

MECHANISMS UNDERLYING THE DECLINE OF MOUNTAIN CARIBOU
(*RANGIFER TARANDUS CARIBOU*) IN BRITISH COLUMBIA

by

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Diplom-Biologe, University of the Saarland, Saarbrücken, 1998

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE STUDIES
(Department of Animal Science)

We accept this thesis as conforming
to the required standard

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THE UNIVERSITY OF BRITISH COLUMBIA

March 2004

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ABSTRACT

The distribution and abundance of mountain caribou (*Rangifer tarandus caribou*) in British Columbia has declined. High predation rates as a consequence of forest management and associated changes to the relative abundances of alternate ungulate prey species have been proposed to cause the population declines. A direct link between changes in the forest age structure and declining caribou population trends, however, is lacking. Understanding the underlying mechanism of the population decline is necessary to develop recovery strategies aimed at maintaining a viable mountain caribou population.

I synthesized demographic and radiotelemetry data from separate studies initiated over the entire distribution of mountain caribou between 1984 and 2002. My primary goal was to use a comparative approach among identified subpopulations to distinguish between three potential repercussions of forest management (food regulation, predation-sensitive foraging, and predation) that might explain the observed declining population trends. I used information on caribou density per area of forests >140 years within subpopulation ranges and cause of mortality to differentiate between the potential repercussions. Predation was the primary cause of caribou mortality over the entire distribution of mountain caribou. In addition, I found increasingly negative rates of increase as caribou density per area of forests >140 years declined (i.e. inverse density dependence). Both results were consistent with the hypothesis that the decline of mountain caribou is caused by high predation rates.

I then quantified the influence of demographic parameters on subpopulation trends and identified environmental factors correlated with variation in these demographic parameters among subpopulations. My results indicated that differences in subpopulation trends were best explained by differences in female adult survival rates.

Female adult survival rates were negatively associated with increasing amounts of young forest stands and thus high proportions of suitable habitat for alternate prey species. Thus, my data supports the mechanistic link between the amount of habitat characteristics suitable for alternate ungulates and decreased survival of adult female caribou.

Finally, I carried out a population viability analysis for mountain caribou. My results indicate that mountain caribou are likely declining to extinction over the majority of their distribution within <100 years.

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ACKNOWLEDGEMENTS

I would like to thank my supervisor tandem of Bruce McLellan (research) and David Shackleton (academic). Both gave me an incredible opportunity by accepting me as their student. Working with Bruce was a great challenge. He always found ways to improve my writing and constantly reminded me that many of my results just confirmed what he knew since long ago, and I would have known if I had spent more time doing fieldwork. Thus he taught me how important it is to get away from my computer back into the field and simply observe my study animals. His ability to ask the right questions and come up with ways to design field studies that allow us to answer these questions were matched only by his enthusiasm for this project. I don't think he knows how much I enjoyed catching Grizzlies in the Flatheads with him. David supported me in every way possible. His door was always open (especially when I didn't want to talk about my research) and I will truly miss a great hiking partner. Throughout this thesis, my supervisory committee provided help whenever I asked for it. Tony Sinclair was especially helpful in organizing my thoughts and straightening my logic. Peter Arcese gave me my first introduction to viability modelling.

For this project, I was able to bring together a truly amazing data set for an endangered species. One of the best experiences of my PhD was how everybody whom I asked was willing to share their data because all were interested in the conservation of mountain caribou. Dale Seip, Jim Young, Trevor Kinley, Dennis Hamilton, and Glen Watts never hesitated to give me access to their data sets. Thanks also to Ian Hatter who always wanted me to present my findings at meetings of the Mountain Caribou Technical Advisory Committee. Kelsey Furk, Nicola Freeman, and Janis Hooge helped me when I was completely lost and confused with how many different approaches there were to store data in digital databases.

I thank Rob Ahrens and Bob Lessard for their discussions and contributions to the viability modelling, Arnold Moy and Yolanta Kulis for helping me with many aspects of working with a Geographical Information System, and Clayton Apps and Chris Johnson for sharing digital forest cover maps. Fred Hovey provided many helpful suggestions (and scripts!) for statistical analyses.

Of the many fellow students I met here at UBC I would like to thank Paulo Corti and Justin Brashares. I count myself lucky to have found a good friend like Paulo and appreciate that I can always say anything that comes to my mind. Justin was a friend who not only read very early drafts of unfinished manuscripts, but who also was always willing to discuss ideas on population dynamics and conservation of large mammals, proposed analyses, suffering that accompanies graduate studies, and most appreciated, future career options. I also much appreciated discussions with Liz Gilles, Tim Karels, Jane Reid, Paul Smith, Shawn Taylor, and Scott Wilson.

Of the many people that are important to me, I first want to thank my partner Cassandra Tucker. Cassandra not only keeps my life balanced but also kindly reminds me from time to time that I need to listen to her needs. In doing so, she not only puts up with me but also helps me to become a better person. Finally, I would like to thank my family. Without the support of my parents Udo A. and Frauke Wittmer, I would have never become the independent and curious person I hope to be. Their financial support throughout my studies is much appreciated. Thanks also to my sister Anke, my niece Sophie, and my brother-in-law Bernd. Anke looked after me like only a true older sister does, used her airmiles to get me a ticket to Germany so that I could spend Christmas at home, and who loved to come over and have coffee with me on Granville Island.

DESCRIPTION OF THE AUTHORS' ROLE

This thesis is a synthesis of data collected by multiple individuals. As lead author, I developed the study design, chose appropriate statistical techniques, analyzed and interpreted all data, and was responsible for producing draft manuscripts suitable for peer review. My research supervisor Bruce McLellan was involved from thesis conception to defence, helping me with the development and refinement of research questions and editing thesis chapters. His contributions are recognized through co-authorship of all subsequent publications.

The contributions of the following individuals are recognized through co-authorship of subsequent publications of selected thesis chapters:

Chapter 2 - Population dynamics of the endangered mountain ecotype of woodland caribou (*Rangifer tarandus caribou*) in British Columbia: I recognize the data contributions from Dale Seip, Trevor Kinley, Glen Watts, Dennis Hamilton and Jim Young.

Chapter 3 - The role of predation in the decline and extirpation of woodland caribou populations: Anthony Sinclair contributed to selecting appropriate methods to analyze the data as well as interpreting the results.

Chapter 5 - A population viability analysis for mountain caribou: the effect of inverse density dependence in female adult survival: Robert Ahrens programmed and contributed scripts to perform the Population Viability Analysis.

CHAPTER 1 - THESIS INTRODUCTION

GENERAL OVERVIEW

Human impacts on natural ecosystems have been accelerating rapidly in the past century, affecting habitats and animals inhabiting them. The impacts are often negative, especially for large mammalian herbivores, but an understanding of how human activities impact population dynamics, requires long term studies with marked individuals followed over long periods (Gaillard *et al.* 2000). Without such studies, conservation and management of endangered species and their habitats will likely be ineffective.

Habitat change, through loss or alteration resulting from human activities, is currently the driving force most frequently identified with loss of biodiversity and extinction of species (Caughley 1994, Wilcove *et al.* 1998, Sih *et al.* 2000). Habitat modifications can either directly (i.e. food availability) or indirectly (i.e. changes in species interactions) influence the dynamics of endangered populations. So far, intensive studies demonstrating direct effects of habitat loss or habitat alterations on changes in demographic rates, are rare and limited mainly to avian species (e.g. Franklin *et al.* 2000, Smith & Hellmann 2002). However, there is much empirical evidence indicating population declines of many large herbivores are also related to landscape modification. This has resulted in increasing attention being paid to changes in demographic parameters and associated changes in habitat conditions, along with predator-prey interactions.

Changes in predator-prey interactions can cause the extirpation of a population where prey are secondary to a predator that depends on another primary prey species (Sinclair *et al.* 1998, Courchamp *et al.* 2003). The extirpation is a result of an absence of density dependence in either functional or numerical response of the predator to the low-density secondary prey population. However, most examples refer to cases where a

non-native species was introduced. There is no reason *a priori* why habitat modifications could not also result in similar changes in native predator-prey systems, if the changes in distribution and abundance of a species are a direct consequence of habitat modifications.

The distribution of woodland caribou (*Rangifer tarandus caribou*) has declined across North America (Bergerud 1974). As a result of the range reduction, woodland caribou are now essentially restricted to Canada with the exception of trans-boundary populations in Alaska and northwestern Idaho. Because of continuing declining population trends and increasing population fragmentation, woodland caribou across Canada have become a high priority species for management and conservation (Cumming 1992, Thomas & Gray 2002).

Traditionally the decline of woodland caribou has been attributed to food limitation during winter and/or summer, and adverse climate (Bergerud 1996), but predation is currently considered the proximate limiting factor across most of their distribution (Bergerud & Elliot 1986, Seip 1992, Stuart-Smith *et al.* 1997, Rettie & Messier 1998, Schaefer *et al.* 1999). Predation may be facilitated by forestry and other changes to caribou habitat that favour early seral stage forest (Rettie & Messier 1998). Although early seral stages are not important as foraging habitats for caribou, changes in the forest age structure towards young-age stands are thought to support higher densities of alternate prey species such as moose (*Alces alces*) that in turn support higher predator densities (Bergerud & Elliot 1986, Seip 1992). In addition, linear corridors associated with industrial operations in forested areas may increase the speed and range of predator movements and thus result in increased predation of caribou (James & Stuart-Smith 2000).

Woodland caribou within the Southern Mountain National Ecological Area of Canada are considered 'threatened' by the Committee on the Status of Endangered

Wildlife in Canada (COSEWIC 2002). A sub-group of these, the mountain ecotype (referred to as mountain caribou) found in the interior wet-belt of southeastern British Columbia (Heard & Vagt 1998), are considered 'endangered' in British Columbia and in Idaho where they are the last remaining caribou in the United States outside of Alaska (U.S. Fish & Wildlife Service 1994, British Columbia Conservation Data Centre 2001). The range of mountain caribou in British Columbia has declined by approximately 40% from historical distributions (Spalding 2000) and the population is currently fragmented into 12 local subpopulations (Heard & Vagt 1998).

During winter, arboreal lichen (*Bryoria* spp. & *Alectoria sarmentosa*) dominate the diet of mountain caribou (Rominger & Oldemeyer 1989, Terry *et al.* 2000) because the deep snowpack of generally 2-5 m in the interior wet-belt mountains buries all plants except trees. Mountain caribou have adapted behaviourally to the deep snow conditions by exhibiting seasonal altitudinal migrations. As the snowpack deepens and consolidates later in winter, it provides a platform from which caribou can access arboreal lichen directly in the forest canopy on high elevation late winter ranges. Because arboreal lichens are more abundant in mature forest stands (Rominger *et al.* 1996, Terry *et al.* 2000), mountain caribou are closely associated with late-successional, coniferous forests (Apps *et al.* 2001). Mature forest stands, especially at lower elevation, are also critical to forest companies for timber harvesting and integrating the needs of caribou and forestry is a significant challenge for resource managers in British Columbia (Stevenson *et al.* 2001).

Due to the significant resource conflict, mountain caribou have been studied intensively. Between 1984 and 2002 separate studies on mountain caribou were initiated that covered their entire distribution. Most studies have focused on foraging behaviour (e.g. Rominger *et al.* 2000, Terry *et al.* 2000) and habitat selection (e.g. Apps *et al.* 2001) at various spatial scales, but population dynamics are also documented (e.g. Seip

1992, Kinley & Apps 2001). Prior to my study, data analysis was limited to within local subpopulations.

STUDY OBJECTIVES

My study attempts to address the specific and broad issues of the impacts of habitat alteration and associated changes in predator-prey interactions, on the dynamics of an endangered species. The general goal of this thesis is to explore the hypothesis that forest management leads to woodland caribou declines by upsetting the large mammal predator-prey system, because a direct link between habitat changes, changes in predator-prey systems, and changes in demographic rates of caribou is lacking.

Caughley (1994) proposed the use of hypothetico-deductive methods within an experimental design to distinguish between potential causes of decline. The application of an experimental design to study an endangered species, however, is often impractical and unethical in natural conditions (Courchamp *et al.* 1999). In addition, because of the large areas over which caribou range, experimental work designed to evaluate the impact of long-term environmental changes, such as habitat loss, on population dynamics is logistically and politically challenging.

When I began thesis design and research in summer 1999, I was encouraged by my research supervisor Bruce McLellan to exploit the fact that mountain caribou, an endangered species, had been intensively monitored across their entire distribution. Thus, I adopted a comparative or inter-population approach to take advantage of this natural experiment (*sensu* Sinclair 1991) that provided variation in population trends and densities while encompassing a variety of external factors potentially influencing population dynamics. The primary goals were to synthesize the sampled data of the separate studies conducted over the entire distribution of mountain caribou and use a comparative approach to improve our understanding of the mechanism of decline.

Ultimately, understanding the underlying mechanism of the population decline is necessary to develop recovery strategies aimed at maintaining a viable mountain caribou population.

The specific objectives of this thesis are:

- 1) to identify the population structure, subpopulation trends and demographic rates of mountain caribou in British Columbia;
- 2) to determine the cause of the decline of mountain caribou using an inter-population rather than an intra-population approach;
- 3) to determine the mechanism of decline by quantifying the influence of demographic parameters on subpopulation trends of mountain caribou and testing the importance of extrinsic factors (habitat factors, population density, and snow conditions) on changes in demographic rates; and
- 4) to develop a predictive population model to evaluate the probability of population persistence.

THESIS ORGANISATION

I prepared this thesis as a series of independent, but related chapters (“paper format”) to be submitted for publication in scientific journals. In Chapter 2, I delineate the population structure of mountain caribou in British Columbia and present estimates of subpopulation sizes and trends. The primary objective of this chapter is to provide estimates of demographic rates that are critical in population viability analyses (PVA). In Chapter 3, I distinguish among alternate hypotheses explaining the observed decline in mountain caribou subpopulations. In particular I use the relationship between population density and availability of suitable winter foraging habitat (i.e. forest stands >140 years) to differentiate between predictions of the food regulation, predation-sensitive foraging and the predation (apparent competition) hypotheses. In Chapter 4, I explain the

mechanism of decline. I first evaluate the contribution of demographic parameters to variation in subpopulation rates of increase. I then use survival analyses techniques where I include covariates representing differences in habitat factors, population density, and snow depth to explain variation in this demographic parameter among subpopulations. In Chapter 5, I carry out a population viability analysis and evaluate the impact of changes in adult female survival rates at low population densities on population persistence using a modelling approach. The final chapter is a synthesis of my findings with respect to the conservation of mountain caribou.

STUDY AREA

Mountain caribou are found in southeastern British Columbia and northern Idaho from near the international border at 49° N latitude to northeast of Prince George at about 55° N latitude (Figure 1.1). Their distribution in 1999 encompassed approximately 58500 km² (Stevenson *et al.* 2001) of mostly mountainous terrain, with elevation varying from about 400 m to >3500 m. Northern portions of this range are generally characterized by highland topography with sloping plateaus and rounded mountains. Mountains in more southerly and eastern portions of the distribution are generally higher and more rugged. Although climate varies across their distribution, the influence of Pacific air masses results in high annual precipitation, most of which falls as snow during winter (Environment Canada 2002). The cool, wet climate results in low frequency and extent of natural fire disturbance, and thus forests are naturally dominated by old age classes (Meidinger & Pojar 1991).

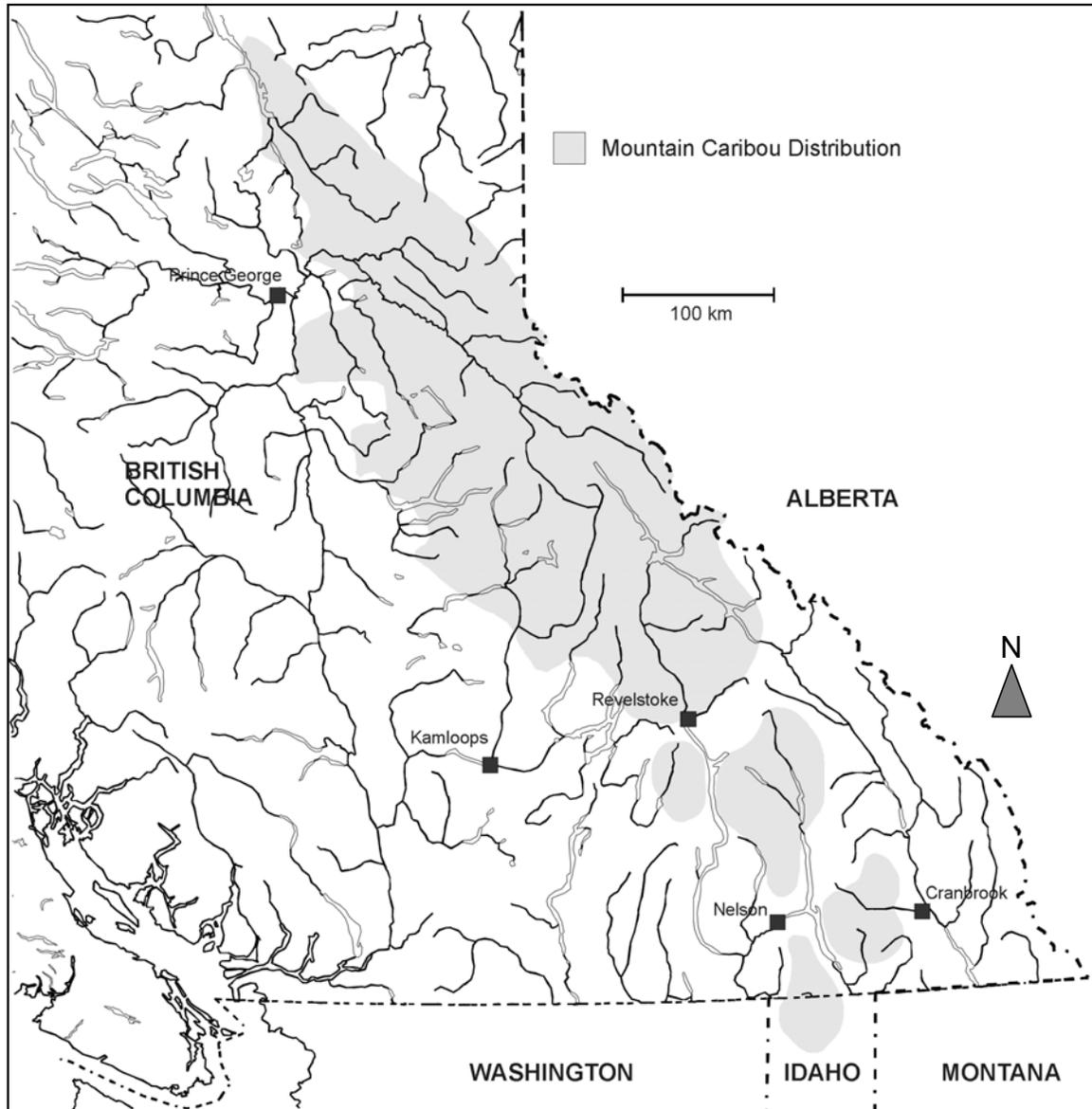


Figure 1.1. Map of the study area with general distribution of mountain caribou in British Columbia and northern Idaho (modified from Apps *et al.* 2001).

Mountain caribou are primarily found in 4 biogeoclimatic zones. In the southern portion of mountain caribou range, lower elevation habitats are within the Interior Cedar-Hemlock (ICH) biogeoclimatic zone (Meidinger & Pojar 1991). Climax ICH forests are dominated by western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*). A moderately developed shrub layer commonly includes black huckleberry

(*Vaccinium membranaceum*) and falsebox (*Pachistima myrsinites*). In the northern portion of mountain caribou range, the ICH is replaced by the Sub-Boreal Spruce (SBS) biogeoclimatic zone. Climax SBS forests are dominated by hybrid white spruce (*Picea glauca x engelmannii*) and subalpine fir (*Abies lasiocarpa*). Common shrubs present are black huckleberry, birch-leafed spirea (*Spirea betulifolia*), falsebox and thimbleberry (*Rubus parviflorus*). At mid elevations, above the ICH and SBS, is the Engelmann Spruce-Subalpine Fir (ESSF) biogeoclimatic zone. Climax ESSF forests are dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir. The shrub layer contains varying amounts of black huckleberry, white-flowered rhododendron (*Rhododendron albiflorum*), black gooseberry (*Ribes lacustre*) and oval-leafed blueberry (*Vaccinium ovalifolium*). High elevations are in the Alpine Tundra (AT) biogeoclimatic zone where trees are absent. Vegetation in the AT consists of a variety of shrubs, grasses, sedges, herbs, bryophytes and lichens that are often widely separated by areas of bare soil, rock, or glaciers. Forestry is the dominant land-use activity across the range of mountain caribou and clear-cutting and replanting is the most common silvicultural system used.

