Proceedings of the Sixth North American Caribou Workshop
Prince George, B.C., Canada,
1-4 March, 1994

Proceedings of the George River Caribou Workshop
Labrador City, Labrador, Canada,
27-29 Jan, 1994

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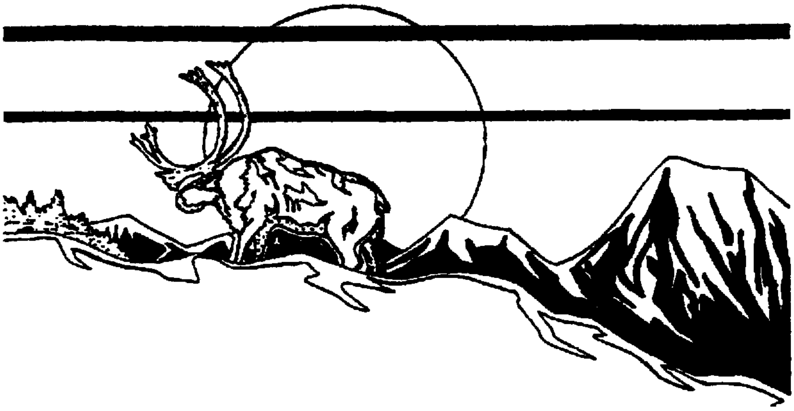

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Proceedings of the Sixth North American Caribou Workshop and the proceedings of the George River Caribou Workshop. (Papers from the George River Caribou Workshop (with asterix) are interspersed where appropriate with the papers from NACW).

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Kent Brown, Debbie Cichowski, Janet Edmonds, Lois Gray, Doug Heard, Chris Ritchie, Dale Seip, Susan Stevenson, Don Thomas, Glen Watts, and Mari Wood.

Preface

The Sixth North American Caribou workshop was attended by over 200 people from across North America, as well as four special guests from Russia. The first day of the workshop featured a session on the population ecology of North American caribou. Caribou in North America naturally occur at densities ranging from several animals/km^2, to less than one caribou/100 km^2. The presentations on population ecology addressed the reasons for these major, naturally occuring differences. The second day of the workshop concentrated on caribou and forest management. Logging and forest products are the primary industries in the Prince George area and the impacts of forestry practices on caribou are an important resource management issue in the area. Consequently, many local habitat biologists and forest industry representatives were especially interested in the presentations on different approaches to integrating forestry and caribou habitat protection across Canada. The third day included a general session with presentations on caribou genetics, physiology, diseases, population parameters, foraging behavior, and management. In addition to the presentations, there were also many excellent poster presentations and some of the papers in these proceedings were presented as posters. On the final day of the workshop, about 50 participants went on a field trip which involved being shuttled by helicopter onto the mountain-tops east of Prince George to see mountain caribou. Participants who were accustomed to seeing caribou living in arctic tundra or boreal forests were very surprised to see and hear about caribou living in large cedar forests and on mountain-tops where snow depths exceeded several meters, and the only available forage was the lichens growing on trees.

We believe that the workshop was a major success with many excellent presentations and posters, as well as opportunities for the participants to meet and discuss caribou research, ecology, and management with their counterparts from across North America. These proceedings include a wide range of excellent papers that provide a permanent record of the workshop. The editors thank the authors and reviewers for their efforts to produce and review these papers.

Section 1.

Population ecology of North American Caribou

The Sixth North American Caribou Workshop,
Prince George, British Columbia, Canada,
1-4 March, 1994.

