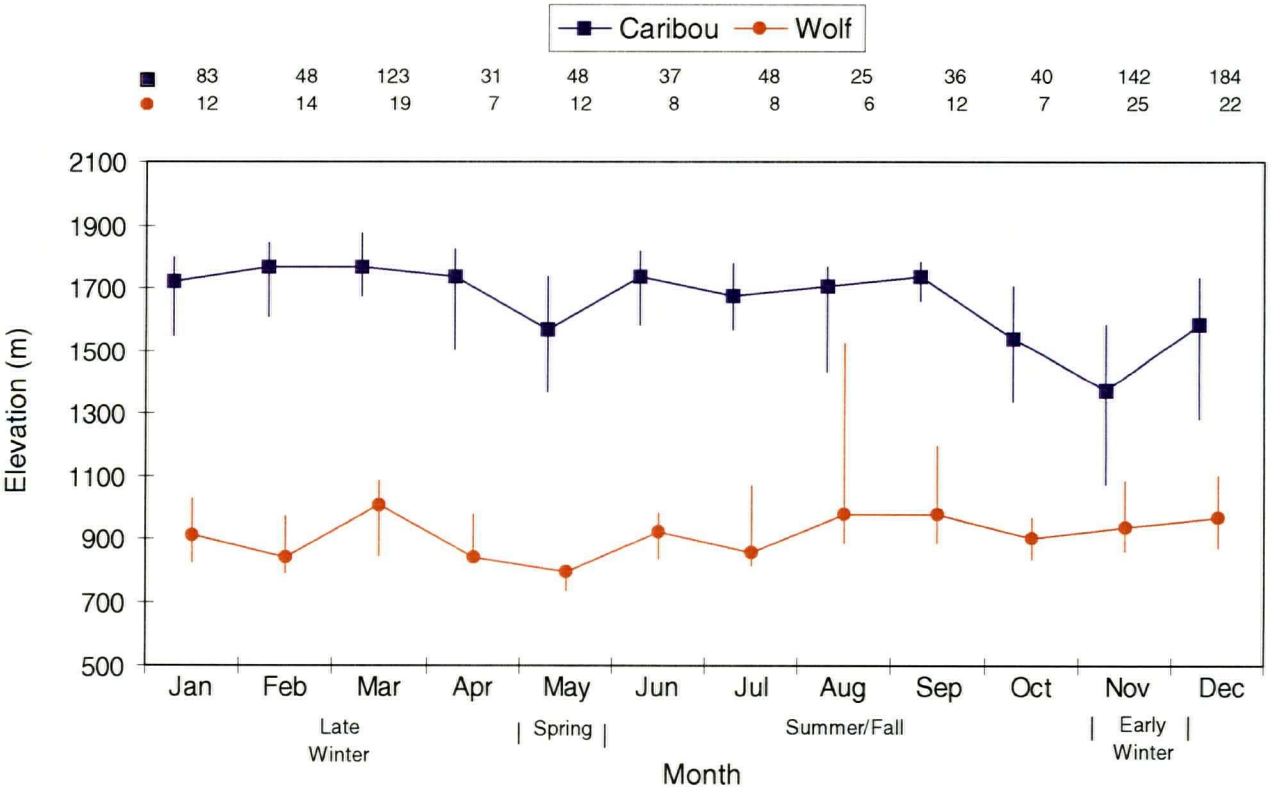

Fig. 5. Quesnel Highlands radio-collared mountain caribou and wolf median monthly elevations and interquartile ranges (1993-96).

= 1.14, $p = 0.255$) (Fig. 4) during the early winter.

During late winter, the elevations used by wolves in the highlands and mountains were generally lowest (Figs. 2,3,4 and 5) with wolves separate from caribou in each study area (all $p < 0.001$). Wolves and moose in both the Columbia Mountains and the Quesnel Lake area used lower elevations than caribou during the late winter (Fig. 2 and 4), yet the elevations used by wolves and moose in the Columbia Mountains did not differ ($\hat{U}$ [59,71] = 0.113, $p = 0.91$), whereas those of wolves and moose at Quesnel Lake did ($\hat{U}$ [47,147] = 2.72, $p = 0.007$).