Mountain goats (*Oreamnos americanus*) and moose are found throughout the range of mountain caribou with moose being rarer in southern areas. White-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and elk (*Cervus elaphus*), are abundant in southern areas. Common predators across the distribution of mountain caribou include grizzly bear (*Ursus arctos*), black bear (*U. americanus*), and wolverine (*Gulo gulo*), while wolves (*Canis lupus*) are more abundant in the north and cougar (*Puma concolor*) are more abundant in the south. Mountain caribou are no longer legally hunted, although a limited number of permits were issued to shoot males until the mid 1990s in some areas (Hatter *et al.* 2002).

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CHAPTER 2 - POPULATION DYNAMICS OF THE ENDANGERED MOUNTAIN ECOTYPE OF WOODLAND CARIBOU (*RANGIFER TARANDUS CARIBOU*) IN BRITISH COLUMBIA

INTRODUCTION

The distribution of woodland caribou (*Rangifer tarandus caribou*) has contracted across North America following human settlement (Bergerud 1974), but predation is generally considered the proximate limiting factor across most of their distribution (Bergerud & Elliot 1986, Seip 1992, Bergerud 1996, Stuart-Smith *et al.* 1997, Rettie & Messier 1998, Schaefer *et al.* 1999). Predation may be facilitated by logging and other changes to caribou habitat that favour early seral stage forest (Rettie & Messier 1998). These young forest stands are thought to promote higher densities of alternate prey species such as moose (*Alces alces*) that in turn support higher predator densities (Bergerud & Elliot 1986, Seip 1992). In addition, linear corridors associated with industrial operations in forested areas may increase the speed and range of predator movements and thus result in increased predation on caribou (James & Stuart-Smith 2000). Because of their declining population trends and increasing population fragmentation with the continued spread of managed forests, conservation of woodland caribou has become a significant concern across much of their distribution in Canada (Thomas & Gray 2002).

Woodland caribou within the Southern Mountain National Ecological Area of Canada are considered 'threatened' by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2002). A sub-group of these, the mountain ecotype (referred to as mountain caribou) found in the interior wet-belt of British Columbia (Heard & Vagt 1998), are considered 'endangered' in British Columbia and also in Idaho where they are the last remaining caribou in the United States outside Alaska (U.S. Fish & Wildlife Service 1994, British Columbia Conservation Data Centre 2001). The distribution of mountain caribou in British Columbia has declined over the past century (Seip &

Cichowski 1996, Spalding 2000) to where they are now found in only 12 recognized subpopulations some of which are contiguous while others appear isolated (Heard & Vagt 1998).

Mountain caribou are closely associated with late-successional, coniferous forests (Rominger & Oldemeyer 1989, Apps *et al.* 2001). Their primary winter food, arboreal lichen (*Bryoria* spp. & *Alectoria sarmentosa*), is abundant in these forests (Rominger & Oldemeyer 1989, Rominger *et al.* 1996, Terry *et al.* 2000) and the deep snowpack of generally >2 m in the mountains during winter is sufficient to provide a platform from which they gain access to lichen in the forest canopy. Many of these old forests are highly valuable to the forest industry and thus there is considerable interest in integrating forest management and mountain caribou habitat requirements (Stevenson *et al.* 2001).

The objectives of this study are to objectively delineate the remaining subpopulations of mountain caribou in British Columbia, and to document their size, trend, pregnancy and recruitment rates, together with causes and temporal distribution of adult mortality. The South Selkirks subpopulation along the British Columbia-Idaho border is excluded because of the long history of augmentation of animals into this subpopulation (Compton *et al.* 1995). I have 3 goals in presenting these demographic data. The first is to document the structure and dynamics of an endangered ungulate population to enable a greater understanding of the pattern of population decline, and to provide estimates of demographic rates that are critical in population viability analyses. The second goal is to present long-term data on the population dynamics of a large herbivore based on an extensive sample of marked individuals in an ecosystem with a full complement of 5 natural predators because such data are particularly scarce (Gaillard *et al.* 2000). Finally, presenting data on the population distribution and

dynamics of an endangered herbivore should enable managers to focus attention where it is most immediately needed to preserve this ecotype of caribou.

METHODS

ANIMAL CAPTURE & TELEMETRY

Between 1984 and 2002, 353 adult caribou (305 f, 48 m) were captured using a net-gun fired from a helicopter in open subalpine habitat during late winter (Table 2.1). A high proportion of the population is visible and available for capture at this time of the year and thus animals were collared in a geographic distribution that approximated the distribution of mountain caribou in British Columbia. All captured caribou were fitted either with mortality-motion sensitive very high frequency (VHF) conventional radiocollars or Global Positioning System (GPS) collars with VHF signals and mortality-motion sensors.

Telemetry relocations were recorded from fixed-wing aircraft 2-4 times each month. Locations were plotted on aerial photographs or topographic maps and the Universal Transverse Mercator (UTM) co-ordinates of each animal were recorded to the nearest 100 m. When the technology became available, a GPS in the aircraft was also used to place located animals. GPS collars were programmed to attempt a fix every 4-6 hours. The number of fixes obtained per caribou differed between the 2 types of telemetry collars. I therefore extracted a random sub-sample of GPS fixes at biweekly intervals to match VHF standards for my analysis.

SUBPOPULATION DELINEATION

I used the telemetry data to examine subpopulation boundaries and estimate the area occupied by each subpopulation following methods of Rettie & Messier (1998). Multi-annual, 100% minimum convex polygon (MCP) (Mohr 1947) home ranges, or the maximum area that individuals were known to cover, were delineated using the animal

Table 2.1. Mountain caribou population structure in British Columbia, Canada, in 2002 excluding the South Selkirks subpopulation; population delineation based on radiotelemetry data with dates of radiotelemetry studies, population range sizes^a, number of radiocollared caribou, number of radiolocations, and number of years caribou were monitored in each subpopulation.

Subpopulation	Date	Area (km ²)	Animal Sample (Females/Males)	Locations (Females/Males)	Caribou Years (Females/Males)	Years AVG±SD Females/Males
Purcells-South	03/94-02/99	771	27 (14/13)	947 (469/478)	37.65 (19.25/18.40)	1.38±1.80/1.42±1.22
Purcells-Central	03/94-02/99	373	9 (5/4)	405 (324/81)	15.47 (11.24/4.23)	2.25±1.93/1.06±0.70
Nakusp	03/95-01/01	2340	34 (25/9)	1605 (1185/420)	91.13 (65.95/25.18)	2.64±1.53/2.80±2.38
Duncan	02/92-07/01	447	5 (4/1)	311 (191/120)	18.17 (11.53/6.64)	2.88±2.55/-
Monashee-South	03/02-09/02	74	1 (1/0)	9 (9/0)	0.47 (0.47/0)	-
Columbia-South	02/92-11/02	1761	20 (17/3)	2034 (1935/99)	85.23 (81.27/3.96)	4.78±2.76/1.32±0.27
Frisby-Boulder	01/94-11/02	613	9 (9/0)	491 (491/0)	20.44 (20.44/0)	2.27±1.09/-
Columbia-North	03/92-11/02	4526	48 (41/7)	2347 (1800/547)	109.56 (85.28/24.28)	2.08±1.78/3.47±1.83
Kinbasket-South	02/92-05/99	759	5 (3/2)	568 (371/197)	25.92 (16.98/8.94)	5.66±2.99/4.47±3.19
Groundhog	04/96-11/02	1277	8 (8/0)	275 (275/0)	18.36 (18.36/0)	2.30±1.59/-
Wells Gray	01/84-03/89	8141	63 (63/0)	3165 (3165/0)	134.93 (134.93/0)	2.14±1.29/-
	02/93-11/02		73 (71/2)	3666 (3648/18)	221.56 (218.12/3.44)	3.07±2.33/1.72±1.07
Allan Creek	03/01-11/02	241	3 (3/0)	55 (55/0)	3.35 (3.35/0)	1.12±0.56/-
Barkerville	02/93-11/02	742	12 (12/0)	860 (860/0)	37.75 (37.75/0)	3.15±1.95/-
North Cariboo Mtn.	03/88-03/92	1779	10 (8/2)	363 (293/70)	35.81 (27.87/7.94)	3.48±0.90/3.97±0.00
George Mtn.	03/88-03/92	199	2 (1/1)	74 (43/31)	6.44 (3.95/2.49)	-
Narrow Lake	03/88-03/92	424	2 (2/0)	85 (85/0)	7.14 (7.14/0)	3.57±0.55/-
Hart Ranges	03/88-03/92	3890	22 (18/4)	668 (607/61)	64.19 (56.02/8.17)	3.11±1.12/2.04±1.30
Total	01/84-11/02	28357^b	353 (305/48)	17928 (15806/2122)	933.57 (819.90/113.67)	2.87±1.16/2.47±1.25

^a estimated from telemetry data using 95% fixed kernel utilization distributions

^b total area occupied by mountain caribou = 29749 km² (including South Selkirks = 1392 km²; Stevenson *et al.* 2001)

movement extension (Hooge & Eichenlaub 2000) in Arcview (ESRI 1996). I plotted the MCP home ranges of all collared animals and placed individuals into a specific subpopulation when its MCP range overlapped at least 1 other member of the subpopulation. Subpopulations were separated where no MCP home ranges of collared animals occurred, although it is possible that some animals moved among subpopulations. I then pooled telemetry locations among animals within each subpopulation and delineated their boundaries and area using a 95% fixed kernel approach (Worton 1989).

SUBPOPULATION SIZES & TREND

Between 1992 and 2002, caribou subpopulations were censused at irregular intervals in March or early April when caribou are in open, high elevation habitats, shortly after new snow fell, using Bell 206 helicopters. In mountainous terrain, a pilot and 2-3 observers flew contours along the forest-subalpine habitat boundary, whereas in plateau habitats the numerous forest openings were searched for caribou tracks. Fresh tracks were followed until the animals were sighted, unless the tracks descended into mature timber and were lost from view. Radiocollars were used as marks and not to locate animals. Caribou were classified as adult males, adult females, or calves. In forested areas where close examination was not always possible, antlered females were sometimes difficult to distinguish from young males and classification was often limited to adults and calves only. When available, the location of the sighting was recorded using a GPS in the helicopter as well as recording them on topographic maps. Survey areas and boundaries were slightly adjusted based on changes in observed animal distribution.

Population estimates and 95% confidence intervals were derived using the joint hypergeometric maximum likelihood estimator (JHE) (Bartmann *et al.* 1987) using the NOREMARK computer program (White 1996). In cases where the lower 95% confidence limit was below the actual number of caribou seen during census flights, I used the

census result as the lower confidence limit. If no radiocollared caribou were present in a subpopulation, a sightability factor based on the long-term average for that area was applied to estimate population size. I then calculated the finite rate of population increase, lambda (λ), adjusted to a yearly time interval as

$$\lambda = (N_t/N_0)^{1/t} \quad (1)$$

where N_t is the number of caribou in year t , N_0 is the number of caribou in the initial year, and t is the number of years between N_0 and N_t (Caughley 1977).

PREGNANCY RATES & RECRUITMENT

Over a portion of the whole sampling period, blood samples were collected during capture from 134 adult female caribou over different years and subpopulations.

Pregnancy rates were estimated as the proportion of females >2.5 years with serum progesterone levels consistent with pregnancy (Rehbinder *et al.* 1981). I used log-likelihood ratios (Zar 1999) to determine if pregnancy rates differed among populations. I estimated calf recruitment in each population from the proportion of calves counted during aerial censuses in late March when calves were \approx 10 months of age. I consider the proportion of calves in March to be true measures of recruitment, because animals of that age likely experience similar mortality rates as older animals (Bergerud 1980, Fuller & Keith 1981). I used log-likelihood ratios to determine if average recruitment rates differed among subpopulations.

CAUSE OF MORTALITY

When the signal from a motion-sensitive radiocollar indicated that a caribou was dead, the site was investigated as soon as possible. The cause of mortality was determined from evidence found at the site and, when possible, from a necropsy that included a measure of bone marrow, visceral, and rump fat deposits. Predation was suggested when there was evidence of bleeding, a struggle, or bite injuries. These cases were usually clear when there was snow on the ground, but less so during the summer. Cases

of predation were then divided into wolf (*Canis lupus*), bear (*Ursus spp.*), cougar (*Puma concolor*), wolverine (*Gulo gulo*) or unknown predator, based on tracks, scats, hair and distribution and nature of the carcass. Non-predation deaths were divided into accidents (i.e. avalanches, birthing, falls), malnutrition, human caused or unknown. In many cases it was difficult to determine the cause of death and I conservatively classified the mortality cause as unknown.

Summer (June 11 to October 21), early winter (October 22 to January 11), late winter (January 12 to April 23), and spring (April 24 to May 20) seasons, into which mortalities were grouped, were based on average dates of elevational movements of caribou in the Columbia Mountains where these movements are more distinctive than in other areas (Apps *et al.* 2001). The calving season was when radiocollared female caribou in the Columbia Mountains were first (May 21) and last (June 10) observed with newborn calves. I tested for seasonal differences in probability of dying adjusted for season length for all natural mortality causes (i.e. excluding human caused mortalities) and predator caused mortalities only using log-likelihood ratios.

ADULT SURVIVAL

I used the staggered entry Kaplan-Meier procedure (Pollock *et al.* 1989) to calculate yearly survival rates of radiocollared adults. I based the survival intervals on the biweekly monitoring interval and began calculations at the beginning of the calving season. I tested for differences in average multiyear survival rates among subpopulations using a one-way ANOVA (Zar 1999). Subpopulations were included in the analysis when ≥ 4 individuals per year were monitored during at least 3 complete years.

STATISTICAL ANALYSES

I used an $\alpha=0.05$ for all statistical analyses. Statistical analyses were performed using

SAS (SAS Institute Inc. 1995) and SYSTAT (SYSTAT Software Inc. 2002). Unless otherwise noted, means are reported $\pm 1SE$ of the mean.

RESULTS

SUBPOPULATION DELINEATION

Based on MCP home ranges of all collared caribou I was able to identify 17 subpopulations of mountain caribou in British Columbia (excluding the South Selkirks subpopulation). The apparent population fragmentation is most pronounced towards the southern limit of mountain caribou distribution in British Columbia (Figure 2.1). Using the fixed kernel estimator, subpopulation ranges varied in size from 74 km² for the Monashee subpopulation to 8141 km² for the Wells Gray subpopulation. All 17 subpopulations combined covered 28357 km² (Table 2.1).

SUBPOPULATION SIZES & TREND

Average sightability of mountain caribou during all censuses between 1992 and 2002 was 84.57%. However, during censuses used to estimate the overall trend, 103 of 128 collared animals were observed corresponding to an average sightability of 80.47%. During 2002, all subpopulations were censused and resulted in an estimate of 1809 mountain caribou (Table 2.2). Before 2002, the entire population was never censused simultaneously, however, the average λ for each subpopulation weighted by the earlier subpopulation estimate results in an overall average λ of 0.96. Trends in individual subpopulations varied, with more southern ones generally decreasing more rapidly than northern subpopulations of which some were relatively stable (Table 2.2). In 2002, 9 of 17 subpopulations consisted of an estimated ≤ 20 individuals and 3 of ≤ 6 individuals.

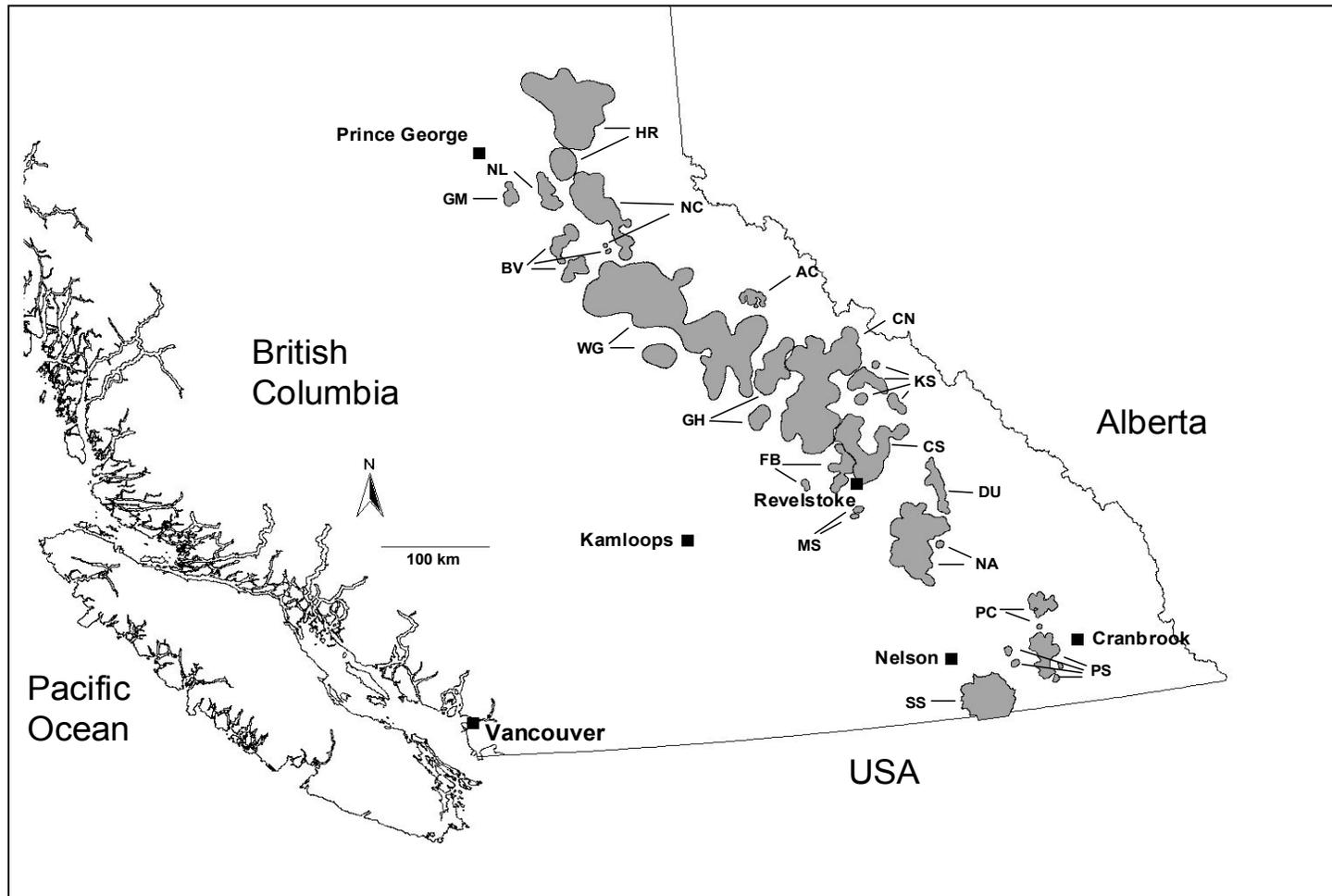


Figure 2.1. Population delineation and current distribution of identified subpopulations of mountain caribou in British Columbia: South Selkirks (SS), Purcells-South (PS), Purcells-Central (PC), Nakusp (NA), Duncan (DU), Monashee-South (MS), Columbia-South (CS), Frisby-Boulder (FB), Columbia-North (CN), Kinbasket-South (KS), Groundhog (GH), Wells Gray (WG), Allan Creek (AC), Barkerville (BV), North Cariboo Mountain (NC), George Mountain (GM), Narrow Lake (NL), Hart Ranges (HR).

Table 2.2. 2002 census results, JHE^a population estimates with 95% confidence intervals, and population trends of mountain caribou subpopulations in British Columbia, Canada, based on late winter population censuses.