Introduction to the Population Ecology of North American Caribou

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Rangifer, Special Issue No. 9, 11-12

Caribou (*Rangifer tarandus*) in North America naturally occur at densities ranging from several animals/km^2 to less than one caribou/100 km^2. Seip (1991) and Bergerud (1992) discussed how those major differences in density across North America appear to be related to the impact of wolf (*Canis lupus*) predation, and the strategies used by caribou to avoid wolves. Caribou living in areas without wolves usually occur at high densities and are regulated by competition for food. Migratory arctic caribou coexist with wolves, but their long distance migrations reduce their exposure to wolves during the calving period. Although wolf predation is often a major limiting factor, migratory arctic caribou coexist with wolves at relatively high densities. In the mountains of western North America, caribou usually aggregate on alpine plateaus or disperse in rugged, high-elevation habitat during the calving period and thereby reduce their exposure to wolves. That strategy is only moderately effective so the caribou coexist with wolves at medium densities. Caribou that live in the boreal forests across North America have the least effective options to avoid wolves, and are often reduced to very low densities or even eliminated. Those caribou often calve on islands, in muskegs, or in rugged terrain to avoid wolves.

The impacts of predation on caribou are usually greater in areas where there are other prey species, such as moose (*Alces alces*), that support higher wolf populations, or in areas where other predators such as bears (*Ursus* spp.) are also present. In some areas high levels of human harvest have significantly reduced caribou populations below natural densities. Consequently, habitat modifications that enhance other ungulates, or improve access for human hunters, can be detrimental to caribou populations.

In this session, we asked the presenters to discuss the population ecology of different caribou herds in North America and to evaluate if they fit the general model outlined above. The first paper by Ouellet *et al.* describes two high density caribou herds that live on wolf-free islands and are regulated by competition for food. The next three papers by Crête *et al.*, Heard *et al.*, and Whitten discuss migratory arctic caribou herds. The papers by Farnell *et al.*, Valkenberg *et al.*, and Seip & Cichowski discuss caribou in mountainous areas of western North America. The paper by Cumming *et al.* describes how caribou in the boreal forests of Ontario spatially separate themselves from wolves and moose. The final paper by Bergerud is a review of caribou population ecology and was the special presentation at the banquet.

The presentations were generally consistent with the hypothesis that major differences in density AMONG caribou herds in different areas of North America are related to differences in the impact of wolf predation, and the ability of caribou to avoid wolves. However, many of the papers also stress the major amount of variablility that occurs WITHIN populations from year to year. Much of that variability appears to be related to the impacts of weather and its interactions with food availability and predation. Some of the past debate surrounding caribou population ecology is clarified by making this distinction between the factors responsible for the order of magnitude differences in density AMONG populations across North America, and the factors responsible for the significant year to year variability that often occurs WITHIN populations. Collectively, these papers provide a clearer understanding of those relationships, and their importance to caribou population ecology.

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The George River Caribou Workshop,
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Science, Utilization, Conservation and Co-Management of the George River Caribou Herd

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Rangifer, Special Issue No. 9, 13-16

Throughout the second half of this century, the George River Caribou (*Rangifer tarandus caribou*) population (GRC) which ranges throughout the Ungava and Labrador Peninsulas of the eastern Canadian provinces of Quebec and Newfoundland, has grown to be one of the world's largest barren-ground caribou herds (Couturier *et al.*, 1990). Recent evidence however, suggests that the herd has exceeded the carrying capacity of its range (Messier *et al.*, 1988, Crête & Huot, 1993) and may no longer be growing (Couturier *et al.*, 1994). These indications have generated concern among aboriginal peoples of Quebec and Labrador whose culture and economy depend on the GRC, and among the non-aboriginal residents who rely on the herd for subsistence, sport hunting and eco-tourism. At present, there is no formal arrangement for the joint management of the GRC between the provincial governments of Newfoundland and Quebec, although wildlife managers from both jurisdictions coordinate management activities on an informal basis. Only in Quebec, has a public advisory committee been established (James Bay Hunting, Trapping and Fishing Coordinating Committee). Anderson & Rowell (1991) have called for the establishment of a joint management agreement which would formalize cooperation between the provinces as well as among aboriginal users and government officials.

Surely, some form of cooperative management between users and government is an idea whose time has come. The George River Caribou Workshop, held on January 27-29, 1994, in Labrador City, Labrador, was conceived in that spirit. Initiated by the Labrador Institute of Northern Studies of Memorial University of Newfoundland, the primary objective of the workshop was to bring together scientists, aboriginal and non-aboriginal users and government representatives to discuss issues pertaining to the status and management of the GRC. We quickly learned that this is no easy task.