Seasonal intermedian distances of mountain caribou, wolves and moose

In all seasons, in both the rugged Columbia Mountains and the highlands around Quesnel Lake, the median elevation of wolves was more closely associated with the median elevation of moose than that of caribou (Table 7). Seasonal intermedian distances of wolves and moose ranged from 46 to 305 m in the Columbia Mountains, while those of wolves and caribou ranged between 198 and 975 m. At Quesnel Lake, the wolf/moose seasonal intermedian distance ranged between 35 and 213 m, compared to a range of 347 to 747 m for wolves and caribou.

Caribou and wolves in highland areas did not always have seasonal intermedian distances lower than those of caribou and wolves in the mountainous study areas. Only during spring and late winter was the Quesnel Lake (highland area) wolf/caribou intermedian distance less than that of wolves and caribou in Wells Gray Provincial Park (Table 7). A similar comparison between wolves and caribou in the Quesnel Highlands and the Columbia Mountains showed that only in late winter did wolves and caribou in the Quesnel Highlands have a seasonal intermedian distance less than that of wolves and caribou in the rugged Columbia Mountains (Table 7).

Table 7. Wolf/mountain caribou and wolf/moose seasonal intermedian distances (m) within study areas.

Season	Mountains			Highlands		
	Columbia Mountains		Wells Gray Prov. Park	Quesnel Lake		Quesnel Highlands
	wolf-moose	wolf-caribou	wolf-caribou	wolf-moose	wolf-caribou	wolf-caribou
Spring	305	579	600	35	347	778
Summer/Fall	76	198	400	213	510	746
Early Winter	46	366	200	68	492	427
Late Winter	61	975	850	137	747	736

DISCUSSION

The hypothesis that wolves show more elevational overlap with moose than with mountain caribou was supported in both highland and rugged mountains. Wolf scat analyses from these two areas further support these conclusions as the main diet item of wolves throughout the year in both the Quesnel Lake area (Seip 1992b) and the Columbia Mountains (see chapter 4) was moose. Similar elevational relationships between wolves and moose were reported in northern British Columbia during the summer (Bergerud et al. 1984; Bergerud and Page 1987) and throughout the year in Wells Gray Provincial Park and the Quesnel Lake area (Seip 1992a).

The hypothesis that mountain caribou in highland areas show less elevational separation from wolves than those living in rugged mountains was not clearly supported. Caribou and wolves in the highlands (Quesnel Lake; Quesnel Highlands) were as likely to use different elevations during each season as were caribou and wolves in rugged mountainous areas (Columbia Mountains; Wells Gray Provincial Park). Even during summer/fall, when wolves were most elevationally mobile and likely to prey upon mountain caribou (Seip 1992a), caribou in the rolling highland areas appeared to space further away from wolves than did caribou in the more mountainous areas. Despite the advantage of greater elevational range to space away from wolves, mountain caribou in the Columbia Mountains were the only population to exhibit

significant elevational overlap with wolves, and then, only during summer/fall. The Columbia Mountains caribou population has not declined and no wolf predation of radio-collared caribou has been observed to date (B.N. McLellan, personal communication). This may indicate that caribou and wolves occupied geographically different areas during summer/fall, similar to caribou and wolves in Wells Gray Park (Seip 1990, 1992a).

Wolves were reported as the main cause of caribou deaths in the highlands near Quesnel Lake (Seip 1992a); however, the elevations used by the two species differed during all four seasons. A brief overlap in elevational use by wolves and caribou may have occurred during the calving period (Bergerud et al. 1984; Bergerud and Elliot 1986; Bergerud and Page 1987) and influenced the predation rate. This does not seem likely though as few adults at Quesnel Lake were killed by wolves during this period (Seip 1992b) and wolf predation on calves was reported to be low in June (Seip 1992a). It appears that without significant elevational overlap, wolves caused a dramatic decline in the caribou population at Quesnel Lake as 80% (8/10) of the wolf predation occurred at elevations below the median elevations of radio-collared caribou (see chapter 2).