Subpopulation	2002 Census Data			Previous Census Data			Lambda
	Census	Collars obs/total	Estimate (95% CI) ^b	Census (Year)	Collars obs/total	Estimate (95% CI)	
Purcells-South	14	0/0	17	63 (1995)	7/7	63	0.83
Purcells-Central	5	0/0	6	15 (1995)	3/3	15	0.88
Nakusp	75	6/9	108 (75-147)	158 (1996)	10/11	173 (158-200)	0.92 (0.88-0.95)
Duncan	17	0/0	20	49 (1996)	2/2	49	0.86
Monashee-South	4	1/1	4	10 (1994)	0/0	12	0.87
Columbia-South	29	2/3	39 (29-58)	105 (1994)	11/12	114 (105-130)	0.87 (0.85-0.90)
Frisby-Boulder	20	5/5	20	27 (1996)	3/4	34 (27-47)	0.92 (0.87-0.95)
Columbia-North	131	6/9	188 (131-257)	203 (1997)	13/15	232 (203-272)	0.96 (0.92-0.99)
Kinbasket-South	12	0/0	14	17 (1997)	5/5	17	0.96
Groundhog	15	2/2	15	37 (1995)	0/0	44	0.86
Wells Gray	225	5/13	526 (235-818)	593 (1995)	16/17	628 (593-695)	0.98 (0.88-1.02)
Allan Creek	5	0/2	17 (5-36)	N/A	N/A	N/A	N/A
Barkerville	41	4/6	58 (41-81)	39 (1994)	2/2	39	1.05 (1.00-1.10)
North Cariboo Mtn.	236	0/0	279	232 (1993)	0/0	274	1.00
George Mtn.	3	0/0	4	20 (1992)	0/0	25	0.83
Narrow Lake	61	0/0	72	67 (1999)	0/0	79	0.97
Hart Ranges	275/357 ^c	0/0	325/422 ^c	313 (1992)	0/0	370	0.99
Total			1809^d			2167	0.96

^a JHE = Joint Hypergeometric Estimator in NOREMARK

^b population estimates in absence of marked animals corrected by multiyear average sightability factor = 84.57%

^c 82 additional caribou counted outside traditional census area

^d total number of mountain caribou in 2002 = 1843 animals (including 34 animals from South Selkirks subpopulation (W. Wakkinen, Idaho Department of Fish & Game, pers. communication))

PREGNANCY RATES & RECRUITMENT

Pregnancy rates were determined from 134 adult female caribou in 8 subpopulations over 11 different years (Table 2.3). Plasma progesterone levels indicated that 123 of the 134 were pregnant. There were no apparent trends in pregnancy rates among years within subpopulations. I did not detect differences in pregnancy rates among subpopulations when data were pooled over years ($G=2.921$, $df=7$, $P=0.892$). The overall pregnancy rate of mountain caribou was $92.4\% \pm 2.24$.

Observed percentages of calves in March in the 17 subpopulations during the 2002 census varied between 0 and 25% (Table 2.4) with a mean of $12.79\% \pm 1.85$. I did not detect differences in recruitment rates among subpopulations in 2002 ($G=18.427$, $df=16$, $P=0.299$). Long-term averages of the percentage of calves in March varied between 0 and 20.78% with a mean of $11.21\% \pm 1.39$. The coefficient of variation of the observed percentage of calves at ≈ 10 months of age varied from 0 to 244.95 (Mean= 48.75 ± 16.15) within subpopulations.

CAUSE OF MORTALITY

Between 1984 and 2002, 155 mortalities of radiocollared caribou were recorded in 15 of the 17 subpopulations. Six deaths (3 f/3 m) were human caused, including 2 vehicle accidents, 2 research related mortalities, and 2 caribou that were illegally shot. Of the 149 natural mortalities, I could confidently categorise 88 into either predation, malnutrition, and accidents, while 61 remained unknown. Of the 88 deaths with a known cause, 82 were females. Fifty-four (66%) of these were killed by predators, 19 (23%) died of accidents, while 9 (11%) deaths were due to malnutrition. Four (67%) of the 6 known causes of death of males were by predators, 1 (16.5%) was an accident, and 1 (16.5%) was due to malnutrition. Causes of death data were pooled over sexes because the ranks of mortality causes were the same.

Table 2.3. Pregnancy rates (animal sample) of 134 adult female mountain caribou (>2.5 years) in British Columbia between 1984-1997, determined from serum progesterone levels.

Year	Purcells-South	Purcells-Central	Duncan	Columbia-South	Columbia-North	Kinbasket-South	Wells Gray	Barkerville
1984							1.00 (12/12)	
1985							1.00 (6/6)	
1986							0.89 (24/27)	
1987							1.00 (4/4)	
1988							1.00 (1/1)	
1992			1.00 (2/2)	0.88 (7/8)	1.00 (2/2)	1.00 (2/2)		
1993				1.00 (3/3)	0.88 (7/8)		0.86 (12/14)	1.00 (3/3)
1994	1.00 (4/4)	1.00 (3/3)					1.00 (4/4)	
1995							1.00 (4/4)	
1996							1.00 (5/5)	1.00 (1/1)
1997	0.75 (3/4)	0.67 (2/3)			0.75 (3/4)	1.00 (1/1)	1.00 (6/6)	0.67 (2/3)
AVG±SE	0.88±0.13	0.84±0.17	1.00±0	0.94±0.06	0.88±0.07	1.00±0	0.98±0.02	0.89±0.11

Table 2.4. Percentage of calves observed during late winter population censuses of mountain caribou subpopulations, British Columbia.

Subpopulation	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	AVG±SE	CV*
Purcells-South				1.59	0	10.71	0		7.69		14.29	5.71±2.48	106.39
Purcells-Central				0	7.69	0	0		0		0	1.28±1.28	244.95
Nakusp					10.13	6.70		7.89			16.00	10.18±2.07	40.58
Duncan					12.24	14.29		7.69			23.53	14.44±3.33	46.11
Monashee-South			30.00								0	15.00±15.00	141.42
Columbia-South			12.38		11.36	15.05					17.24	14.01±1.33	18.97
Frisby-Boulder					25.93	11.43					25.00	20.78±4.69	39.05
Columbia-North						11.82					9.92	10.87±0.95	12.35
Kinbasket-South						5.88					8.33	7.11±1.23	24.38
Groundhog				10.81							13.33	12.07±1.26	14.78
Wells Gray				17.88							15.56	16.72±1.16	9.81
Allan Creek											20.00	N/A	N/A
Barkerville			15.38	8.33	6.67	20.00	11.54	25.00	10.53	25.71	17.07	15.58±2.32	44.64
North Cariboo Mtn.		9.91						10.08			8.90	9.63±0.37	6.63
George Mtn.	0										0	0	0
Narrow Lake								10.45			11.48	10.96±0.51	6.63
Hart Ranges	12.14							10.93			16.81	13.29±1.79	23.35
Total											12.79±1.85	11.21±1.39	

*CV = coefficient of variation

When adjusted for season length, I found differences in the distribution of natural mortality causes among seasons ($G=14.828$, $df=4$, $P<0.01$) with caribou being more likely to die during the calving and summer season (Figure 2.2). Caribou are also more likely to die due to predation during calving and summer than during other seasons ($G=19.303$, $df=4$, $P<0.001$). Due to small samples, I pooled the 17 subpopulations into a northern and southern group with the division at the Groundhog - Columbia-North boundary. I found similar known causes of mortality in each group, however, wolves and bears were the major predators in the north while cougar, bears and wolverine were the major predators in the south (Figure 2.3).

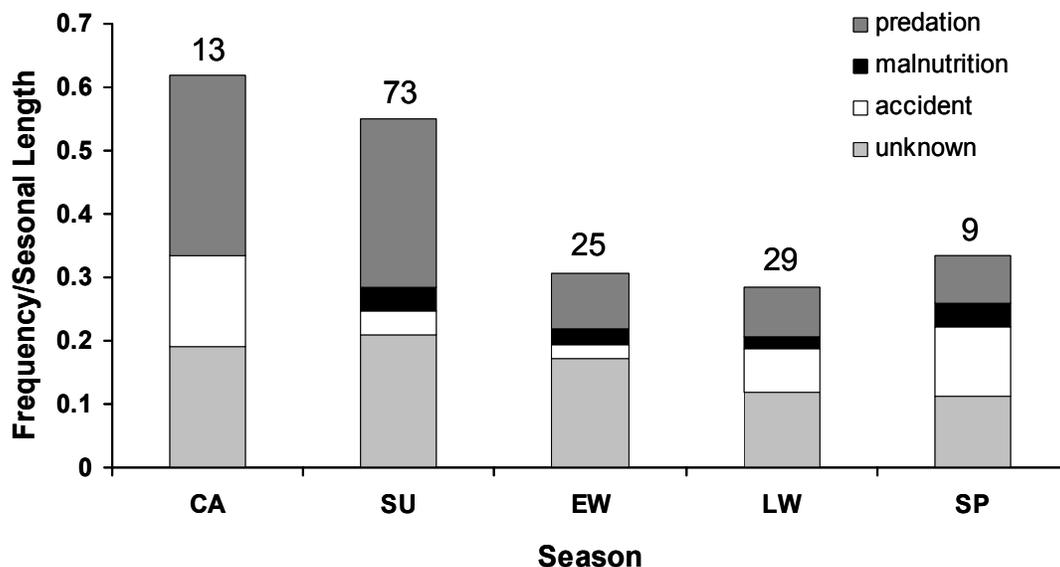


Figure 2.2. Pooled (females/males) proportion of mountain caribou with natural mortality cause dying during calving (CA: May 21 - June 10), summer (SU: June 11 - October 21), early winter (EW: October 22 - January 11), late winter (LW: January 12 - April 23) and spring (SP: April 24 - May 20) in British Columbia, Canada, adjusted for seasonal length (days); labels above the bars indicate total number of mortalities.

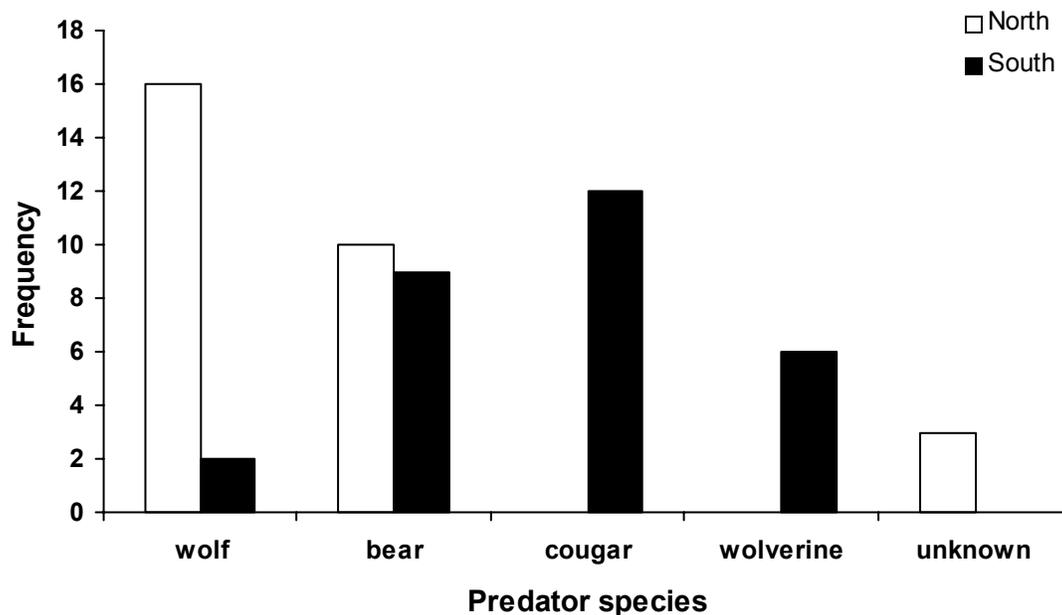


Figure 2.3. Pooled (female/male) causes of mountain caribou mortalities by identified predator species in the northern and southern part of their distribution in British Columbia; division between groups at the Groundhog - Columbia-North boundary.

ADULT SURVIVAL

Too few males were sampled to compare survival rates between sexes. The sample size of female caribou was sufficient in 10 out of 17 subpopulations. Multi-year average annual survival rates varied between 0.55 ± 0.10 in the Purcells-South subpopulation and 0.93 ± 0.04 in the Hart Ranges subpopulation and were significantly different among subpopulations (ANOVA: $F=2.657$, $df=254$, $P=0.048$) (Table 2.5). Annual survival rates also varied considerably among years within subpopulations (CV ranges from 6.76 to 37.22) and among subpopulations.

Table 2.5. Average yearly adult female survival rates \pm SE of mountain caribou subpopulations (animal sample) with ≥ 4 collared individuals per year in British Columbia from 1984 to 2002.

Year	Purcells-South (13)	Nakusp (23)	Columbia-South (17)	Frisby-Boulder (9)	Columbia-North (38)	Groundhog (7)	Wells Gray (121)	Barkerville (10)	North Cariboo Mtn. (8)	Hart Ranges (18)
1984-85							0.71 \pm 0.11			
1985-86							0.71 \pm 0.10			
1986-87							0.91 \pm 0.05			
1987-88							0.80 \pm 0.06			
1988-89								1.00	0.92 \pm 0.07	
1989-90								0.88 \pm 0.12	0.88 \pm 0.08	
1990-91								0.86 \pm 0.13	1.00	
1991-92										
1992-93			0.93 \pm 0.07							
1993-94	0.29 \pm 0.17		0.92 \pm 0.07		0.90 \pm 0.09		1.00			
1994-95	0.67 \pm 0.19		1.00		0.78 \pm 0.14		0.80 \pm 0.09			
1995-96	0.75 \pm 0.22	0.91 \pm 0.09	0.83 \pm 0.11	1.00	0.62 \pm 0.15		0.77 \pm 0.10			
1996-97		0.79 \pm 0.11	0.80 \pm 0.13	1.00	0.88 \pm 0.12		0.77 \pm 0.09			
1997-98	0.50 \pm 0.25	0.73 \pm 0.11	0.63 \pm 0.17	0.50 \pm 0.25	0.71 \pm 0.11		0.90 \pm 0.05	1.00		
1998-99		0.92 \pm 0.07	0.80 \pm 0.18		0.87 \pm 0.09	1.00	0.80 \pm 0.07	1.00		
1999-00		0.92 \pm 0.08	1.00		0.69 \pm 0.15	0.83 \pm 0.15	1.00	0.60 \pm 0.22		
2000-01			1.00		0.60 \pm 0.22	0.80 \pm 0.18	0.83 \pm 0.08	1.00		
2001-02			0.75 \pm 0.22	1.00	0.86 \pm 0.13	0.50 \pm 0.25	0.84 \pm 0.08	0.75 \pm 0.15		
TOTAL	0.55\pm0.10	0.85\pm0.04	0.87\pm0.04	0.88\pm0.13	0.77\pm0.04	0.78\pm0.10	0.83\pm0.03	0.87\pm0.08	0.91\pm0.04	0.93\pm0.04
CV*	37.22	10.31	14.52	28.57	14.96	26.57	11.44	21.35	8.55	6.76

*CV = coefficient of variation

DISCUSSION

The distribution and abundance of mountain caribou in British Columbia has contracted greatly over the past century (Spalding 2000) and it appears that trend is continuing. Although no subpopulation that was monitored over the past 19 years has become extinct, several have experienced significant reductions and are in imminent danger of extinction. The spatial pattern of decline is for the population to become increasingly fragmented into small, isolated subpopulations. Isolation of subpopulations is most pronounced towards the southern limits of the distribution of mountain caribou but population fragmentation also occurs at the core of the population. This increasing fragmentation of mountain caribou into discrete populations with limited interactions among groups is consistent with previous observations of woodland caribou (Stuart-Smith *et al.* 1997, Rettie & Messier 1998) and is likely to accelerate the extinction process by increasing risks associated with demographic and environmental stochasticity (Caughley 1994). Although population extinction and recolonization is the basis of metapopulation theory (Hanski & Gilpin 1991), the trend in the range contraction from the outer boundaries of mountain caribou distribution suggests a directional change in conditions that could result in extinction.

Estimates of mean annual adult survival rates of woodland caribou in North America commonly range from 0.84 to 0.93 (Bergerud 1980, Fuller & Keith 1981, Stuart-Smith *et al.* 1997, Rettie & Messier 1998, Mahoney & Virgl 2003). The survival rates I observed in some subpopulations during this study are substantially lower than nearly all previously reported estimates for woodland caribou except those found in one other rapidly declining population (i.e. 0.70/year; Schaefer *et al.* 1999). I found considerable temporal variation in adult female survival (CV >10) in all but the 2 subpopulations at the northern limit of mountain caribou distribution in British Columbia. High levels of temporal variation in adult female survival have previously been observed in declining caribou

populations, and have been associated with high levels of predation from wolves that were primarily sustained by an alternative prey species (Gasaway *et al.* 1992). In addition, my results also revealed differences in mean adult survival rates of female mountain caribou among subpopulations. The spatial and temporal variability in adult survival rates in this study are different from survival rates generally reported for large herbivores (Gaillard *et al.* 2000) and indicate that data sampled from large, viable populations may not adequately reflect the dynamics of small, declining populations.

Pregnancy rates in this study were high and did not differ among subpopulations. The relative consistency of pregnancy rates irrespective of population trajectory appears typical for woodland caribou (Schaefer *et al.* 1999) and most other ungulates, with the exception of increasing age of primiparity with population density (Gaillard *et al.* 2000). Rettie & Messier (1998) suggest that this insensitivity implies an absence of nutritional factors in population decline and thus indicate a potential for population recovery. My results also suggest that recruitment rates were unrelated to population trajectories. These results do not support Bergerud (1974) who suggested that caribou populations with 12-16% calves at 10-12 months of age are likely stable and that those with less than 10% calves are declining. Unlike pregnancy rates, however, recruitment rates showed a similar temporal variation as adult female survival rates suggesting that recruitment may be linked to adult survival by a common mortality agent, presumably predation (Seip & Cichowski 1996, Schaefer *et al.* 1999).

The major proximate cause of population declines of mountain caribou appears to be predation on adult caribou, but identified primary predators differ between northern and southern subpopulations. In northern subpopulations, wolf and bear predation dominated the cause of death. Recent studies of woodland caribou have stressed the importance of alternate ungulate prey, primarily moose, leading to greater wolf numbers and increased predation on caribou (Bergerud & Elliot 1986, Seip 1992, Schaefer *et al.*

1999, Rettie & Messier 2000). In such a predator-prey system, the numerical response of wolves becomes independent of caribou densities and caribou can only persist where they can separate themselves from alternate prey species (Rettie & Messier 2000). Although bears have been identified as an important source of mortality of caribou calves (e.g. Adams *et al.* 1995, Mahoney & Virgl 2003), my results suggest that bear predation may also act as an important limiting factor of adult (female) caribou especially because bear predation is likely additive to wolf predation.

In southern mountain caribou subpopulations, bear, wolverine and in particular cougar predation dominated the cause of death. I suggest that the large mammal predator-prey system in southern British Columbia may also have been disrupted. Successful game animal management focussing on white-tailed deer, mule deer, and elk, may have stimulated an increase in cougar numbers with the resulting increase in predation rates on caribou. Effects of changes in the predator-prey system may have been influenced by habitat alterations that increased the amount and distribution of early-seral habitats preferred by deer and elk (Kinley & Apps 2001). All 9 identified subpopulations in this predator-prey environment showed negative population trajectories. This absence of population growth over the entire distribution suggests changes in the predator-prey system at large spatial scales and indicates that mountain caribou may not be viable in the current predator-prey environment without the use of predator control.

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CHAPTER 3 - THE ROLE OF PREDATION IN THE DECLINE AND EXTIRPATION OF WOODLAND CARIBOU POPULATIONS

INTRODUCTION

Large mammal populations can be regulated by extrinsic factors, such as food supply, that affect life history traits and rates of population increase (Sinclair 1989, Choquenot 1991, Mduma *et al.* 1999). In large herbivores, the relationship between population rate of increase (r) and population density can be non-linear (convex), with r declining faster at high population abundances (Sibly & Hone 2002, Sinclair & Krebs 2002). In addition, density-independent factors, such as weather fluctuations, can also affect population growth rates (Post & Stenseth 1998). Because not all age and sex classes have similar responses to variations in density or weather, it is difficult to distinguish clearly between density dependence and density independence (Milner *et al.* 1999, Coulson *et al.* 2001). Therefore, in the absence of predators, population dynamics of large herbivores are strongly influenced by the interaction of density-dependent competition for resources and environmental stochasticity (Sæther 1997, Gaillard *et al.* 2000).

Population declines of many large herbivores as a result of landscape modification and overexploitation have recently prompted increased attention on the effect of rarity on population dynamics. Due to factors such as inbreeding, demographic stochasticity, and loss of cooperative interactions with conspecifics, the per capita rate of increase may decrease as populations reach small sizes or low densities (Courchamp *et al.* 1999a, Stephens & Sutherland 1999, Sinclair & Krebs 2002). These factors produce an inverse density-dependent decline, and populations may decline to extinction below a threshold density (Dennis 2002). Despite the important consequences of inverse density dependence for the conservation and recovery of endangered populations, there are few

examples of accelerated population declines at low density, due to the inherent difficulties of studying small populations (Sutherland & Norris 2002).