The GRC occupies a range that crosses a provincial boundary, parts of which are still disputed. Furthermore, the GRC range encompasses several distinct cultural and language groups (french-speaking Quebecois, metis, Inuit of Quebec and Labrador, Innu (Montagnais, Naskapi and Cree) and non-aboriginal English-speaking Labradorians). Clearly, meaningful partnerships can only be forged if these differences are recognized and respected. Early in our discussions, the workshop coordinating committee decided that simultaneous translation into the various languages of the participants was critical to ensure the workshop's credibility and success. Generous grants from the government of Canada (Department of Indian and Northern Affairs and the Office of the Secretary of State) allowed us to provide translation among four different languages. As well, we decided that the workshop would be structured around a small number of keynote addresses to allow ample time for discussion and exchange of ideas among all workshop participants.

Four workshop objectives were identified: (1) to consider present and past assessments of caribou numbers and population trends in the GRC (2) to explore the role of environmental factors such as climate and habitat change on population dynamics (3) to consider actual and potential human activities on the population and distribution of the caribou (4) to discuss caribou management strategies and the co-management concept. The workshop was organized around four half-day sessions focused on each of these objectives and each session featured three or four keynote speakers. An evening panel discussion of the social and cultural significance of the GRC was also organized, and the third day was devoted to an open discussion of workshop presentations, research needs and co-management concepts. The following is a brief overview of the results of this workshop. All keynote addresses are presented in this volume.

We were overwhelmed by the positive response to this workshop. More than 100 people participated, including representatives from each of the aboriginal groups mentioned above, from the federal, provincial and local governments, from the Labrador West Caribou Hunters' Association, the Labrador East Hunters' Association and several independent outfitters and local residents. Klein's plenary address, "Caribou management strategies in the circumpolar north" (this volume), provided a global perspective to the workshop discussions. Issues of caribou management of the GRC are not unique and the variety of management options which Klein reviewed provided much for participants to consider. In closing, Klein pointed out that all of the large migratory herds of caribou in North America have reached peak population levels and, under these conditions, a wide range of management strategies appear to work well. Klein cautioned that the difficult challenges will arise when caribou populations decline. Klein's comments were a timely preface to the session on Population Dynamics in which Couturier & Russell (this volume) presented evidence from the 1993 census indicating that the GRC population is no longer increasing. In a another presentation, Crête *et al.* (this volume) presented data on recruitment and survival that suggested that the population may, in fact, be declining.

As the GRC population has increased in recent decades, the herd's range has expanded and shifted southward and westward. Possible reasons for population and distribution trends were examined in the session on Habitat and Distribution. Climatic variation and its effects on snowfall patterns and winter range conditions may result in fluctuations in caribou density (Huot *et al.*, this volume). However, Maarouf *et al.* (this volume) concluded that the available data do not substantiate a major regional climatic trend consistent with this hypothesis. Instead, recent work by Huot *et al.* (this volume) and correspondent climatic data (Maarouf *et al.*, this volume) provide evidence that the quality of the summer range, and not the winter range, has deteriorated in recent years. Evidence was presented that animals were in poor condition (Huot *et al.*, this volume), and as a result, reduced productivity may be a cause of reduced population growth. Finally, Heard & Williams (this volume) posed the provocative suggestion that the recent southward shift in the distribution of the GRC caribou may result in significant increases in wolf predation as the caribou winter further into the boreal forest.

An evening panel on the cultural, social and economic significance of the GRC raised concerns about the effects on caribou of military low-level flying, hydroelectrical development, road construction and human access. The generally poor condition of the animals was also noted. Both aboriginal and non-aboriginal shareholders expressed strong support for the idea of co-management of the herd. The value of traditional knowledge in understanding the GRC and wildlife in general was emphasized. Anecdotal evidence was provided, of many caribou being slaughtered and not utilized in both Labrador and Quebec.