My results suggest that elevational separation is inadequate in explaining the large variation in mountain caribou deaths attributed to wolf predation in the highland and mountainous study areas examined (see chapter 2). Differences in wolf densities (Bergerud and Elliot 1986) and the relative densities of moose and caribou (Cumming et al. 1996; Seip and Cichowski 1996) may be the primary factors influencing the susceptibility of mountain caribou to wolf predation within highland and mountainous areas in any given season (see chapter 2). It would be useful if future studies were conducted in both highland and mountainous areas to examine how different mountain caribou, moose and wolf densities influence the elevational relationships of these species. Additionally, where elevational separation between caribou and wolves does not occur, the geographic locations of caribou and wolves should be compared to determine if any spatial

separation exists. These studies should also be of longer duration than those conducted thus far in order to ascertain the seasonal and annual variability within mountain caribou, wolf and moose spatial interactions.

CHAPTER 4

THE SEASONAL DIETARY IMPORTANCE OF MOOSE TO WOLVES IN THE COLUMBIA MOUNTAINS

INTRODUCTION

Early this century, the distribution and abundance of moose increased rapidly in parts of British Columbia (Edwards 1954; Hatter 1949; Spalding 1990). This was possibly due to the clearing and burning of forests for land settlement and railway development (Hatter 1949). Bergerud (1974) and Bergerud and Elliot (1986) suggested that the increased availability of moose stimulated an increase in wolves that also preyed upon and reduced or eliminated caribou populations lacking an adequate antipredator strategy. With an ample alternate ungulate prey source available, a decrease in caribou would not necessitate reduced wolf numbers (Bergerud 1988b; Seip 1992b). Wolves in the Quesnel Lake area were reported to be sustained primarily by moose (Seip 1992b); however, studies of the importance of moose in wolf diet in other areas of mountain caribou range are scarce. The objective of this chapter is to test the hypothesis that wolves in mountain caribou range are sustained primarily by moose throughout the year.

METHODS

The seasonal importance of moose for two packs of radio-collared wolves in the Columbia Mountains was estimated from 79 wolf scats collected between December 1993 and November 1995. Scats were classified as either summer (May 1 -Nov 7) or winter (Nov 8 - Apr 30). In summer, scats were collected at den and rendezvous sites, and also monthly along an extensive network of logging roads. During winter, scats were collected at kill/scavenge sites, along roads, and while backtracking wolves in snow. Logging roads in the study area were checked just after snowmelt in the spring for winter-deposited scats (Forbes and Theberge 1992). Since coyotes

(*Canis latrans*) inhabited this study area, only scats > 30 mm in diameter (Weaver and Fritts 1979) or smaller scats associated with a wolf den, rendezvous site or wolf tracks were collected (Fuller and Keith 1980).

Hair from scats was identified to species using the methods of Adorjan and Kolenosky (1969), Kennedy and Carbyn (1981), and Spilborghs (1996). White-tailed and mule deer hair could not be separated. Frequently, multiple scats collected at the same kill or rendezvous site contain hair from the same kill and are not independent samples (Huggard 1991). In an attempt to minimize this bias, the effective sample size for these sites was taken as the number of prey species represented in the scats. The regression equation proposed by Weaver (1993) was used to estimate the relative weight of each prey species consumed by wolves, based on the frequency of occurrence of each prey species in scats. Paired t-tests (SYSTAT 1992) were used to determine whether moose was the primary diet item of wolves in each season. In testing the wolf diet hypothesis statistically, "primary diet item" was defined as being >50% of the biomass consumed by wolves. Levels of significance were set at $p < 0.05$.

RESULTS

Frequency of occurrence of wolf diet items

Moose occurred approximately twice as often in winter scats (50%) than in summer scats (22.0%), whereas the frequency of caribou remains in wolf scats differed little between summer and winter seasons, with each containing 14.0% and 18.2% respectively (Table 8). Deer remains were found only in winter wolf scats and then, occurred infrequently (6.8%). Beaver, a common food item of wolves in the Columbia Mountains in the summer, comprised 42.0% of the total diet. Although several other species were found in both summer and winter wolf scats, each occurred infrequently (Table 8).