Studies of the effects of density dependence and density independence on population growth are commonly based on time series analyses within single populations. Not only is it often difficult to attribute cause and effect with time series analyses (Bjørnstad & Grenfell 2001), but the effects of population density are often masked by time lags in density responses or confounding density-independent factors (Shenk *et al.* 1998). Caughley (1994) proposed the use of hypothetico-deductive methods within an experimental design to distinguish between potential causes of decline. The application of a classical experimental design to study an endangered species, however, is often impractical and unethical in natural conditions (Courchamp *et al.* 1999a). To overcome this limitation, Sinclair (1991) suggested taking advantage of natural experiments that provide variation in population densities and the external factors influencing population dynamics.

The distribution of sedentary woodland caribou (*Rangifer tarandus caribou*) has contracted across their range in North America (Bergerud 1974, 1996). Because of declining population trends and increasing population fragmentation, woodland caribou are now considered 'threatened' over large areas of their distribution by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2002). The densities of remaining caribou populations are low and typically vary between 0.01-0.04/km² in boreal habitats and 0.04-0.12/km² in mountainous habitat (Thomas & Gray 2002). Food limitation during winter and/or summer, adverse climate, and increased predation facilitated by accelerated forest harvesting and associated increases in ungulate species and predators, have all been proposed to affect population dynamics of caribou in North America (Bergerud 1996, Rettie & Messier 1998). However, to select appropriate

recovery strategies for endangered populations, we need to distinguish between the possible causes that drive populations to low numbers or even to extinction.

Here I use data sampled over the entire distribution of the mountain ecotype of woodland caribou in the interior wet-belt of British Columbia, commonly referred to as mountain caribou (Heard & Vagt 1998), taking advantage of differences in initial population densities and external factors influencing these densities. My study objectives are to determine rates and causes of the decline of mountain caribou using an inter- rather than an intra-population approach. Specifically, using information on rates of decline relative to population density per area of suitable winter foraging habitat and cause of mortality, I aim to distinguish between the following 3 potential causes of decline (Table 3.1):

Table 3.1. Predictions of population rate of increase and cause of mortality according to three hypotheses proposed to explain the decline of mountain caribou in British Columbia (food regulation caused by habitat loss, predation-sensitive foraging (PSF) caused by habitat loss, predation with caribou being secondary prey).

Cause of decline	Rate of increase (r)	Cause of mortality
Food	Highest at low densities (density dependent)	Malnutrition
PSF	Highest at low densities (density dependent)	Predation
Predation	Lowest at low densities (inverse density dependent)	Predation

1. FOOD REGULATION DUE TO HABITAT LOSS

As food availability increases, population growth rate generally increases to a maximum for the species (Caughley 1976, Sibly & Hone 2002). Loss of suitable habitat may directly precipitate population declines if increased population densities in the remaining habitat result in increased mortality or reduced reproduction (Sutherland 1996). As a result of the unusual high snow accumulation (>2 m) in the interior wet-belt of British

Columbia during winter, mountain caribou depend almost exclusively on long-strand arboreal lichen (*Bryoria* spp. & *Alectoria sarmentosa*) (Rominger & Oldemeyer 1989, Rominger *et al.* 1996, Terry *et al.* 2000). Arboreal lichen is more abundant in old forest stands, thus, mountain caribou are closely associated with late successional forests (i.e. >140 years) (Apps *et al.* 2001). Logging these forests might have led to increased caribou densities in remaining patches of old forest stands, reducing per capita food availability during winter to below a critical threshold. Following the ratio-dependent theory of consumer-resource interactions proposed by Arditi & Ginzburg (1989), I investigated population rate of increase relative to the ratio of population size per area of suitable winter foraging habitat (forest >140 years). If the declines of caribou populations were caused by a per capita decrease in food availability, I expected rates of increase (r) to be highest at low population densities measured by the number of animals per area of forests >140 years of age (Figure 3.1). In addition, if food availability was causing population declines, then I would expect low pregnancy rates and the majority of animals to die as a consequence of malnutrition.

2. PREDATION-SENSITIVE FORAGING DUE TO HABITAT LOSS

Predation and food can jointly limit population size because caribou could respond to declining amounts of suitable winter foraging habitat by increasing the time that they spend foraging in riskier habitat, and thus increase their vulnerability to predators.

Predation-sensitive foraging affects the population dynamics of prey because predators often kill animals that are foraging in riskier habitats which they use due to declining food supplies in safer habitats (Sinclair & Arcese 1995). The predation-sensitive foraging hypothesis differs from the food regulation hypothesis in that the decline of caribou is still caused by habitat loss (food depletion causes a change in foraging behaviour), but mortality is primarily due to predators. Thus, if the decline of caribou is a consequence of predation-sensitive foraging, I expected rates of increase (r) to be highest at low

population densities, again measured as the number of caribou per area of forests >140 years (Figure 3.1). In contrast to the food regulation hypothesis, I expected the majority of animals to die from predation. In addition, caribou should be killed by predators during winter when food resources are more limited.

3. PREDATION

Predators can cause the extirpation of a population where prey are secondary to a predator that depends on another prey species (Sinclair *et al.* 1998). The extirpation is a result of an absence of density dependence in either functional or numerical response of the predator to the low-density secondary prey population. If the numerical response of a predator to the prey is of type 0 (i.e. numerical response independent of secondary prey densities), and the functional response is of type II, the proportional effect of the total response will be uniformly inversely density-dependent (Messier 1995). At the lower range of prey densities, however, predators may show an approximation of a type I response (page 167, Caughley & Sinclair 1994). At these low prey densities, predators will likely spend no time actively searching for the secondary prey but will continue to prey upon them incidentally when encountered. Thus, if the numerical response of a predator to the secondary prey is of type 0, and the functional response is of type I, the proportional effect of the total response will be linear and result in constant mortality rates of the secondary prey at very low densities.

The susceptibility of woodland caribou to predation has led to patterns of habitat use that separate them from other ungulates in the same geographic area (Bergerud & Page 1987, Seip 1992). Changes in the forest age structure may compromise the ability of caribou to avoid other prey species and their predators. This is, because young forest stands are thought to support higher densities of moose (*Alces alces*) and deer (*Odocoileus* spp.) that in turn support higher predator densities (Bergerud & Elliot 1986, Seip 1992). If the decline of mountain caribou is caused by high levels of predation

where caribou are preyed upon secondarily by predators that depend on other primary prey, I predicted rates of increase (r) of caribou to be lowest at low population densities per area of forests >140 years (Figure 3.1). The inverse density-dependent predation rates are due to increasing per capita mortality as populations decline and might cause extirpation of caribou populations. At the very lowest caribou densities, however, where caribou are incidentally preyed upon, and assuming near equal predator densities across the distribution of caribou, I expected rates of increase (r) to be equal among subpopulations. This result is predicted as a consequence of a consistent proportional per capita mortality rate where the functional response is near linear. In addition, I predicted caribou to die primarily due to predation.

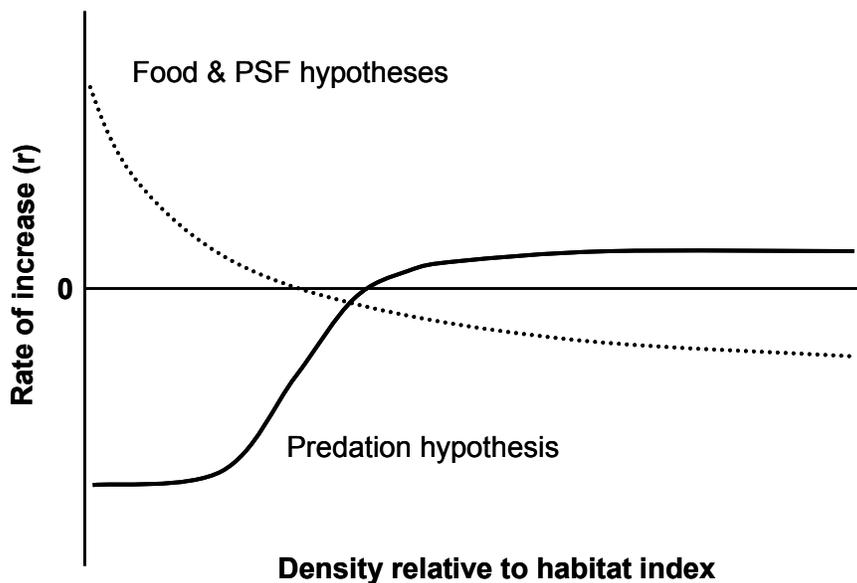


Figure 3.1. Predicted relationship between population rate of increase (r) and number of individuals per area of forests >140 years for a) food regulation & predation-sensitive foraging (PSF) hypothesis and b) predation hypothesis (modified from Caughley & Sinclair 1994, Sinclair *et al.* 1998).

METHODS

TELEMETRY AND POPULATION TRENDS

Field methods were as reported in Chapter 2. Briefly, VHF- and GPS-collared caribou were relocated at 1-2 week intervals and their status confirmed. When the signal from a motion-sensitive radiocollar indicated that a caribou was dead, the site was investigated as soon as possible. The cause of mortality was determined from evidence at the site and, when possible, from a necropsy that included a measure of bone marrow, visceral, and rump fat deposits. Predation was suggested when there was evidence of bleeding, a struggle, or bite injuries. These cases were usually clear when there was snow on the ground, but less so during the summer. Non-predation deaths were divided into accidents (i.e. avalanches, birthing, falls), malnutrition, human caused, or unknown. In many cases it was difficult to determine the cause of death and I conservatively classified the mortality cause as unknown.

Subpopulations were surveyed from helicopters at irregular intervals in March or early April when mountain caribou are in open, high elevation habitats shortly after new snow fell. Population estimates and 95% confidence limits were derived from the census results using the joint hypergeometric maximum likelihood estimator (JHE) (Bartmann *et al.* 1987) in the NOREMARK computer program (White 1996). In cases where the lower 95% confidence limit was below the actual number of caribou seen during census flights, I used the census result as the lower confidence limit. In the absence of marked individuals in the subpopulation I applied a sightability correction factor of 84.57% based on long-term averages pooled over all years and populations (Chapter 2). I then calculated the instantaneous rate of increase (r) for each subpopulation, as

$$r = (\ln N_{2002} - \ln N_0) / t \quad (1)$$

where N_{2002} is the number of caribou in year 2002, N_0 is the number of caribou in the initial year, and t is the number of years between N_0 and N_{2002} (Caughley & Sinclair

1994). Subpopulations were delineated *a posteriori* based on telemetry locations of radiocollared animals (Chapter 2), so reliable estimates of population trends are limited to the period between 1992 and 2002.

POPULATION DENSITIES RELATIVE TO HABITAT INDEX

I extracted forest age variables from 1:20000 digital inventory planning files (Resource Inventory Branch 1995) rasterized to 250 m resolution. Forest age data were updated to the year 2002 and assumed to be indicative of forest composition over the period when caribou population dynamics were studied. Following Apps *et al.* (2001) I grouped forest age into 4 age classes (Age 1=1-40 years, Age 2=41-100 years, Age 3=101-140 years, Age 4 >140 years). I then estimated the area of forests >140 years encompassed within each distinct subpopulation range using the ArcView Geographical Information System (ESRI 1996) because of the importance of these forests as foraging habitat during winter (Rominger & Oldemeyer 1989, Rominger *et al.* 1996, Terry *et al.* 2000). I divided subpopulation size by the area of forests >140 years within each subpopulation's range estimated from telemetry data described in Chapter 2, to derive an index of caribou densities per area of suitable winter foraging habitat.

TEST OF PREDICTIONS

I examined predictions of subpopulation decline by plotting subpopulation size in forest stands >140 years against instantaneous rate of increase of each subpopulation. I determined goodness-of-fit of curves from regression analysis (Zar 1999). Statistical analyses were performed using Systat 10.2 (SYSTAT Software Inc. 2002). Results are considered significant when $\alpha < 0.05$. Means are reported $\pm 1SE$ of the mean unless otherwise noted.

RESULTS

RATE OF INCREASE

The instantaneous rate of increase was negative for 12 out of the 15 subpopulations for which I was able to determine trends (Mean=6.93 \pm 0.49 years) (Table 3.2). The 95% confidence interval of the rate of increase in the Wells Gray subpopulation (-0.1322 to 0.0233) overlapped zero, and while this corresponded with an 85% chance of decline, it was statistically indistinguishable from a stable population. Based on available information, only 1 subpopulation (Barkerville) increased significantly over the time it was monitored, while 1 subpopulation (North Cariboo Mountain) appeared stable. Trends in individual subpopulations varied from -0.1871 to 0.0496, with smaller populations declining at the fastest rate (GLM: $R^2=0.510$, $df=13$, $F=13.555$, $p=0.003$) (Figure 3.2). Rates of increase also varied geographically with more southern populations generally decreasing at higher rates than more northern ones.

Table 3.2. Subpopulation sizes (N_{2002} , N_0) used to estimate instantaneous rate of increase (r) with 95% confidence intervals, area covered by suitable forest resources (>140 years) and density estimations for 15 mountain caribou subpopulations in British Columbia (subpopulations ordered from south to north).

Subpopulation	N_{2002}	N_0	Years	r	LCI*	UCI*	Forest >140 yrs. (km ²)	Density >140 yrs.
Purcells-South	17	63	7	-0.1871	-	-	214	0.08
Purcells-Central	6	15	7	-0.1309	-	-	193	0.03
Nakusp	108	173	6	-0.0785	-0.1242	-0.0513	957	0.11
Duncan	20	49	6	-0.1493	-	-	125	0.16
Columbia-South	39	114	8	-0.1341	-0.1608	-0.1009	562	0.07
Frisby-Boulder	20	34	6	-0.0884	-0.1424	-0.0500	265	0.08
Columbia-North	188	232	5	-0.0421	-0.0876	-0.0113	1952	0.10
Kinbasket-South	14	17	5	-0.0388	-	-	193	0.07
Groundhog	15	44	7	-0.1537	-	-	435	0.03
Wells Gray	526	628	7	-0.0253	-0.1322	0.0233	3587	0.15
Barkerville	58	39	8	0.0496	0.0063	0.0914	543	0.11
North Cariboo Mtn.	279	274	9	0.0020	-	-	775	0.36
George Mtn.	4	25	10	-0.1833	-	-	95	0.04
Narrow Lake	72	79	3	-0.0309	-	-	287	0.25
Hart Ranges	325	370	10	-0.0130	-	-	1948	0.17

*LCI = lower confidence interval; UCI = upper confidence interval

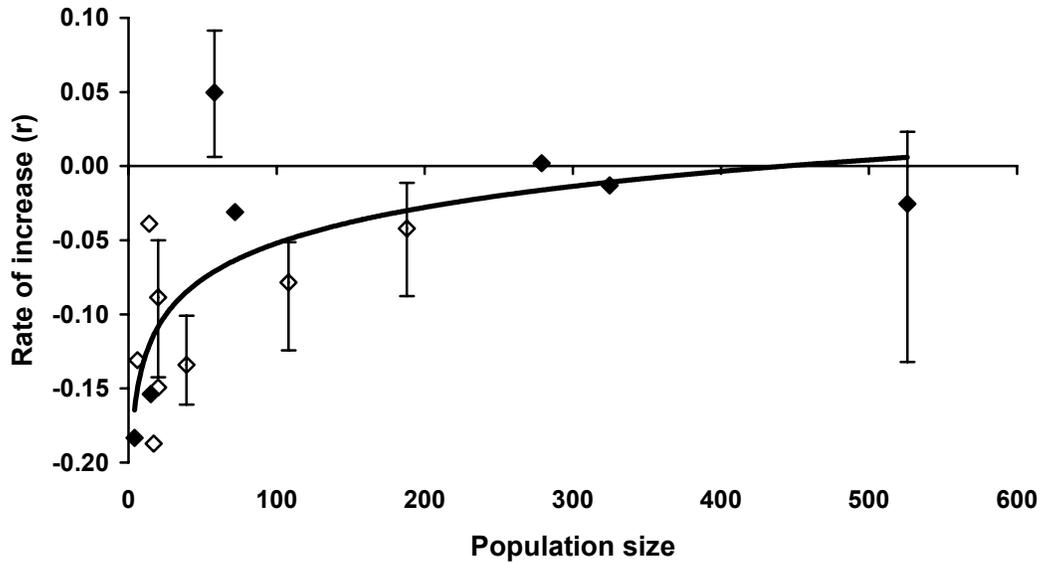


Figure 3.2. Correlation between average yearly instantaneous rate of increase (r) and total population size in 2002 of 15 subpopulations of mountain caribou in British Columbia (error bars indicate 95% confidence limits based on sampling variance of population estimates; line indicates goodness-of-fit curve from regression analysis); open diamonds (\diamond) indicate (southern) subpopulations with significant cougar predation, closed diamonds (\blacklozenge) indicate (northern) subpopulations with significant wolf predation (Chapter 2).

CAUSE OF MORTALITY

A total of 155 mortalities of radiocollared caribou distributed over all 15 subpopulations were recorded. Six deaths (3 f/3 m) were human caused, including 2 vehicle accidents, 2 research-related mortalities, and 2 caribou that were illegally shot. Of the 149 natural mortalities, I could confidently categorise 88 into predation, malnutrition, or accidents (Table 3.3). Of the 88 deaths with a known cause, 82 were females. I pooled causes of death data over sexes because the ranks of mortality causes were the same. Fifty-eight (66%) of the known mortality causes were due to predation. Predation was the primary cause ($\geq 50\%$) of mortality in 11 of the 13 subpopulations with known causes of mortality. Apparent malnutrition was confirmed for 10 caribou from 4 subpopulations.

Table 3.3. Cause of mortality and proportion of mortalities with known cause killed by predators of the mountain ecotype of woodland caribou, British Columbia, Canada (males).

Subpopulation	Accident	Malnutrition	Predation	Proportion predation	Unknown
Purcells-South	-	-	9 (1)	1.00	3
Purcells-Central	1	-	-	0	1
Nakusp	1	-	4 (1)	0.80	6 (1)
Duncan	-	1 (1)	2	0.67	-
Columbia-South	4 (1)	-	5	0.56	4
Frisby-Boulder	1	-	-	0	1
Columbia-North	5	2	9 (1)	0.56	7
Kinbasket-South	-	-	-	-	1 (1)
Groundhog	-	-	2	1.00	4
Wells Gray	7	6	22	0.63	27 (1)
Barkerville	1	-	2	0.67	2
North Cariboo Mtn.	-	-	1	1.00	1
George Mtn.	-	-	1 (1)	1.00	-
Narrow Lake	-	-	-	-	1
Hart Ranges	-	1	1	0.50	3 (2)
TOTAL	20	10	58	0.66	61

POPULATION DENSITIES RELATIVE TO HABITAT INDEX

The instantaneous rate of increase declined faster with decreasing caribou densities per area of suitable habitat (GLM: $R^2=0.388$, $df=13$, $F=8.231$, $p=0.013$), indicating a type II (predator-prey) interaction with depensatory predation on secondary prey (Figure 3.3).

On the basis of information available (shape of the goodness-of-fit curve from the regression analysis) there appears to be no evidence that over the entire distribution, the overall rate of decline is decelerating at low caribou densities.

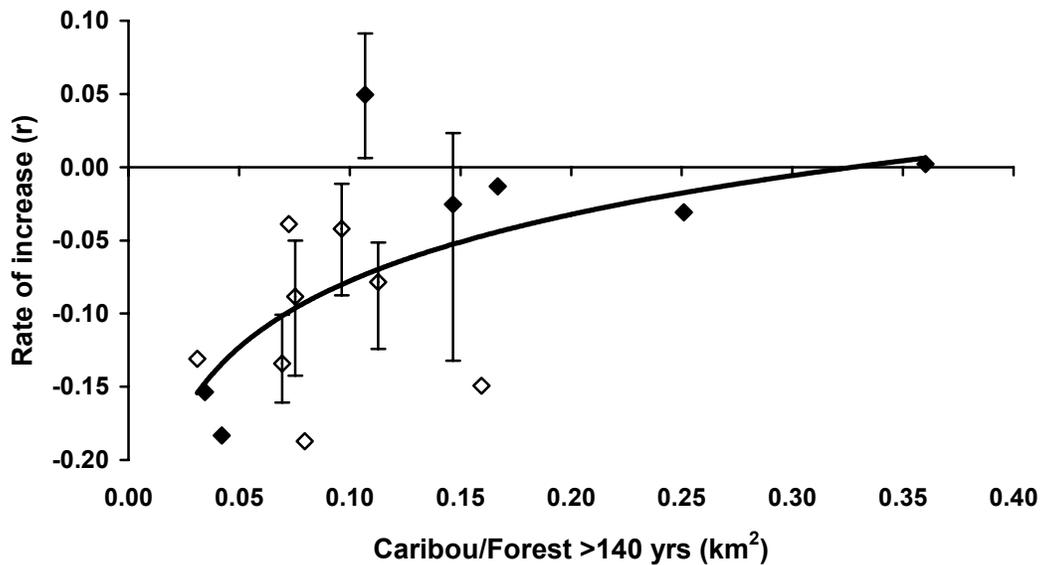


Figure 3.3. Correlation between average annual instantaneous rate of increase (r) and number of caribou per area of suitable winter foraging habitat (forest >140 years (km^2)) of 15 subpopulations of mountain caribou in British Columbia (error bars indicate 95% confidence limits based on the sampling variance of population estimates; the line indicates the goodness-of-fit curve from regression analysis); open diamonds (\diamond) indicate (southern) subpopulations with significant cougar predation, closed diamonds (\blacklozenge) indicate (northern) subpopulations with significant wolf predation (Chapter 2).