Information arising from the sessions on population dynamics and distribution set the tone for subsequent sessions on Caribou - Human Interactions and The Co-Management Concept. In his overview, Harrington (this volume) identified hunting (subsistence, sport and commercial), low-level military jet fighter training (Harrington & Veitch, 1991) and hydro-electric development as the three sources of human impact within the range of the GRC, which are of greatest concern. Harrington also emphasized the importance of considering the cumulative effects of these human activitites as well as those of climatic and other environmental changes. Finally, Harrington warned about the danger of concluding that there are no negative consequences of environmental interventions when we are dealing with complex ecosystems and when no substantive evidence can be brought to bear on the issue. Erring on the side of caution, that is assuming that environmental interventions have impacts until proven otherwise, is the safest way to proceed (Montevecchi & Bouman, 1994). Information on the impacts of these human activities is generally poor. In contrast, based on monitoring by Hydro Quebec, Jean Doucet suggested that impacts of hydro-electric development on the GRC have been negligible and may in fact have been beneficial. Guy Bellefleur of the Conseil des Atikanekw et des Montagnais spoke about the negative consequences for caribou of low-level military flying and hydro-electric and forestry practices which involve the opening of roads and consequent access to wildlife habit. Mr. Bellefleur pointed out that some aboriginal groups were greatly concerned with recent increases in sport hunters.

Throughout the workshop, local residents expressed great concern over these possible impacts, although perspectives often varied. For example, with regard to hunting, members of the Labrador West Caribou Hunters' Association expressed concern about subsistence (food) hunting, while members of the Labrador East Caribou Hunters' Association raised issues concerning the future of sport hunting. Likewise, the Labrador Inuit Association has until recently operated a successful commercial harvest of the GRC, while the Labrador and Quebec Innu generally oppose commercial ventures on religious grounds.

Despite these sometimes disparate perspectives, there was support from all of the aboriginal and non-aboriginal user groups for the establishment of a co-management board. Composed of government and non-government representatives from Newfoundland and Labrador, and Quebec, the board would advise government on issues of caribou management. Not surprisingly, the final workshop session on co-management was of particular interest to participants. Presentations by Peter (this volume), Thompson (this volume) and David Kritterdlik reviewed the history and evolution of the Porcupine Caribou Management Board, the Split Lake Caribou Management Board and the Beverly-Qamanirjuaq Management Board, respectively, providing useful management perspectives and strategies. Agreement on the concept of co-management of the GRC was tempered with a great deal of disagreement about how best to initiate and develop such a process. A primary issue of contention centred on whether non-aboriginal shareholders should be formally represented on a co-management board (their preference) or represented by government (aboriginal people's preference). Unsettled aboriginal land rights in the region probably acted to preclude meaningful resolution of such substantive issues. Notwithstanding the lack of agreement on these issues, everyone felt they had learned from the exchange of information, ideas and interactions.

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The Sixth North American Caribou Workshop,
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Population Ecology of Caribou Populations without Predators: Southampton and Coats Island Herds

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Abstract: This paper is a review of the ecology of two caribou populations inhabiting predator-free northern islands, Coats and Southampton Island. Findings are analyzed in light of the hypothesis that in absence of predation or high human harvest, food competition results in delayed puberty, reduced calf production, increased winter starvation of caribou and regulates populations at high densities (>2 km^{-2}). Caribou were hunted to extinction on Southampton Island (Northwest Territories, Canada) by mid-century. In 1967, 48 caribou were captured on neighbouring Coats Island and released on Southampton Island. Southampton Island is characterized by a high per capita winter food availability in summer and in winter. The population on Southampton Island has been increasing at a rapid rate of growth since re-introduction (λ=1.27). Fast population growth was possible because females invested early in reproduction and over winter survival rate was high. The population on Coats Island is also characterized by high per capita food availability in summer but low food availability in winter. The population size has undergone some marked fluctuations, abrupt declines followed by relatively rapid recovery and, contrary to predictions, densities were always less than 1 km^{-2}. Low population densities on Coats Island result primarily from low food availability. This review suggests that in the absence of predation or high human harvest competition for food regulates caribou population abundance. However, caribou numbers can fluctuate markedly among years because inter-annual variation of weather conditions affects forage accessibility in winter. This review also emphasizes the importance of distinguishing between factors that determine absolute population density and variation in density among years (in our case probably plant production and winter weather conditions which influence forage accessibility) from the regulatory factors, processes that stop population increase (competition for winter food leading primarily to density dependent changes in mortality from starvation) when examining population dynamics.