Table 8. Frequency of occurrence and percent biomass of wolf diet items by season in the Columbia Mountains.

Wolf diet items	Summer		Winter	
	Frequency of occurrence	% Biomass	Frequency of occurrence	% Biomass
Caribou	7	18.9	8	12.7
Moose (adult)	7	42.0	22	77.5
Moose (calf)	4	5.7	-	-
Deer	-	-	3	3.4
Beaver	21	21.8	-	-
Other*	11	11.6	11	6.4
No. of scats	44		35	
No. of items	50		44	

Note: Percent biomass is based on the regression equation: $y = 0.439 + 0.008x$, where x is animal mass (Weaver 1993). Animal masses used were as follows: caribou, 124.7 kg (based on a ratio of 22 bulls : 78 cows : 21 calves (McLellan et al 1994b) and D.C. Thomas, unpublished data); adult moose, 343.4 kg (J. Woods, Banff NP unpublished data); moose calf in July, 40.0 kg (Banfield 1974); adult deer (mule and white-tailed combined), 74.2 kg (J. Woods, Banff NP unpublished data); beaver, 14.0 kg (Leege & Williams 1967).
*Includes wolf, hoary marmot, red-backed vole, red squirrel, grouse, snowshoe hare, abattoir scraps, and deer mouse.

Percent biomass of wolf diet items

During winter, wolves in the Columbia Mountains were sustained primarily by moose (t-test = 4.12, df = 34, $p < 0.001$), with moose clearly the most important species (77.5%; Table 8). All five wolf kills found while backtracking wolves during the winter of 1994-95 were moose, confirming this result. Caribou, the second most prominent diet item, contributed 12.7% of the biomass consumed by wolves. Deer, the only other ungulate found in winter scats, constituted a mere 3.4% of wolf diet during this season.

Wolves in the Columbia Mountains were not sustained primarily by moose in the summer (t-test = -0.25, df = 43, $p = 0.403$), yet moose was still the most important species in the summer diet. Three prey items accounted for 88.4% of the biomass consumed. In order of importance these were: moose (47.7%; 42% adult, 5.7% calves), beaver (21.8%) and caribou (18.9%).

DISCUSSION

Bergerud (1974) and Bergerud and Elliot (1986) suggested that in areas with both moose and caribou, wolves would prey primarily on moose. The estimate of winter wolf diet items in the Columbia Mountains supported this hypothesis, but the estimate of summer wolf diet items did not. Still, moose was the main diet item of Columbia Mountains wolves throughout the year and as reported at Quesnel Lake (Seip 1992b), moose were clearly of greater dietary importance to wolves than caribou. Unfortunately, moose census data corrected for sightability were not available for the Columbia Mountains, so testing whether wolves used moose and caribou equal to their availability was not possible. Uncorrected moose census data did indicate that moose were common in the Columbia Mountains during the study (J. Krebs, personal communication).

Wolves in the Columbia Mountains relied to a greater extent on beaver during the summer, and less on moose than wolves in the Quesnel Lake area (Seip 1992b). Differences in the relative availability of beaver (Theberge et al 1978) in the two areas may explain this variation, as wolves often prey heavily on beaver when available (Peterson 1977; Potvin et al. 1992; Voigt et al. 1976). It is also possible that the high occurrence of beaver in the sample of summer wolf scats is an artifact of collecting a disproportionate number (95%) of wolf scats at lower elevations during this season.

During summer, radio-collared wolves in the Columbia Mountains were located 25% of the time in roadless, high-elevation areas, and often these areas were not visited as the probability of finding wolf scats at or near the bi-monthly relocation site of a radio-collared wolf was low. Assuming wolves consumed diet items at elevations proportionally equal to those of their relocations, and that scats would be left in proximity to kill or scavenge sites (Huggard 1991), the summer wolf scat sample may have been biased towards lower elevation prey species (i.e., beaver), and against higher elevation prey species (i.e., caribou and hoary marmots). Therefore,

caution should be used when interpreting the estimates of wolf summer diet in the Columbia Mountains.