DISCUSSION

The principal objective of my study was to differentiate between 3 hypotheses (food, predation-sensitive foraging (PSF), and predation) of causes for the population decline in the mountain ecotype of woodland caribou in British Columbia. The food hypothesis predicted that the decline of mountain caribou is due to increased intraspecific competition for food resources as a consequence of loss of mature lichen bearing forest stands through logging. Consequently, I predicted that malnutrition would be the primary cause of mortality, pregnancy rates would be low, and that the highest rates of increase would occur at low population densities per area of suitable winter foraging habitat. My results showed that predation was the primary cause of mortality, pregnancy rates were

high and constant ($92 \pm 2\%$) (Chapter 2), and that rates of increase were lowest at low population densities relative to area of suitable winter foraging habitat. Thus, my results were inconsistent with the food hypothesis.

The PSF hypothesis proposed that resource restriction and predation interact such that as food supply decreases, caribou increase their risk of predation due to more time spent foraging in riskier habitat. Consequently, I predicted that predation would be the primary mortality cause, and most would occur during winter when foods should be most limited. In addition, I predicted that the highest rates of increase would occur at low population densities per area of suitable winter foraging habitat. My result of predation being the primary cause of mortality was consistent with predictions of the PSF hypothesis, however, predation predominately occurred in summer (Chapter 2) when food was more abundant. Additionally, my results indicate that rates of increase were lowest at low population densities per area of suitable winter foraging habitat, also inconsistent with the PSF hypothesis.

The predation hypothesis proposed that predators drive caribou populations to extinction when they are a secondary prey and predators depend on some other primary prey. Consequently, I predicted consistently low survival rates of caribou even at low population densities per area of suitable winter foraging habitat and that predation would be the primary cause of mortality. My results support both predictions of the predation hypothesis. Predation was the primary cause of mortality in almost all subpopulations of mountain caribou in British Columbia, and I found negative rates of increase even at very low caribou density per area of suitable winter foraging habitat. Counter to my expectations, however, the increasingly negative rate of increase continued even when caribou densities were very low, suggesting a lack of refuge effect at low numbers.

Theoretical studies have argued for the potential importance of inverse density dependence in the dynamics of small populations (e.g. Lande *et al.* 1994, Brassil 2001,

Dennis 2002, Fowler & Ruxton 2002). The primary consequence of inverse density dependence is an increase in the extinction risk when populations fall below a critical density threshold (Dennis 1989). Although inverse density dependence has been described across many taxa including mammals, empirical evidence remains rare (Sæther *et al.* 1996, Courchamp *et al.* 1999a) because of difficulties in measuring population growth rates at low densities (Morris 2002). Consequently, demographic studies in large herbivores continue to focus mainly on density dependence and density independence (Gaillard *et al.* 2000).

Several mechanisms have been hypothesized to cause inverse density dependence. Most studies have focused on intraspecific inverse density dependence as mediated by social interactions among conspecifics, including increased efficiency of mating with higher density (e.g. Kuussaari *et al.* 1998) and increased efficiency of cooperative behaviours with density (e.g. Clutton-Brock *et al.* 1998, Courchamp *et al.* 1999b, 2000). Conversely, inverse density dependence as mediated by complex interspecific relationships involving more than two species, such as predator-prey interactions, have seldom been considered (Courchamp *et al.* 1999a). Sinclair *et al.* (1998) provided empirical evidence of inverse density dependence from altered predator-prey systems in Australia, where an introduced predator species (red fox, *Vulpes vulpes*) drove a remnant population of small marsupial (eastern barred bandicoot, *Perameles gunnii*) to extinction. The extinction was a consequence of increased per capita mortality at low population densities as predicted from a type II total response.

My results provide evidence of inverse density dependence as a consequence of high mortality rates caused by predation in a large herbivore in a multi-prey, multi-predator system with a full complement of 5 natural predators. The trend in population decline may suggest a type II predator response influencing the rate of increase even at

very low prey densities. However, it is unlikely that inverse density dependence continues to operate at very low densities, because predators would spend virtually no time searching for or handling caribou, and thus predation on caribou would be completely incidental. Instead, I suggest that the number of prey and predators was not consistent across the range of all caribou subpopulations. In general, ranges of caribou subpopulations with low numbers and very low rates of increase were in areas with younger forest stands and thus likely had higher primary prey and higher predator numbers (Chapter 4).

The continued high rate of decline at low densities has important implications for the population dynamics of woodland caribou over their entire distribution in North America. Predation is generally considered the proximate factor limiting woodland caribou populations across most of their distribution (Bergerud & Elliot 1986, Bergerud 1996, Stuart-Smith *et al.* 1997, Rettie & Messier 1998, Schaefer *et al.* 1999). It has been hypothesized that predation might be facilitated by logging and other changes to caribou habitat that favour early seral stage forest (Rettie & Messier 1998). These young forest stands are thought to support higher densities of alternate prey species, primarily moose, that in turn support higher predator densities (Bergerud & Elliot 1986, Seip 1992). My results provide evidence that the loss of mature forests has not yet had a significant effect on caribou populations by increasing intraspecific competition for food (i.e. arboreal lichen) but that it compromises the predator avoidance strategy of caribou where they fail to separate themselves from increasing alternate prey populations and their predators. Their failure to reduce predation risk exposes caribou to an increasing predator population that has a numerical response to alternate (primary) prey consumption. Because I studied the dynamics of mountain caribou over their entire distribution in British Columbia, I consider that my results provide evidence that this

mountain ecotype of caribou has become secondary prey and most subpopulations are declining to extinction due to high predation rates.

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CHAPTER 4 - UNDERLYING MECHANISMS OF THE DECLINE OF AN ENDANGERED LARGE HERBIVORE

INTRODUCTION

A successful recovery strategy for an endangered species requires (1) determining which demographic rates (e.g. survival, reproductive output, and recruitment) of the organism are depressed, and (2) identifying which intrinsic or extrinsic factors cause the depressed rates (Caughley 1994). To determine which rates are depressed, studies attempt to quantify the contribution of demographic rates to changes in population growth rates. For large herbivores, population growth rates are most sensitive to changes in adult female survival, followed by changes in fecundity of prime aged females, and fecundity of young females, and are least sensitive to changes in juvenile survival (Tuljapurkar & Caswell 1997, Gaillard *et al.* 2000). However, because temporal variation in adult female survival and fecundity are generally low, variation in population growth rate is suggested to be predominantly caused by changes in juvenile survival (Saether 1997, Gaillard *et al.* 1998, 2000). These conclusions have been drawn from long-term studies of individually marked animals in large, stable populations, and often in ecosystems where predators have been reduced or extirpated.

Factors found to cause changes in demographic rates of large herbivores commonly include population density, resulting in intraspecific competition for food, and climatic variation (Saether 1997, Gaillard *et al.* 2000, Sinclair & Krebs 2002). Although habitat loss is the driving force most frequently identified with loss of biodiversity and extinction of species (Caughley 1994, Wilcove *et al.* 1998, Sih *et al.* 2000), examples of the direct effect of habitat loss or habitat alterations on changes in demographic rates remain rare (Boyce 2002). The paucity of examples might be due to the difficulty of measuring habitat degradation within single populations over time in an experimental

design. However, population dynamics and the demographic rates that define those dynamics are also affected by spatial variation. Studies estimating spatial variation by comparing population dynamics among different spatial units such as territories in other taxa, have been successful in linking changes in demographic rates to habitat conditions (e.g. Northern Spotted Owls (*Strix occidentalis caurina*); Franklin *et al.* 2000).

Although woodland caribou (*Rangifer tarandus caribou*) remain widely distributed in Canada, their range has declined significantly from historical distributions (Bergerud 1974, Thomas & Gray 2002). In some areas, range recession has been generally northward and has been linked to the advancing northern edge of forest harvesting (Schaefer 2003). Predation, however, is generally considered the proximate limiting factor leading to population declines of woodland caribou (Bergerud & Elliot 1986, Bergerud 1996, Stuart-Smith *et al.* 1997, Rettie & Messier 1998, Schaefer *et al.* 1999). Predation has been suggested to be precipitated by timber harvesting that creates landscapes of early seral stages (Rettie & Messier 1998). These early successional forests lead to increases in the abundance of other ungulate species such as moose (*Alces alces*; Rempel *et al.* 1997), which in turn support higher densities of predators (Schwartz & Franzmann 1991, Ballard *et al.* 2000). As a consequence, caribou can be extirpated where they are secondary prey and when predators are maintained by other prey species (Chapter 3). Besides providing improved habitat for the primary prey, roads and linear corridors associated with industrial operations in forested areas may also improve predator efficiency by enhancing their searching efficiency (James & Stuart-Smith 2000). If woodland caribou are to be maintained, the hypothesis that forest management leads to woodland caribou declines by upsetting the relative stability of the predator-prey system is clearly important to understand. However, a direct link between habitat changes, changes in predator-prey systems, and changes in demographic rates of caribou is lacking.

Mountain caribou are an ecotype of woodland caribou that live in the interior wet-belt mountain ranges of western Canada and the USA (Heard & Vagt 1998). The winter snowpack in these mountains is generally 2-5 m in depth and buries all plants except trees. The deep snow, however, provides a platform from which caribou can reach their winter food of arboreal lichen (*Bryoria* spp. & *Alectoria sarmentosa*) that is abundant on old, coniferous trees (Rominger *et al.* 1996, Terry *et al.* 2000). Due to declining population trends and increasing population fragmentation, mountain caribou within the Southern Mountain National Ecological Area of Canada are currently considered 'threatened' by the Committee of the Status of Endangered Wildlife in Canada (COSEWIC 2002). As in other woodland caribou, the decline of mountain caribou has been linked to high predation rates (Seip 1992, see also Chapter 3).

My study had 2 objectives. The first was to quantify the influence of demographic rates on subpopulation trends of mountain caribou. To meet this objective, I test the hypothesis of Saether (1997) and Gaillard *et al.* (1998, 2000) - although population trends of large herbivores are most sensitive to changes in adult female survival, it is usually changes in recruitment that actually cause trends to change because recruitment varies widely in response to fluctuating conditions while adult survival remains relatively constant. My second objective was to examine the importance of several environmental factors on changes in demographic rates. Here I was able to use a comparative approach among identified subpopulations because population dynamics of mountain caribou have been studied over their entire distribution. Factors influencing demographic rates included amount and distribution of habitat attributes that have been suggested to precipitate caribou declines, as well as snow depth and population density. Understanding how differences in environmental conditions among subpopulations influence variation in demographic rates might ultimately allow us to develop effective conservation strategies.

METHODS

FIELD METHODS AND POPULATION ESTIMATES

Field methods were as reported in Chapter 2. Briefly, VHF- and GPS-collared caribou were relocated from fixed-wing aircraft at 1-2 week intervals. During telemetry flights the status of collared animals was also confirmed. When the signal from a motion-sensitive radiocollar indicated that a caribou was dead, the site was investigated as soon as possible. During the site investigation, it was confirmed if a caribou had died or simply dropped its collar.

Caribou subpopulations were surveyed from helicopters at irregular intervals in March or early April when caribou are in open, high elevation habitats shortly after new snow fell. Population estimates and 95% confidence limits were derived from the census results using the joint hypergeometric maximum likelihood estimator (JHE) (Bartmann *et al.* 1987) in the NOREMARK computer program (White 1996). In cases where the lower 95% confidence limit was below the actual number of caribou seen during census flights, I used the census result as the lower confidence limit. In the absence of marked individuals in the subpopulation I applied a sightability correction factor of 84.6% based on long-term averages pooled over all years and populations (Chapter 2). I then calculated the annual instantaneous rate of increase (r) adjusted to an interval of 1 year for subpopulations where 2 or more complete population censuses were conducted in separate years between 1992 to 2002, as

$$r = (\ln N_{2002} - \ln N_0) / t \quad (1)$$

where N_{2002} is the number of caribou in year 2002, N_0 is the number of caribou in the initial year, and t is the number of years between N_0 and N_t (Caughley & Sinclair 1994).

RECRUITMENT & ADULT SURVIVAL

I estimated recruitment in each subpopulation from the percentage of the subpopulation classified as calves during aerial censuses in late March when calves were \approx 10 months

old. I consider the percentage of calves in March to be true measures of recruitment, because animals of that age likely experience similar mortality rates as older animals (Bergerud 1980, Fuller & Keith 1981).

I estimated adult caribou survival (ϕ), defined as the probability that a caribou survives to year $t+1$, given it was alive at year t (Lebreton *et al.* 1992). I derived estimates of (ϕ) using known-fate mark-recapture models in Program MARK (White & Burnham 1999). I estimated annual survival for a year that began at the beginning of the calving season, following seasonal definitions described in Chapter 2. Individuals were recorded as alive or dead within the year with multiple resightings of individuals equating to single encounters. Initiating survival calculations at the onset of calving while animal capture was 2 months earlier, reduced bias in survival rates if there had been any mortality related to capture. To reduce the effects of small sample sizes, I only included populations monitored for at least 3 complete years with at least 4 caribou collared during each year. A total of 59 years from 10 of the identified 17 subpopulations met these requirements to be included in the analysis. I limited my analysis to adult females because 2 out of 3 populations with sufficient data to make comparisons showed significant differences in survival rates between females and males (Wittmer, unpublished data).

DEMOGRAPHIC RATES AND POPULATION GROWTH

I estimated population rates of increase (r) as a function of both recruitment and adult survival. I used the Akaike information criterion (AIC) difference for small samples (ΔAIC_c), and Akaike weights (ω) to evaluate and select the most parsimonious model following an information theoretic approach (Burnham & Anderson 2002). The model with the lowest AIC_c value is the one that explains the greatest amount of variation using the fewest variables and is taken as the model most supported by the observed data.

Akaike weights can then be interpreted as the approximate probability that each model is the best model from the set of proposed models (Anderson *et al.* 2000). In 2 subpopulations, the telemetry data used to estimate adult survival rates, predated the census data used to estimate population trends. Thus, I limited this analysis to 8 subpopulations to ensure that estimates of demographic rates were within the time period used to estimate population trends.

COVARIATES OF ADULT SURVIVAL

Covariates with survival rates were based on factors measured within the range of each subpopulation. The range boundary of each subpopulation was determined using the 95% adaptive kernel density estimator (Worton 1989) using all locations of animals radiocollared in each subpopulation (Chapter 2). For each individual, I attached covariates associated with the subpopulation range occupied by that individual. Thus, the sampling unit to which inferences were made was individuals within subpopulations. Unfortunately, I could not use alternate prey availability or predator abundance directly to measure their effect on caribou survival rates because such data were not available over the whole distribution of mountain caribou. My study relies on differences among the habitat, environmental variation, and caribou densities of the subpopulations. Some of these differences are summarized in Table 4.1.

Landscape habitat covariates: I selected habitat covariates based on the hypothesis that caribou declines are associated with increasing proportions of young forest stands (Rettie & Messier 1998). I extracted forest age variables from 1:20000 digital forest inventory planning files (FIP; Resource Inventory Branch 1995) rasterized to 250 m resolution. Forest age data were updated to the year 2002 and covered the entire distribution of mountain caribou. I then estimated the proportion of the total landbase of each subpopulation range that consisted of forest stands that were 1-40 (PROP1) and 41-100 (PROP2) years old, and non-forested (alpine, rock, and ice) (Table 4.2) using the

ArcView Geographical Information System (ESRI 1996). I did not include the proportion of the subpopulation range that was old forest because I previously found that forests of these ages were not correlated to the rate of increase of caribou subpopulations (Chapter 3). Also, the amount of old forest is approximately the remainder after the other categories are used. The distribution of forest stands of different ages may also be important for mountain caribou. Therefore, I determined the mean patch size (MPS1, MPS2), edge density (ED1, ED2), and mean distance to the nearest neighbouring forest patch of the same forest age class (MNN1, MNN2) within the subpopulation ranges, using the patch analyst extension (Elkie *et al.* 1999) within ArcView.

Climate covariates: Arboreal lichen does not grow lower on trees than the maximum snowdepth, so large interannual variation in snowpack may result in too little snow accumulation in some years for caribou to reach lichen in the lower canopy (Goward 1998). Thus, I explored the effects of among year variability in snow depth on survival, using variation in annual snow depth as an indicator of winter severity. This is consistent with an among-year study approach of climatic variation described by Rotenberry & Wiens (1991). Snow data were obtained from automated snow pillow stations within the identified subpopulation ranges of mountain caribou. Snow pillow stations are maintained by the Ministry of Sustainable Resource Management (2002) and ranged in elevation from 1520 m to 2010 m. I assumed that data from the snow pillow stations were representative of conditions experienced by caribou in distinct subpopulations on high elevation late winter ranges. Snow accumulation (cm) was measured on the first day of each month from January to April. For each caribou subpopulation, I then calculated the average yearly snow accumulation during this period (i.e. late winter). To estimate the variation in snow depth during the census period, I determined the coefficient of variation (Zar 1999) in snow accumulation encompassing all years included to estimate effects on survival rates.

Table 4.1. Forest habitat and forest age characteristics associated with 10 subpopulation ranges of mountain caribou in British Columbia (subpopulations are ordered south - north).

Subpopulation	Range (km ²)	Percent non-forested	Percent 1-40 years	Percent 41-100 years
Purcells-South	771	7.00	18.29	30.88
Nakusp	2340	35.05	9.53	9.08
Columbia-South	1761	48.37	6.07	10.39
Frisby-Boulder	613	36.41	6.69	7.96
Columbia-North	4526	40.22	8.82	4.22
Groundhog	1277	37.99	12.62	12.29
Wells Gray	8141	40.81	5.74	7.00
Barkerville	742	6.37	6.32	6.61
North Cariboo Mtn.	1779	43.65	10.72	0.53
Hart Ranges	3890	36.85	7.42	2.53

Table 4.2. Covariates used for analysis among-population variability in survival of female adult mountain caribou.

Covariates	Definition
(1) Proportion of habitat	Proportion of non-forested (alpine) habitat within subpopulation range (NONFOR) Proportion of forest habitat age 1-40 years within subpopulation range (PROP1) Proportion of forest habitat age 41-100 years within subpopulation range (PROP2)
(2) Distribution of habitat	Mean patch size of forest habitat age 1-40 years within subpopulation range (MPS1) Mean patch size of forest habitat age 41-100 years within subpopulation range (MPS2) Edge density around forest habitat age 1-40 years within subpopulation range (ED1) Edge density around forest habitat age 41-100 years within subpopulation range (ED2) Mean nearest neighbouring forest patch age 1-40 years within subpopulation range (MNN1) Mean nearest neighbouring forest patch age 41-100 years within subpopulation range (MNN2)
(3) Climate variable	Coefficient of variation of average yearly snow accumulation (Jan-Apr) (SNOW)
(4) Population density	Population density within subpopulation range (DEN)

Population density: For each subpopulation I estimated population density by dividing the population size in the year 2002 by the total range size. Range size was estimated using the 95% adaptive kernel density estimator using all locations of animals radiocollared in each subpopulation (Chapter 2).

MODELLING THE EFFECTS OF COVARIATES ON ADULT SURVIVAL

At first, I considered a model with area effects (ϕ , area) in the survival probabilities. I then modelled the variation in female survival probabilities among subpopulations as a function of the covariates. All covariates were standardized prior to the analysis following guidelines outlined by Cooch & White (2001). Relationships among survival probabilities and covariates cannot be investigated directly, because survival estimates generated by mark-recapture models are not independent (Lebreton *et al.* 1992). Instead, I constrained area-dependent survival probabilities within survival models as linear functions of environmental variables, where the design matrix was linked to the model parameters by the logit link function in program MARK (White & Burnham 1999). The effects of covariates were assessed by comparison with constant (ϕ , intercept) and area dependent (ϕ , area) models. I used AIC values to assess whether constraints improved model fit (Burnham & Anderson 2002) and thus, whether survival probabilities covaried with environmental parameters.

Following Gaillard *et al.* (1997), I first modelled survival as a function of a single covariate x : $\text{Logit } \phi = \text{Ln}[\phi/(1-\phi)] = a + bx$. I then added a second covariate y to the best model with a single covariate, as: $\text{Logit } \phi = a + bx + cy$. To avoid autocorrelation, habitat covariates were only paired among different forest age classes. Finally, I added a third covariate to the best model with 2 covariates to test for further model improvement. Models were ranked and compared using ΔAIC_c and Akaike weights (ω) (Lebreton *et al.*

1992, Burnham & Anderson 2002). I considered models within 2 AIC_c units of the selected model competing models (Burnham & Anderson 2002).

To account for possible model overdispersion, I determined the variance inflation factor \hat{c} , by dividing the model deviance of the global model (i.e. the most parameterised model) by its degrees of freedom. $\hat{C} > 1$ indicates that the empirical sampling variance is greater than the theoretical variance, which can be adjusted by inflating \hat{c} to account for the observed overdispersion. The estimate of \hat{c} from the global survival model was 1.366, within the range for adequate global model fit (Anderson *et al.* 1994), indicating moderate overdispersion. I adjusted AIC_c for overdispersion using \hat{c} to derive $QAIC_c$ (Anderson *et al.* 1994).

RESULTS

SUBPOPULATION TREND

The rate of increase based on repetitive censuses indicated that 7 out of 10 subpopulations with sufficient data were declining (Table 4.3). The 95% confidence interval of the rate of increase in the Wells Gray subpopulation (-0.1322 to 0.0233) overlapped zero, and corresponds to a 85% chance of decline. Rates of increase of individual subpopulations varied from -0.1871 to 0.0496 with more southerly populations generally decreasing at higher rates than more northern ones.

RECRUITMENT AND ADULT SURVIVAL

The mean percentage of calves \approx 10 months old observed during March censuses varied from 5.71 and 20.78% among subpopulations and averaged 12.88% \pm 1.33 (Table 4.3). The coefficient of variation of the observed percentage of calves varied from 6.63 to 106.39 (Mean=31.66 \pm 9.36) within subpopulations. Survival rates of males (0.872 \pm 0.036) appeared slightly higher than those of females (0.834 \pm 0.014), but too few males were sampled for a meaningful comparison between sexes or among subpopulations.

Table 4.3. Instantaneous rate of increase (r), 95% confidence limits (CI), multiyear average adult female yearly survival rates and multiyear average percentage of calves during population censuses in late March of mountain caribou subpopulations (subpopulations are ordered south - north).

Subpopulation	r (CI)	Female survival rates (AVG±SE)	CV* female survival	Percent calves (AVG±SE)	CV* prop. calves
Purcells-South	-0.187 (N/A)	0.52±0.11	37.22	5.71±2.48	106.39
Nakusp	-0.079 (-0.124/-0.051)	0.85±0.04	10.42	10.18±2.07	40.58
Columbia-South	-0.134 (-0.161/-0.101)	0.87±0.04	14.45	14.01±1.33	18.97
Frisby-Boulder	-0.088 (-0.142/-0.050)	0.88±0.08	28.57	20.78±4.69	39.05
Columbia-North	-0.042 (-0.088/-0.011)	0.78±0.04	13.47	10.87±0.95	12.35
Groundhog	-0.154 (N/A)	0.78±0.10	26.60	12.07±1.26	14.78
Wells Gray	-0.025 (-0.132/0.023)	0.84±0.02	12.17	16.72±1.16	9.81
Barkerville	0.050 (0.006/0.091)	0.83±0.08	23.57	15.58±2.32	44.64
North Cariboo Mtn.	0.002 (N/A)	0.91±0.06	8.55	9.63±0.37	6.63
Hart Ranges	-0.013 (N/A)	0.93±0.04	6.76	13.29±1.79	23.35
TOTAL		0.83±0.01	18.18±3.21	12.88±1.33	31.66±9.36

*CV = coefficient of variation

Annual survival rates of female caribou varied considerably among subpopulations (Table 4.3). Multiyear average survival rates ranged from 0.52 ± 0.11 in the Purcells-South subpopulation to 0.93 ± 0.04 in the Hart Ranges subpopulation. The coefficient of variation of female adult survival rates varied from 6.76 to 37.22 (Mean= 18.18 ± 3.21) within subpopulations. The temporal variation in adult female survival was larger than the temporal variation in the percentage of calves ≥ 10 months of age in 4 of the 10 subpopulations.

EFFECT OF DEMOGRAPHIC RATES ON POPULATION GROWTH

This analysis was limited to 8 subpopulations because estimates of demographic rates in 2 subpopulations predated the time period used to estimate population trends. I constructed 3 plausible regression models to explain variation in rates of increase among subpopulations (Table 4.4). The first model used only female adult survival, the second used only recruitment to ≈ 10 months of age and the third used female adult survival and recruitment as independent variables. The model using only average adult female survival was the most parsimonious and is 2.68 times more likely than the model using recruitment. The model using both adult female survival and recruitment did not improve model fit, because adult survival rates were correlated to recruitment rates (Figure 4.1).

Table 4.4. Akaike's information criterion (AIC_c) scores for small sample sizes, AIC_c differences (Δ), AIC_c weights (ω), and number of model parameters (k) for candidate models developed to explain variation in population growth rates (r) among mountain caribou subpopulations (n).

Model	n	k	AIC_c	ΔAIC_c	$AIC_c \omega$
Adult female survival	8	3	-34.15	0	0.72
Recruitment	8	3	-32.17	1.98	0.27
Adult female survival + Recruitment	8	4	-24.81	9.34	0.01

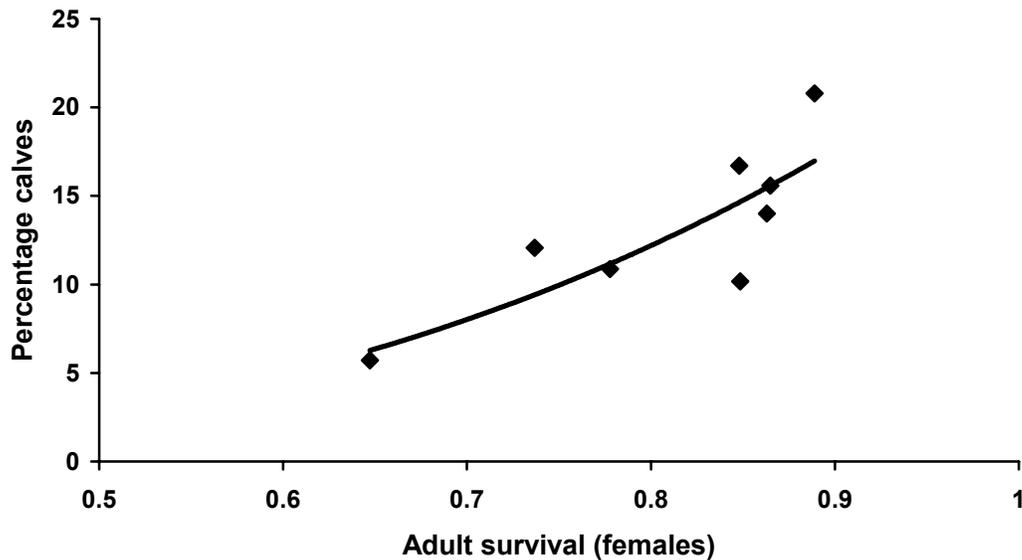


Figure 4.1. Correlation between multiyear average female adult survival rates and multiyear average percentage of calves of mountain caribou during population censuses in late March.

EFFECT OF ENVIRONMENTAL CONDITIONS ON ADULT SURVIVAL

I analyzed 53 models (1 variable & 2 variables) to evaluate the effects of population density, variation in snow depth, and habitat conditions on female adult survival. I excluded all models using >2 covariates because they did not improve model fit. Adult survival declined with increasing proportions of young forest stands (PROP1, PROP2), increasing amounts of forest edge (ED1, ED2), mean patch sizes of forests age 41-100 years (MPS2), and increasing variation in annual snow depth during late winter (SNOW). Adult survival increased with higher proportions of non-forested habitat (NONFOR), population densities (DEN), mean patch sizes of forest age 1-40 years (MPS1), and greater inter-patch distances to young forest stands (MNN1, MNN2).

Using the criteria of 0-2 ΔQAIC_c for defining the top model set, suggested that up to 12 models should be considered (Table 4.5). The top ranked model, $(\phi, \text{area}) = \text{PROP2}$, was 1.73 times as likely to be the best candidate model as the second

ranked model, (ϕ , area)=PROP1. Despite substantial model selection uncertainty, several main survival effects were consistent across top models supporting their importance to caribou survival (Table 4.5). The proportion of young forests age 1-100 years was a main effect in 11 of the 12 top models (\sum QAIC_c weights for models in the top set with proportion of young forests=0.56). The effects of forest fragmentation were included in 5 of the 12 top ranked models (\sum QAIC_c weights=0.21). The effects of population density (DEN) and non-forested (NONFOR) were present in the top model set, but with lower Akaike weights (\sum QAIC_c weights=0.12 & 0.04 respectively). Effects due to variation of annual snowfall (SNOW) were not present in the top model set.

Table 4.5. Top model set of covariates explaining variation in female adult survival among subpopulations; adjusted Akaike's information criterion (QAIC_c) scores for small sample sizes, QAIC_c differences (Δ), QAIC_c weights (ω), and number of model parameters (k) (see Table 4.2 for model codes).

Model	k	QAIC _c	Δ QAIC _c	QAIC _c ω
PROP2	2	472.44	0.00	0.09
PROP1	2	473.53	1.09	0.05
PROP1+MNN2	3	473.63	1.20	0.05
PROP1+PROP2	3	473.64	1.20	0.05
PROP1+MPS2	3	473.73	1.29	0.05
PROP2+NONFOR	3	473.92	1.49	0.04
PROP2+ED1	3	474.13	1.70	0.04
NONFOR+DEN	3	474.16	1.72	0.04
PROP1+DEN	3	474.18	1.74	0.04
PROP2+DEN	3	474.33	1.90	0.04
PROP2+MPS1	3	474.35	1.91	0.04
PROP2+MNN1	3	474.44	2.00	0.03

DISCUSSION

TEMPORAL VARIATION IN ADULT SURVIVAL AND RECRUITMENT

My first objective was to quantify the influence of demographic rates on the population trend of mountain caribou in British Columbia. Because pregnancy rates in mountain

caribou during this study were high with low temporal or spatial variation (Chapter 2), I limited my analysis to the influence of adult survival and recruitment on population trend. I found considerable temporal variation in annual survival rates of females (CV >10%) in 8 out of 10 subpopulations. The CV in adult female survival across all subpopulations ranged widely between 6.8% and 37.2%, but even when pooled over subpopulations, the mean CV of 18.2% was substantially higher than the temporal variability in adult survival rates generally reported for single populations of large herbivores (e.g. mean CV for Cervids = 9.4%; Gaillard *et al.* 2000). I also found recruitment rates of mountain caribou to vary considerably over time. When pooled over subpopulations, the average CV in recruitment rates of 31.7% was only about 1.7 times greater than the temporal variation in adult survival rates. Also, in 4 of the 10 subpopulations, the temporal variation in recruitment rates was lower than the temporal variation in survival rates of adult female caribou.

I also found considerable spatial variation in demographic rates among subpopulations. Mean annual survival rates of females varied between 0.52 and 0.93. Survival rates of females in some subpopulations during this study were substantially lower than survival estimates of woodland caribou previously reported (Stuart-Smith *et al.* 1997, Rettie & Messier 1998, Mahoney & Virgl 2003). The low survival rates found in some subpopulations, however, were similar to female survival rates in another rapidly declining woodland caribou population (i.e. 0.70; Schaefer *et al.* 1999). Recruitment rates also varied among subpopulations ranging from 5.7% to 20.8% calves observed at \approx 10 months of age. The proportion of calves in most subpopulations was below the 15% that Bergerud (1974) suggested was needed to maintain stable populations. My results indicated that recruitment rates were highly correlated with female survival rates, suggesting that both may be linked by a common mortality agent (Seip & Cichowski 1996, Schaefer *et al.* 1999). Finally, my results indicate that the variation in rate of

increase among populations is best explained by differences in adult female survival rates.

Analyses of life history characteristics of long-lived herbivores have shown that population growth rates are most sensitive to changes in adult female survival and least sensitive to changes in juvenile survival (Tuljapurkar & Caswell 1997, Gaillard *et al.* 2000). The importance of adult female survival on rate of population change has been documented in many ungulates including Soay sheep (*Ovis aries*) (Coulson *et al.* 2001) and red deer (*Cervus elaphus*) (Albon *et al.* 2000). However, many studies demonstrate the reverse pattern where changes in population growth are predominately caused by juvenile survival, because adult female survival is very stable over time while juvenile survival is highly variable (Saether 1997, Gaillard *et al.* 1998, 2000).

Studies of caribou have generally found high temporal variation in adult female survival. Similar to my results, Gasaway *et al.* (1992) reported high temporal variation in adult female survival in a declining caribou population that was associated with high levels of predation from wolves that were primarily sustained by an alternative prey species. In addition, Crête *et al.* (1996) have shown that in a declining caribou population, decreased female survival accounted for most of the between-year variation in population growth rates. The caribou studies often differ from many others that have described the population dynamics of large herbivores in that (1) caribou populations were often declining, (2) their decline is likely due to high predation rates where caribou are a secondary prey and predators are maintained by a variety of alternate prey species, and (3) across most of the caribou distribution, the full complement and abundance of their natural predators remain. For example, in my study area there are 5 predator species that are known to prey on adult caribou (Chapter 2). The predator-prey dynamics of these complex systems may lead to periods of high predation rates on all

age classes of caribou when they lack an adequate anti-predation strategy such as migration or spatial separation from predators and their prey.

EFFECTS OF LANDSCAPE HABITAT CHARACTERISTICS ON ADULT SURVIVAL

My second objective was to test the importance of several environmental factors on changes in demographic rates. I limited my analysis to factors influencing the adult survival rates, because variation in population rates of increase were best explained by adult survival and recruitment rates were correlated with adult survival. I also limited my explanatory factors to those available such as snow depth, forest age and distribution, and caribou density. I could not include either alternate prey or predator numbers, because these were unknown. Of the factors that I analyzed, habitat and population density appeared to have the greatest effect on survival of adult females.

From the 12 top models explaining differences in adult survival among subpopulations, 11 had the proportion of their range covered by 1-100 year-old forests as an explanatory covariate. In these 11 models, survival was negatively associated with increasing amounts of young forest stands (1-100 years). The top ranked model included only the proportion of forests aged 41-100 years as the explanatory variable. I suggest that 41-100 year old forests do not support ideal conditions for either caribou or alternate prey species, but is an indication of changes to the forest age structure and thus the forest ecosystem (predator-prey), over longer periods of time. In addition, differences in the amount of 41-100 year old forests among subpopulations are likely an indication of dryer climates with a more frequent fire history, and thus is generally better habitat for a variety of other prey species and their predators. The second ranked model included the proportion of the subpopulation range that consisted of 1-40 year old forest stands. Forests of this age, being recently logged or burned areas, are good habitat for moose, other ungulates, and their predators (e.g. Schwartz & Franzmann 1991). Thus, my data support the mechanistic link between the amount and configuration of habitat

characteristics suitable for moose and other alternate ungulates within a subpopulations range, and survival of adult female caribou in that subpopulation. Other covariates present in the top model set indicated that the distribution of young forest stands such as edge density (ED1) were also negatively correlated to caribou survival.

Conversely, survival was positively correlated with an increase in population density in combination with the proportion of young forests. This supports my observation that the decline of mountain caribou continues even at very low densities because of increases in alternate prey species as a result of forestry practices (Chapter 3). Because of this increase in alternate prey species, the total response of predators might become independent of the secondary prey (i.e. caribou) and thus result in population extinction (Sinclair *et al.* 1998). Survival was also positively correlated to the mean patch size of young forest stands (1-40 years). Woodland caribou have been known to initially feed in young forest stands immediately after fire (Schaefer & Pruitt 1991). Also, there is usually a time delay before moose respond to habitat alterations (Schwartz & Franzmann 1989). Based on my results, habitat change is most probably responsible for much of the variation in adult female survival.

At the subpopulation scale, effects of variation in snow depth during this study were of minor importance. I expected variation in snow depth to be possibly significant in the subpopulations that occasionally have a >4 m snowpack. In these subpopulations caribou are forced to the valley bottoms early in the winter because arboreal lichen does not persist below 4 m above the ground (Goward 1998) and herbaceous plant foods are buried by early winter snowfalls. In areas with less snowfall, lichen persist lower in the canopy and can be reached by caribou without relying on a deep snow platform. Long term directional climate trends, however, may have significantly contributed to the overall decline of mountain caribou in British Columbia (Spalding 2000). Lower snowpacks

during the past century may have contributed to the observed increase in distribution and abundance of alternate prey species and thus of predators across the ecosystem.

An analysis of this spatial extent has inherent problems. Foremost was the lack of data on important factors such as alternate prey and predator numbers. There was also uncertainty and data quality variation in the habitat classification maps available. The forest age maps differed in accuracy between operable and non-operable forested land and all forested land in National or Provincial Parks. The very broad scale of my analysis and habitat categories, however, was unlikely affected by inaccuracies at the detailed scales of these map layers. The temporal scale of my analysis was limited to a maximum of 14 years - not even the life span of an individual caribou. Factors such as one unusual winter could have disrupted the predator-prey system in the area of 1 or more subpopulations and had an effect not typical of the area. Other temporal scales such as historic distribution and spatial scales such as the individual home range may produce different results and should be appropriately analyzed. There was also uncertainty associated with model selection that was expressed in terms of Akaike weights. The model selection process, however, did not result in 1 clearly best model so other possibilities were probable. Finally, because I compared data sampled over the entire distribution of mountain caribou, I likely included sampling variation, the variation attributable to estimating a parameter from sampled data (White *et al.* 2002).

These levels of uncertainty, however, do not negate the result of my study that differences in the amount and distribution of young forest stands as a result of forest management practices had the greatest effect on adult survival. My results should be considered as hypotheses generated from observational data and should be tested using more controlled field experiments.

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CHAPTER 5 - A POPULATION VIABILITY ANALYSIS FOR MOUNTAIN CARIBOU: THE EFFECT OF INVERSE DENSITY DEPENDENCE IN FEMALE ADULT SURVIVAL

INTRODUCTION

Population viability analysis (PVA) is commonly used to assess the probability of a population reaching some threshold, such as extinction, under either current conditions or those predicted from proposed management regimes (Boyce 1992, Reed *et al.* 2002). The importance of a PVA often lies less with predicting absolute time to extinction, and more in the identification of factors that most affect population growth or the likelihood of extinction (Reed *et al.* 2002). To make reliable predictions about population persistence, PVA should incorporate both empirical data from the system of interest and an estimation of the degree of stochasticity inherent in the system (Engen *et al.* 2001). When used in this manner, PVA can be a valuable tool for both scientists and managers for predicting the probable fate of a population, along with the demographic parameters that most influence that fate.

Understanding how demographic parameters change with population density, is important for making predictions about population persistence (Boyce 1992, Henle *et al.* 2004). Our understanding of density-dependent processes, however, are usually based on results from large, viable populations where the per capita growth rate typically decreases with increasing population density (i.e. density dependence) (Sinclair 1989). Oppositely, at very small population sizes, the per capita growth rate may decrease with decreasing population densities (Courchamp *et al.* 1999, Stephens & Sutherland 1999). Several mechanisms have been hypothesized to cause this inverse density dependence including Allee effects and depensatory predation.

Recent theoretical studies have demonstrated the potential importance of inverse density dependence for the persistence of small populations (Lande *et al.* 1994, Brassil

2001, Dennis 2002). However, empirical evidence of inverse density dependence remains rare (Sæther *et al.* 1996, Courchamp *et al.* 1999) because it is inherently difficult to measure population growth rates at low densities (Morris 2002). Consequently, resource managers frequently ignore the potential importance of negative changes in demographic parameters with declining population density when attempting to predict population persistence.