This estimate of wolf diet in the Columbia Mountains and the Quesnel Lake wolf diet estimate (Seip 1992b) support the view that wolves inhabiting mountain caribou range are largely sustained by moose. Both studies, however, lack sufficient data to test for annual and pack level variations in wolf diet across a range of moose and caribou densities. Future mountain caribou studies in which wolves are also radio-collared, should seek to address this inadequacy.

CHAPTER 5

GENERAL CONCLUSION AND MANAGEMENT RECOMMENDATIONS

Wolves were suggested to be the primary factor limiting mountain caribou although they were sustained largely by moose (Bergerud and Elliot 1986; Seip 1992a). Mountain caribou in areas of highland topography were suggested to be most susceptible to wolf predation as, unlike those in more rugged mountains, they had less ability to space away from wolves and moose (Seip 1992a).

The importance of moose in the seasonal diet of wolves was one element of the spatial separation model (Seip 1992a) investigated. Wolf scat contents from the Columbia Mountains supported the hypothesis that wolves in mountain caribou range are sustained primarily by moose. This was particularly evident during winter when few alternate prey species were available to wolves. Similar to wolves at Quesnel Lake (Seip 1992b), mountain caribou were a minor part of Columbia Mountains wolf diet. Since moose appear to be the main prey of wolves in southern B.C. and wolf abundance may be strongly associated with the density of moose, attempts should be made to maintain moose densities at their present levels, particularly in highland areas.

The importance of wolf predation as a mountain caribou mortality factor was another element of Seip's (1992a) model that was examined. The caribou mortality data indicated that wolf predation on mountain caribou was higher at Quesnel Lake than in the Columbia Mountains, supporting the hypothesis that wolf predation on mountain caribou is greater in highland areas than in mountainous areas. There was no evidence though indicating that caribou in highland areas continually experience high levels of wolf predation. Possibly wolves prey on mountain caribou in a density-dependent manner (Seip and Cichowski 1996). Mountain caribou in rugged mountains experience limited wolf predation while avalanches, bear, wolverine, and cougar

predation appear as more common mortality factors.

Acquiring a more comprehensive understanding of the importance of wolf predation on mountain caribou populations in both highland and mountainous areas will require more caribou mortality data than are presently available. Radio-collaring more caribou in and of itself, will not necessarily increase the sample size of caribou deaths with known causes. Increasing the frequency of successive relocation flights (Heisey and Fuller 1985) and reducing response times to caribou mortality sites should help in differentiating among possible mortality factors, lessen the number of caribou deaths of unknown cause and increase sample sizes required to further test the wolf predation hypothesis.

The remaining element of the spatial separation model (Seip 1992a) investigated was the degree of elevational separation between wolves and moose, and wolves and mountain caribou in highland and mountainous areas. The radio-telemetry data supported the hypothesis that wolves show more elevational overlap with moose than with mountain caribou. No support, however, was demonstrated for the hypothesis that mountain caribou in highland areas show less elevational separation from wolves than did caribou in rugged mountains. Differences in wolf density (Bergerud and Elliot 1986) and the relative densities of moose and caribou (Cumming et al. 1996; Seip and Cichowski 1996) may explain the large variation in the number of mountain caribou mortalities attributed to wolf predation in the highland and mountainous study areas examined to date.

Although the wolf/caribou radio-telemetry data used in this thesis incorporates all the current spatial data simultaneously collected on these species, it explains the elevational relationships of wolves and caribou within a relatively short period of time. To determine the annual and seasonal variation in the elevational interactions of mountain caribou, wolves, and moose it is recommended that future studies addressing this issue be of longer duration. Further, to fully test

the spatial separation model (Seip 1992a), the elevational and geographic distributions of mountain caribou, wolves and moose should both be examined. Additionally, the degree to which habitat alteration (timber harvesting and fires) influences wolf, mountain caribou, and moose densities and ultimately, their interactions is still largely unknown. Research directed towards understanding how wolves and their prey respond numerically and spatially to different landscape changes in both highland and rugged mountainous areas should be a primary component of future wolf/caribou/moose radio-telemetry studies.

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