Mountain caribou are an ecotype of woodland caribou (*Rangifer tarandus caribou*) found exclusively in the wet-belt of interior British Columbia and extreme northern Idaho (Heard & Vagt 1998). These caribou are considered 'threatened' by the Committee on the Status of Endangered Wildlife in Canada, because of increasing population fragmentation and declining population sizes (COSEWIC 2002). This decline appears to be caused by high mortality rates of adult females, with predation being the primary cause of mortality across the ecotypes' distribution (Chapter 2, 3, 4). It has been suggested that high predation rates are a result of caribou being secondary prey to predator populations, which are suspected to be increasing due to expanding populations of alternate prey (Seip 1992, Chapter 3). The increase in availability of alternate prey likely occurs in areas with high proportions of early seral stages produced by timber harvesting and wildfire. As a result the per capita predation is higher at low caribou densities and population growth rates of mountain caribou subpopulations become increasingly negative with declining population size (Chapter 3).

The objective of this study is to carry out a PVA and estimate the risk of extinction for mountain caribou in British Columbia. First, I initialize stochastic population projection models (Beissinger & Westphal 1998) for the identified subpopulations of mountain caribou to estimate the mean time to extinction. I then examine female adult survival rates relative to population densities, and finally, explore the effect that reduced female adult survival rates at low population densities has on mean time to extinction.

Thus, my overall focus is to examine the reliability of estimating population projections in relation to our level of understanding of changes in demographic parameters at low population densities.

METHODS

POPULATION STRUCTURE

The population structure of mountain caribou was delineated from telemetry locations sampled from >350 radiocollared adult caribou (Chapter 2). Based on the extensive radiotelemetry data, I identified 17 subpopulations (excluding the South Selkirks subpopulation) with no recorded movements of collared caribou among subpopulations. The South Selkirks subpopulation was excluded because this subpopulation was augmented by caribou translocations until recently (Compton *et al.* 1995). I adopted the population structure delineated in Chapter 2 but also excluded the Monashee-South subpopulation from this analysis because a lack of reliable estimates of the subpopulation range size made it impossible to reliably estimate population density. For each of the remaining 16 subpopulations I developed fully-randomized, individual-based models to project subpopulation persistence (Beissinger & Westphal 1998).

MODEL PARAMETERS

All 16 subpopulations were censused concurrently in 2002, and I used the obtained population estimates to initialize the PVA model. Animals were grouped into 2 sexes and 3 age categories (adults >2 years, juveniles 1-2 years, calves <1 year). I used the following estimates of demographic rates with mean ± 1 SE of the mean to account for uncertainty in the estimation of demographic rates.

(1) Population density: I divided subpopulation size in the year 2002 by the area of the subpopulation's range estimated from telemetry data (Chapter 2) to derive an index of caribou density within each subpopulation.

(2) Sex ratio: During census flights in late March, antlered females were often difficult to distinguish from young males. Thus, in the absence of reliable estimates of sex ratios for individual subpopulations I assumed fixed sex ratios with 58% females and 42% males, within the range of sex ratios commonly reported for woodland caribou (e.g. Schaefer *et al.* 1999: 38.87% males; Stuart-Smith *et al.* 1997: 46.5% males).

(3) Adult survival rates: I estimated adult survival rates from radiocollared animals using known-fate models in MARK (White & Burnham 1999). Estimates of survival rates of adult females were available for 10 subpopulations (data from Chapter 4). Too few males were sampled to estimate survival of adult males for individual subpopulations. Thus, I pooled telemetry data of all males over all subpopulations to estimate an average survival rate for male mountain caribou. I bounded adult survival at 0.95, slightly above the maximum average survival rate of 0.93 estimated for adult females in the Hart Ranges subpopulation (Chapter 4), because average annual adult survival rates >0.95 have not been previously reported (Stuart-Smith *et al.* 1997, Rettie & Messier 1998, Schaefer *et al.* 1999).

(4) Birth rate: I estimated birth rates (Br) from pregnancy rates determined from blood progesterone levels consistent with pregnancy (Rehbinder *et al.* 1981). Blood samples were taken from 134 adult females (>2 years) across 8 subpopulations and 11 different years (data from Chapter 2). I then estimated the expected number of calves born in late May - early June as:

$$\text{Births} = Nf_t * Br \quad (1)$$

where Nf_t is the number of females at time t . Each adult female gives birth to only 1 calf per year. I assumed the sex ratio of calves at birth to be equal.

(5) Calf survival: I estimated calf survival (S_c) until 10 months, from the proportion of calves per adult female during population censuses the following late winter (data from Chapter 2). Calf survival was bounded at a maximum population density of 0.17 individuals/km² by assuming linear density dependence. Such an assumption is necessary to prevent exponential population growth in populations with high adult survival rates. A population density of 0.17 individuals/km² is higher than densities of 0.03-0.13 commonly reported for woodland caribou with unexploited predator populations (Bergerud 1992, Thomas & Gray 2002).

(6) Juvenile survival: In the absence of actual data on survival rates of juveniles, I assumed that juvenile survival equals adult survival in the identified subpopulations because animals \approx 10 months of age are likely to experience similar mortality rates as older animals (Bergerud 1980, Fuller & Keith 1981).

(7) Age of first reproduction: Woodland caribou can give birth as early as 2 years of age (Rettie & Messier 1998). In the absence of reliable empirical data for mountain caribou, however, I conservatively estimated age of first reproduction at 3 years commonly reported for barren-ground caribou (e.g. Whitten *et al.* 1992).

Due to variation in animal samples among subpopulations, estimates of demographic rates were not available for all subpopulations, so I replaced missing values with long-term averages pooled over all years and subpopulations. Demographic data for the demographic rates of the 16 subpopulations are summarized in Table 5.1.

Table 5.1. Summary of values of demographic rates used to initialize the PVA for mountain caribou in British Columbia.

Subpopulation	Population size	Density (km²)	Sex ratio (female:male)	Survival (females)	Survival (males)	Birth rate	Calf survival
Purcells-South	17	0.0220	58:42	0.52±0.11	0.87±0.04	0.92±0.02	0.28±0.16
Purcells-Central	6	0.0161	58:42	0.83±0.01	0.87±0.04	0.92±0.02	0.28±0.16
Nakusp	108	0.0462	58:42	0.85±0.04	0.87±0.04	0.92±0.02	0.28±0.16
Duncan	20	0.0447	58:42	0.83±0.01	0.87±0.04	0.92±0.02	0.28±0.16
Columbia-South	39	0.0221	58:42	0.87±0.04	0.87±0.04	0.92±0.02	0.28±0.16
Frisby-Boulder	20	0.0326	58:42	0.88±0.08	0.87±0.04	0.92±0.02	0.28±0.16
Columbia-North	188	0.0415	58:42	0.78±0.04	0.87±0.04	0.92±0.02	0.28±0.16
Kinbasket-South	14	0.0184	58:42	0.83±0.01	0.87±0.04	0.92±0.02	0.28±0.16
Groundhog	15	0.0117	58:42	0.78±0.10	0.87±0.04	0.92±0.02	0.28±0.16
Wells Gray	526	0.0646	58:42	0.84±0.02	0.87±0.04	0.92±0.02	0.28±0.16
Allan Creek	17	0.0705	58:42	0.83±0.01	0.87±0.04	0.92±0.02	0.28±0.16
Barkerville	58	0.0782	58:42	0.83±0.08	0.87±0.04	0.92±0.02	0.28±0.16
North Cariboo Mtn.	279	0.1568	58:42	0.91±0.06	0.87±0.04	0.92±0.02	0.28±0.16
George Mtn.	4	0.0201	58:42	0.83±0.01	0.87±0.04	0.92±0.02	0.28±0.16
Narrow Lake	72	0.1698	58:42	0.83±0.01	0.87±0.04	0.92±0.02	0.28±0.16
Hart Ranges	325	0.0835	58:42	0.93±0.04	0.87±0.04	0.92±0.02	0.28±0.16
AVG*				0.83±0.01	0.87±0.04	0.92±0.02	0.28±0.16

*AVG = long-term averages pooled over all subpopulations

MODEL STRUCTURE & SIMULATIONS

I assumed that the majority of calf mortality in caribou occurs within the first 2 weeks after calving (Whitten *et al.* 1992, Adams *et al.* 1995). Calves are, therefore, assumed to be born at the beginning of time step t , at the onset of the calving season and all calf mortality occurs immediately after. The total population size N_{t+1} is determined after calf births and deaths. Thus, the individual-based single population models were of the following basic structure:

$$N_{t+1} = S(f)_{t,a} * N(f)_{t,1+} + S(m)_{t,a} * N(m)_{t,1+} + S(c)_{t,1} * Br_t * N(f)_{t,3+} \quad (2)$$

where $S(f)_{t,a}$ is the adult survival rate of females, $N(f)_{t,1+}$ is the total number of females ≥ 1 year old, $S(m)_{t,a}$ is the adult survival rate of males, $N(m)_{t,1+}$ is the total number of males ≥ 1 year old, $S(c)_{t,1}$ is the calf survival rate, Br_t is the birth rate and $N(f)_{t,3+}$ is the total number of adult females of ≥ 3 years of age.

I chose a maximum time interval of 1000 years to estimate the frequency distributions of extinction probabilities and considered a time period of 200 years to estimate mean time to extinction. Each model was simulated 2000 times. For each time step (i.e. 1 year), model parameters were drawn randomly around the parameter mean (Table 5.1). In addition, I accounted for demographic stochasticity by testing each individual against a demographic rate (e.g. survival rate) for that year to determine its fate. Population parameters were updated at the beginning of each calving season. Subpopulations were considered extinct if $N_{t+1}=0$, however, adult females could only give birth when there was at least 1 male in the subpopulation. I then estimated mean time to extinction for mountain caribou from the proportion that subpopulations went extinct during every simulated time step.

DENSITY & ADULT SURVIVAL

In Chapter 3, I showed that the decline in mountain caribou is accelerated at small subpopulation sizes and at small subpopulation densities per amount of suitable winter

foraging habitat. In addition, I showed that variation in rates of increase among subpopulations is best explained by variation in survival rates of adult females among subpopulations and that survival rates are positively correlated with increasing subpopulation densities (Chapter 4). Based on the available data, I estimated average female survival rates as a function of subpopulation density to evaluate the potential impact of inverse density dependence in female adult survival on the mean time to extinction. Thus, each value of adult female survival used in the model was drawn at random from values observed in the field at a similar subpopulation density (Shaffer 1983, Burgman *et al.* 1993), using the coefficient of variation to estimate the variance around the mean (Chapter 4).

RESULTS

Using current estimates of demographic rates and excluding potential effects of inverse density dependence, 14 of the 16 subpopulations have cumulative extinction probabilities of 1.0 within the considered time period of 200 years (Figure 5.1). I present extinction probabilities as median times to extinction because the frequency distribution of extinction probabilities were not normally distributed (Figure 5.2). The predicted median times to extinction were <100 years for all 14 of the subpopulations that are predicted to go extinct (Table 5.2). The 95% confidence intervals of 4 of these 14 subpopulations, however, overlap the 100-year time interval. Both, the George Mountain and the Purcells-Central subpopulations have the shortest predicted median time to extinction with 12 and 17 years, respectively. Median times to extinction were significantly shorter in subpopulations with small initial population sizes (GLM: $R^2=0.692$, $df=13$, $F=29.140$, $p<0.001$) (Figure 5.3). Assuming constancy in demographic parameters, only the Hart Ranges subpopulation does not appear to be at risk of extinction within the time frame of this analysis.

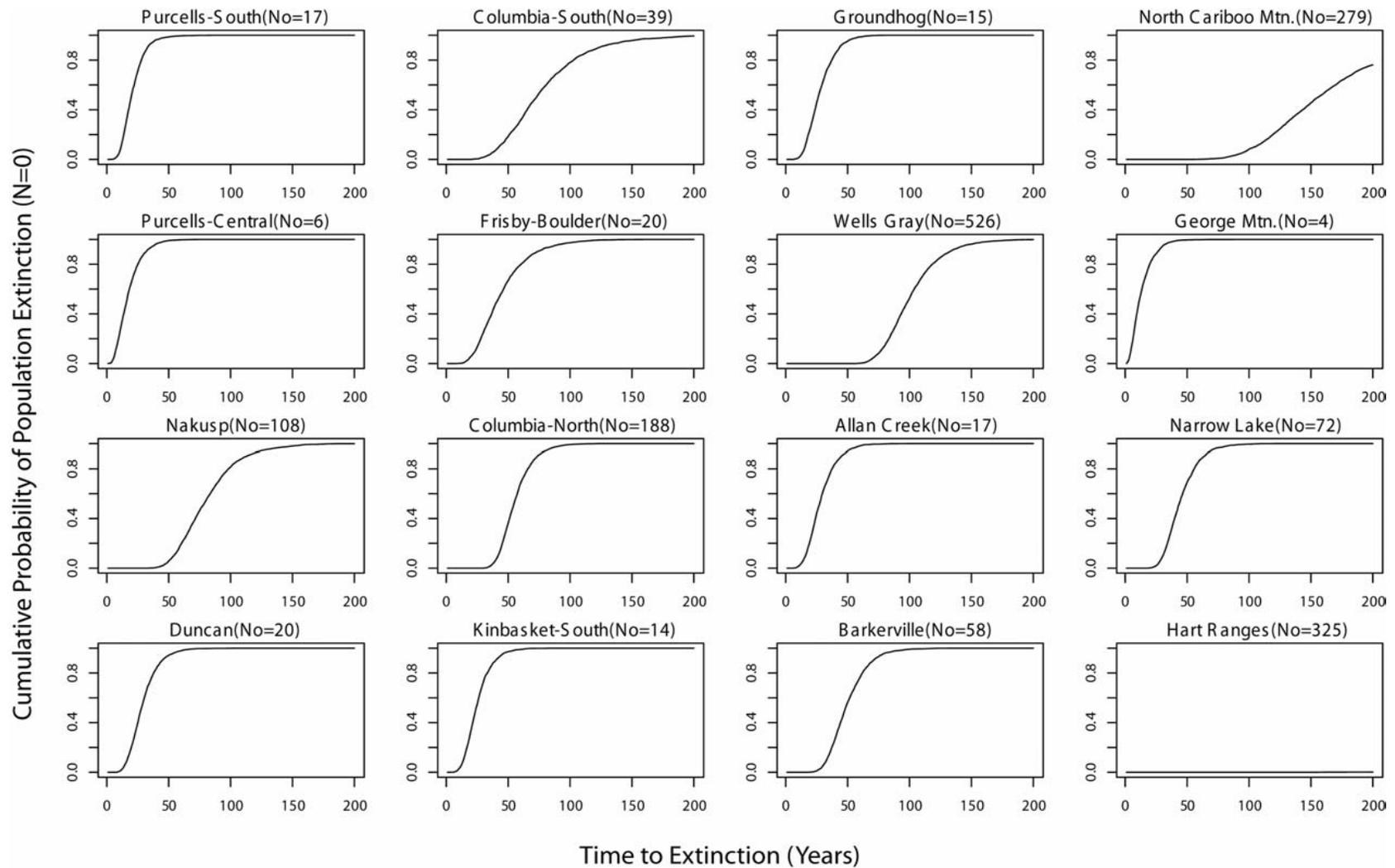


Figure 5.1. Cumulative probability of population extinction for 16 mountain caribou subpopulations in British Columbia, assuming constancy in current estimates of demographic parameters.

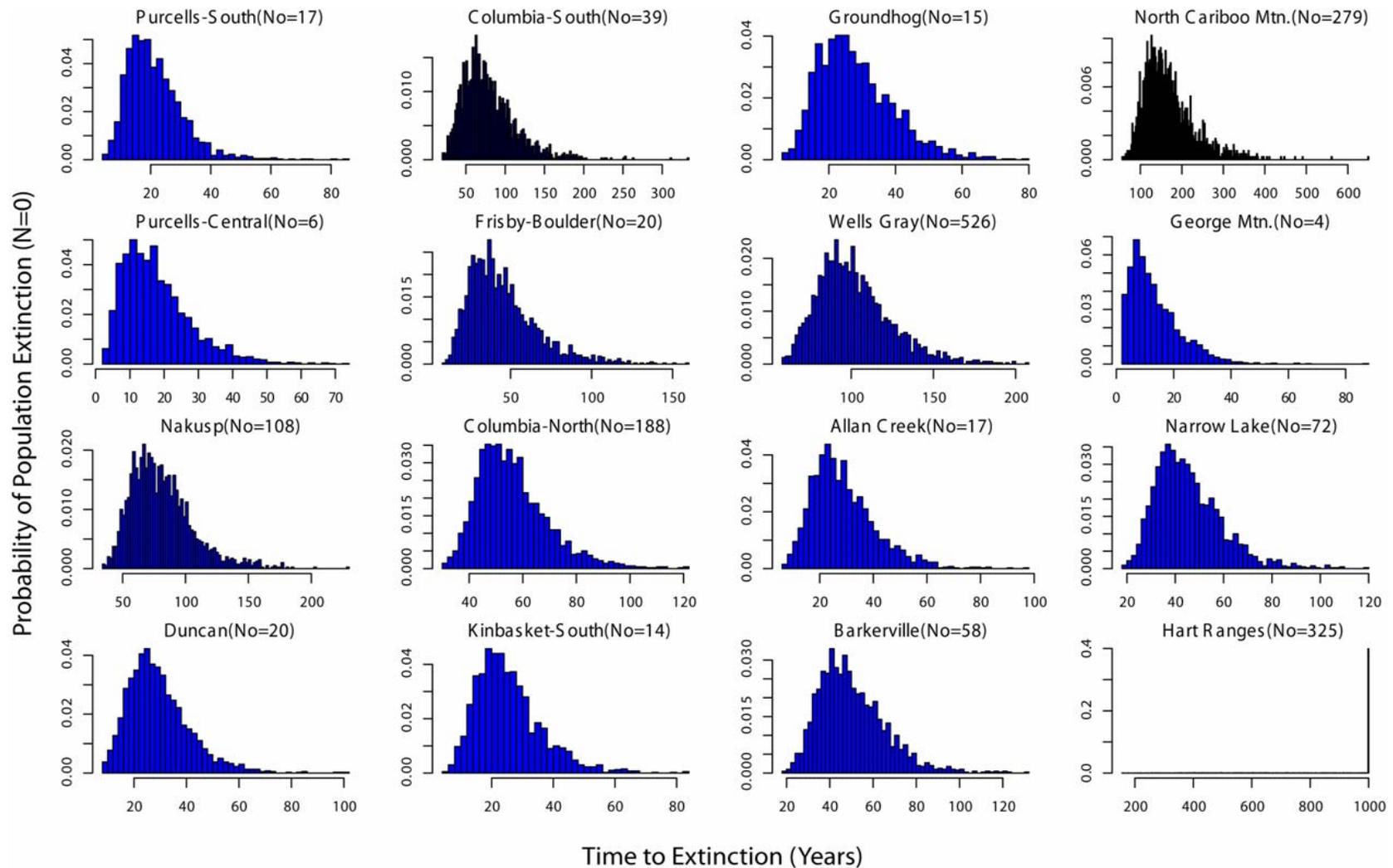


Figure 5.2. Frequency distributions of probabilities of population extinction for 16 mountain caribou subpopulations in British Columbia, assuming constancy in current estimates of demographic parameters (note different scales on x-axis).

Table 5.2. Median (95% confidence intervals) and modal times to extinction for 16 mountain caribou subpopulations in British Columbia, assuming constancy in demographic parameters.

Subpopulation	Median	95% CI	Mode
Purcells-South	20	9-44	17
Purcells-Central	17	5-44	17
Nakusp	78	47-146	68
Ducan	28	13-59	26
Columbia-South	73	33-169	48
Frisby-Boulder	41	17-102	38
Columbia-North	55	37-90	52
Kinbasket-South	24	10-52	19
Groundhog	27	12-55	25
Wells Gray	99	68-158	91
Allan Creek	27	12-58	25
Barkerville	48	28-87	42
North Cariboo Mtn.	156	85->200	152
George Mtn.	12	3-36	8
Narrow Lake	43	26-80	43
Hart Ranges	-	-	-

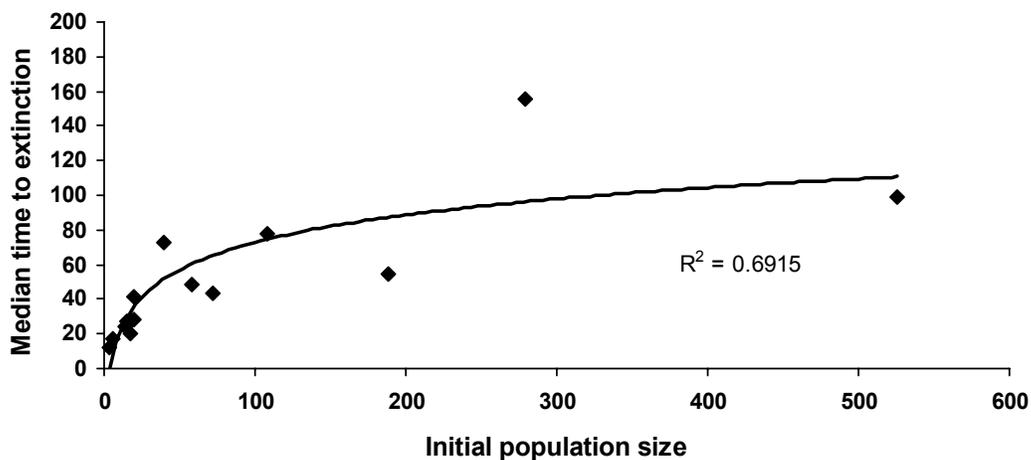


Figure 5.3. Correlation between initial population size and median time to extinction of 15 subpopulations of mountain caribou in British Columbia with predicted median times to extinction of <200 years.

When the observation that survival of adult females decreases with decreasing population densities is included in the model (Figure 5.4), all 16 subpopulations are predicted to decline to extinction within <100 years, with no 95% confidence intervals overlapping 100 years (Figure 5.5, Table 5.3).

Differences in median times to extinction between the scenario assuming constancy in demographic parameters and the scenario assuming inverse density dependence in female adult survival rates were negative for 13 subpopulations. When pooled over subpopulations (excluding the Hart Ranges subpopulation), estimated persistence times decreased by approximately 21% when assuming inverse density dependence in female adult survival. Differences were greatest in subpopulations with large initial population sizes.

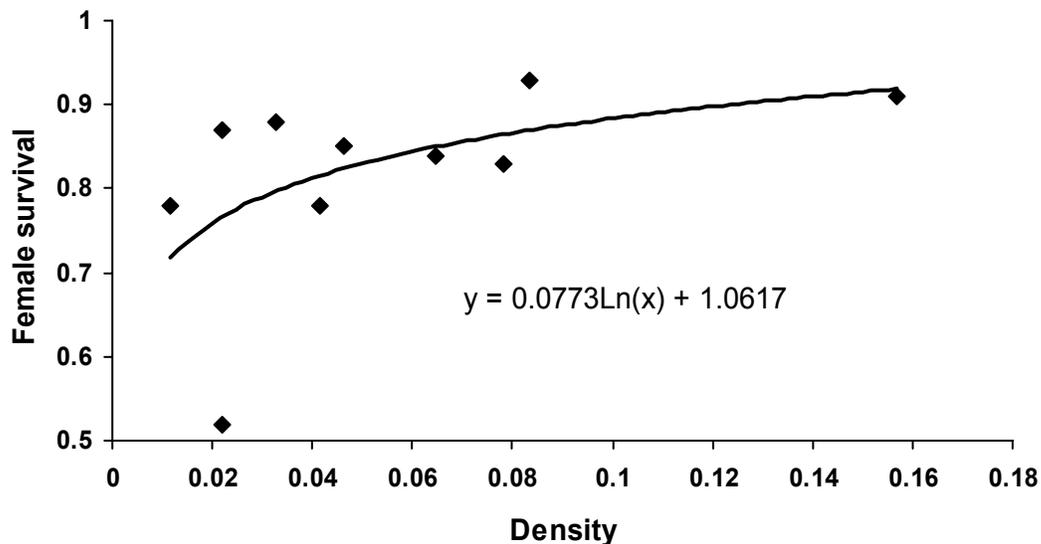


Figure 5.4. Relationship between survival of adult females and population density estimated for 10 subpopulations of mountain caribou in British Columbia.

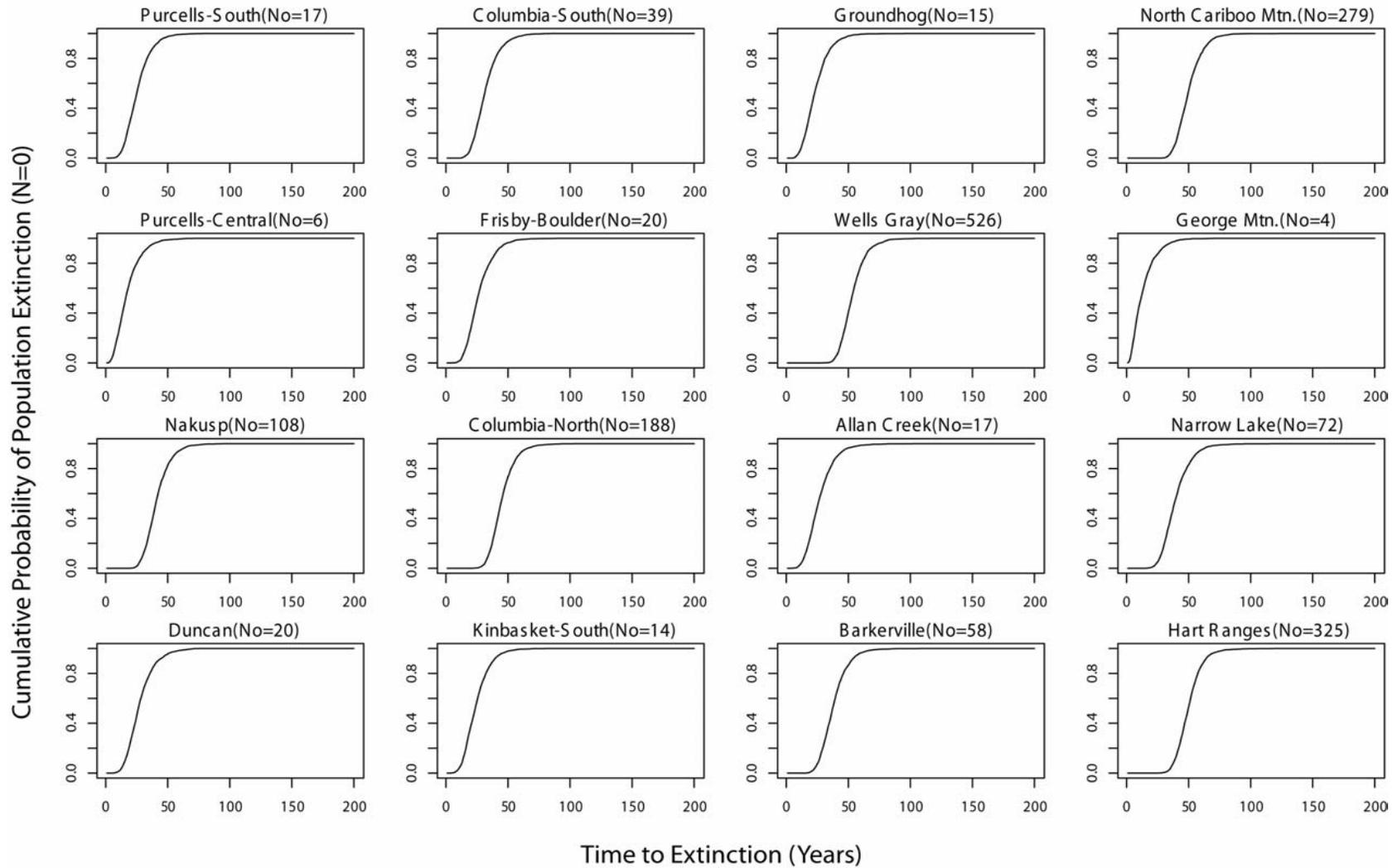


Figure 5.5. Cumulative probability of population extinction for 16 mountain caribou subpopulations in British Columbia, assuming inverse density dependence in survival of adult females.

Table 5.3. Median (95% confidence intervals) and modal times to extinction for 16 mountain caribou subpopulations in British Columbia, assuming inverse density-dependence in survival of adult females.

Subpopulation	Median	95% CI	Mode
Purcells-South	25	11-50	26
Purcells-Central	16	5-44	13
Nakusp	40	26-66	40
Ducan	26	12-56	26
Columbia-South	31	17-58	32
Frisby-Boulder	26	12-54	19
Columbia-North	44	30-70	38
Kinbasket-South	24	10-49	17
Groundhog	23	9-49	22
Wells Gray	53	39-79	49
Allan Creek	26	11-55	22
Barkerville	37	22-64	37
North Cariboo Mtn.	50	35-74	50
George Mtn.	12	3-39	7
Narrow Lake	38	23-65	38
Hart Ranges	50	35-74	50

DISCUSSION

Assessing the likelihood of population persistence is an important task of conservation biologists (Beissinger 2002). My results suggest that if conditions remain constant, mountain caribou in British Columbia are declining towards extinction; 10 of the 16 subpopulations have projected median times to extinction of <50 years. Only three subpopulations (Wells Gray, North Cariboo Mountain, Hart Ranges) have initial population sizes that appear large enough for caribou to persist for >90 years. The extensive sample of radiocollared animals showed no apparent movements among subpopulations (Chapter 2), therefore it is unlikely that smaller subpopulations will experience significant immigration typical for maintenance of metapopulation dynamics (Hanski & Gilpin 1991), that would increase their persistence time. Thus, these results support my conclusions in Chapter 2, that the spatial pattern of decline is associated

with an increasing population fragmentation, and the smallest of these subpopulations have the shortest predicted times to extinction.

My results also suggest, that neglecting inverse density dependence where it occurs will lead to an underestimation of time to extinction and, conversely overestimates of population persistence. Biologically, the observed 21% overestimation of population persistence when inverse density dependence was ignored is a significant decrease in the projected time to extinction. For example, the North Cariboo Mountain subpopulation had their predicted mean time to extinction reduced by approximately 70%. Most significantly, however, the Hart Ranges subpopulation was only considered at risk of extinction when inverse density dependence was included in the model.

Reliable estimates of population persistence depend on our understanding of the effects of population density on demographic parameters at low densities typical for endangered populations. However, few studies have considered these effects using empirical data (Henle *et al.* 2004). The most common method used to simulate the effects of negative changes in demographic parameters at low population densities, is to apply a quasi-extinction level where $N > 1$ (e.g. Dennis 1989, Akçakaya *et al.* 1995, Bascompte 2003). A population is considered doomed to extinction once it reaches or falls below the quasi-extinction level. The influence of quasi-extinction levels on persistence time depends on both the initial population size and the population growth rate. It should always be considered in PVA modelling if populations start from very low numbers and exhibit low population growth rates (Henle *et al.* 2004). Due to a lack of data, however, quasi-extinction levels are frequently estimated and thus can only approximate population dynamics at small population densities. The inverse density dependence in adult female survival that I included, differs from an extinction threshold in that it is based on empirical observations of survival rates across a range of

population densities. Contrary to a quasi-extinction threshold, larger populations were more affected by the inverse density-dependent effects than smaller populations.

It is likely that the projected scenarios I presented are optimistic, even when I assumed that adult female survival rates will decline at smaller population densities. Differences in survival rates of mountain caribou among subpopulations are primarily correlated with habitat alterations creating early seral stages (Chapter 4). These young forest stands support higher densities of alternate prey species such as moose (*Alces alces*) that in turn support higher predator densities (Bergerud & Elliot 1986, Seip 1992). In such altered predator-prey systems, caribou are secondary prey, and predator numbers depend on the alternate primary prey species. Timber harvesting is currently still operating in mountain caribou habitat (Stevenson *et al.* 2001) and will for some time into the future, therefore habitat conditions for alternate prey species may remain suitable or even continue to improve. As a consequence, it is likely, that adult survival will continue to decrease due to increases in incidental predation.

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CHAPTER 6 - GENERAL DISCUSSION: IMPLICATIONS FOR MOUNTAIN CARIBOU CONSERVATION

INTRODUCTION

Historically, woodland caribou (*Rangifer tarandus caribou*) ranged across most of northern North America including the northern United States from Maine to Washington (Banfield 1961). With the exception of the small South Selkirks population in extreme northern Idaho, all those caribou populations in the conterminous United States have since disappeared. Woodland caribou were also more abundant and widespread in Canada. Across much of Canada, populations at the southern limit of their distribution have also disappeared resulting in a northward shift of the southern range boundary (Banfield 1961, Bergerud 1974, Thomas & Gray 2002, Schaefer 2003). As a result, woodland caribou today are virtually endemic to Canada. It is a species of concern over much of its remaining distribution requiring special management in most provinces (Cumming & Beange 1993, Cumming 1998, Edmonds 1998, Rettie *et al.* 1998, Thomas & Gray 2002) including in British Columbia (Hatter *et al.* 2002).

Historic and contemporary causes of decline of woodland caribou likely have varied. Historically, food limitation during winter and/or summer, adverse climate, and overhunting, or some combination of these factors, have been proposed to have impacted population dynamics of woodland caribou in North America (Bergerud 1974, 1996, Spalding 2000). Currently, however, increased predation, facilitated by accelerated forest harvesting and associated increases in ungulate species and predators, is generally considered to be the proximate factor leading to population declines of woodland caribou (Bergerud & Elliot 1986, Rettie & Messier 1998). Population-level effects of increased predation are exacerbated by the low reproductive potential of caribou relative to other ungulate species (Bergerud 1974). The hypothesis

that forest management leads to woodland caribou declines by upsetting the relative stability of the predator-prey system is important if woodland caribou are to be maintained, but a direct link between habitat changes and changes in population dynamics of caribou is lacking.

OBJECTIVES

The objective of this study was to enhance our understanding of the underlying mechanism for the decline of mountain caribou, an ecotype of woodland caribou, in British Columbia. Mountain caribou had been studied intensively across their entire distribution, therefore I adopted a comparative or inter-population approach (*sensu* Sinclair 1991). This allowed me to study variation in population trends and densities, while considering a variety of external factors influencing population dynamics. Specifically, I addressed the hypothesis that forest management leads to mountain caribou declines by altering the predator-prey system. Ultimately, understanding the cause of decline of mountain caribou is essential to develop effective conservation strategies.

FINDINGS

APPARENT EXTINCTION PROCESS

My results predict that mountain caribou are declining towards extinction within <100 years. The distribution of mountain caribou has become increasingly fragmented and isolated, particularly towards the southern part of their distribution. Similarly, most subpopulations are declining with more southern ones decreasing most rapidly. Population fragmentation has resulted in several (n=9) subpopulations with ≤ 20 individuals referred to as sink populations (Pulliam 1988). The extinction risk for such small populations is accelerated by the effect of demographic stochasticity; the random

variation in individual fitness that is independent among individuals (Shaffer 1981, Lande 1993). These sink populations are no longer viable without natural immigration from other subpopulations, because of an increasing isolation of subpopulations especially towards the southern extremity and the resulting loss of connectivity to somewhat larger subpopulations. Although, no subpopulation that was monitored until the end of my analysis in 2002 had become extinct, the George Mountain subpopulation appears to be extirpated based on results of a population census in 2003 (Dale Seip, B.C. Ministry of Forests, pers. communication). However, the Purcells-South subpopulation that dropped from 63 in 1995 to 13 by 2000 (Chapter 2), has since increased moderately, perhaps as a result of intensified hunting pressure on cougars (*Puma concolor*) (Guy Woods, B.C. Ministry of Water, Land and Air Protection, pers. communication).

CAUSE OF DECLINE

Predation was the primary cause of mortality across most of the distribution of mountain caribou in British Columbia. In addition, I found smaller subpopulations to have the most negative rates of increase even though they had very low caribou densities per area of mature lichen-bearing forests. These findings are consistent with the prediction that mountain caribou subpopulations decline because of high predation rates by predators that depend on some other primary prey (Seip 1992). The trend in population decline I observed is likely a consequence of differences in the numbers of alternate prey and predators across the range of all caribou subpopulations. The inverse density dependent decline suggests that in the current predator-prey system, there may not be a point at which caribou numbers stabilize at very low densities.

ADULT SURVIVAL & HABITAT CHARACTERISTICS

Differences in rates of increase among subpopulations were best explained by variation in adult female survival. The temporal variability in adult survival in this and other caribou studies (e.g. Gasaway *et al.* 1992) is different from what is generally reported for large

herbivores (Gaillard *et al.* 2000). The dynamics of caribou may differ from the dynamics of other large herbivores because (1) caribou often experience high predation rates where they fail to effectively separate from alternate prey species, and (2) the full complement and abundance of their natural predators remain across most of the caribou distribution.

Of the factors that I analyzed, habitat and caribou population density had the greatest effect on adult female survival. My findings support the hypothesis that there is a mechanistic link between habitat characteristics suitable for moose (*Alces alces*) and other ungulates and decreased survival of adult female caribou (Rettie & Messier 1998).

IMPLICATIONS FOR MOUNTAIN CARIBOU CONSERVATION

The decline of mountain caribou due to high predation rates appears to be a result of major environmental changes. It is probable that a combination of factors including landscape changes due to forest management, management efforts to increase other cervid populations, and changes in predator management policy, have all influenced ecosystem wide changes in the large mammal predator-prey system. In such an altered ecosystem, predators can cause extinction where rare prey species are incidentally killed while predators depend on some other primary prey species (Sinclair *et al.* 1998).

Some of the factors altering the predator-prey system, such as changes to the forest age structure, likely cannot be rectified in time to maintain mountain caribou. Other factors can be changed. Although overall numbers of some predators and their prey can be changed through hunting regulations, it has been suggested that some individual cougars (Katnik 2002) and specific wolf (*Canis lupus*) packs kill a disproportionate number of caribou. If this hypothesis can be validated, localised reductions of cougars and wolves where predation of caribou is high, might present an effective management strategy to reduce the impact of predators on caribou populations. Given the likelihood

that changes in the predator-prey system have occurred and continue to occur over large areas of the distribution of mountain caribou, it is possible, however, that the remaining subpopulations are no longer viable without continued management of predators. However, there are practical and ethical difficulties inherent in seeking to kill predators (National Research Council 1997, Courchamp *et al.* 2003) as a means of protecting rare species, so we must address the question of whether mountain caribou recovery is acceptable if ongoing predator control is required to maintain them.

Given the objective that mountain caribou conservation is the policy priority, other conservation strategies should be explored. Along with predator management, alternate prey levels should be actively reduced by increasing hunting levels. In addition, guidelines for the management of alternate ungulates need to address the priority of caribou conservation. These need to actively implement management strategies that discourage the increase in other ungulates. Although reactive policies such as translocations have not resulted in an increase in population size in the trans-boundary South Selkirks subpopulation (Compton *et al.* 1995), even with the control of predators, several of the smallest subpopulations may become extirpated without augmentation with additional animals.

WHERE TO FROM HERE?

In my thesis, I did not address all factors that potentially impact the population dynamics of mountain caribou. For example, Simpson & Terry (2000) suggested that an increase in human activities such as the recreational use of snowmobiles may negatively affect mountain caribou population dynamics. The primary concern is related to habitat displacement of caribou from preferred high elevation late winter ranges, that can increase energy expenditure and thus reduce body condition. In elk (*Cervus elaphus*), for example, heavy snowmobile activity has been shown to cause physiological stress

responses in terms of increased fecal glucocorticoid concentrations (Creel *et al.* 2002). Further analyses are required to determine the impact of recreational activities on mountain caribou especially as these activities are increasing and diversifying (e.g. heli-recreation activities).

Finally, like any research project, my results have generated new questions and hypotheses, many of which should be tested using experimental approaches. For example, in Chapter 4, I made the assumption that increased proportions of young forest stands will result in an increase in the abundance of alternate ungulate species such as moose. While this has been shown in many moose studies (see Franzmann & Schwartz (1998) for an extensive review), the assumption has not been verified in the deep snow system of the interior wet-belt mountains of British Columbia. In addition, to further explore the mechanistic link between forest age and increases in alternate ungulate abundances, we must understand the long-term population responses of species such as moose, to the mosaic of forest age stands over time typically generated by current logging practices. We also need to investigate changes in functional and numerical responses of predator populations to increases in alternate prey populations, along with the consequences of such changes for mountain caribou. After the abrupt decline of its primary prey, a predators searching time would increase resulting in an increased probability of encountering caribou and thus higher predation rates. A controlled large scale experimental reduction of moose offers a promising approach to address this question.

Although variability in yearly snow accumulation during late winter did not explain variation in survival of adult females among subpopulations, increased temporal variability in the snowfall pattern as predicted from global warming (e.g. Easterling *et al.* 2000, Walther *et al.* 2002), could have important implications for mountain caribou. For example, a series of several years with low snow accumulation could result in a rapid

local increase in deer (*Odocoileus* spp.) populations and thus of predators (e.g. cougar). Conversely, during a series of winters with high snow accumulation, historically more typical for the interior wet-belt ecosystem, the deer populations would be expected to drastically decline. Thus, to predict the consequences of such weather patterns and the associated changes in the abundance of alternate prey populations on the population dynamics of mountain caribou, requires also an understanding of the response of predators to abrupt changes in the abundance of their primary prey.

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