Key words: *Rangifer,* population dynamics, food, snow, density

Rangifer, Special Issue No. 9, 17-26

Introduction

Caribou were hunted to extinction on Southampton Island (Northwest Territories, Canada) by 1955. In 1967, 48 caribou were captured on neighbouring Coats Island and released on Southampton Island, two northern predator-free environments. The dynamics of these two populations differ sharply. The Southampton Island herd has been increasing since its re-introduction, whereas, during the same period of time Coats Island population showed marked fluctuations. In recent years, several aspects of the ecology of these populations have been studied (e.g. Adamczewski *et al.*, 1987a, 1987b, 1988, 1993; Gates *et al.*, 1986a, 1986b; Heard & Ouellet, 1994; Ouellet, 1992; Ouellet *et al.*, 1994).

In a recent review, Seip (1992) suggested that in absence of major predators or high levels of human harvest, caribou and reindeer (*Rangifer tarandus*) populations generally increase until they become regulated by a density dependent competition for food. Competition for food results in decreased nutrient intake, increased energy costs, reduced pregnancy rates, low calf survival and higher mortality rates. Populations of *Rangifer* regulated by competition for food resources often attain densities over 2 km^{-2}. The main objective of this paper is to review the population ecology of two caribou herds inhabiting northern predator-free islands, Southampton and Coats Islands, in light of the above suggestions. A second objective is to speculate about the future of the re-introduced Southampton Island caribou population.

Study areas

Coats (5 600 km^2) and Southampton (43 000 km^2) Islands are at the north end of Hudson Bay, Northwest Territories, Canada. In winter, open water prevents caribou movements between these two islands and the mainland. The climate is typical of the Arctic (Thompson, 1967 *in* Parker, 1975). Strong winds and a short growing season characterized the climate of these islands. Mean annual temperature is - 11 °C with mean daily temperature above freezing only in July and August. Annual precipitation averaged 300 mm. Snowfall is twice as high as at Baker Lake on the mainland at similar latitude (132 vs 57 cm). Snow cover persist from mid September to mid June. Except for an elevated area of granite and gneiss at the northern end, Coats Island consist of low flat limestone plains. The west half and most of the southeast of Southampton Island is also flat but the reminder of the island is steep to rolling Precambrian shield (Adamczewski *et al.*, 1988; Gates *et al*, 1986b; Parker, 1975).

Methods

The paper is primarily a review of all published information regarding the population ecology of Southampton and Coats Islands herds. We incorporated to the paper previously unpublished results of an aerial survey that we conducted on Coats Island during the summer 1991 to estimate caribou numbers. To relate observed changes in caribou numbers to winter harshness we also calculated a winter severity index.

Aerial survey

An aerial strip transect survey was conducted on the 23 and 24 of June 1991 to estimate population size on Coats Island. Sample units were the same 31 strip transects that were flown in 1984 (see Gates *et al.* 1986b) where the starting point was selected randomly. Observers counted caribou within 400 m wide strip on each side of the Cessna 337 aircraft which was flown at 122 m of altitude and at an airspeed of 185 km hr^{-1}. Transects were systematically spaced 4.3 km apart resulting in 20 % coverage. The census zone was not stratified. The only caribou that could be classified in all cases were neonatal calves. Calculations followed Jolly (1969).

Relative winter severity index

A relative winter severity index was calculated according to Gunn *et al.* (1989) based on snow accumulations recorded at the Coral Harbour weather station (Southampton Island). The index is based on percent deviations from the long-term mean (1974-1994) of accumulated snow depth on the last day of the month, for the periods of early winter (September - November), mid winter (December - February), and late winter (March - May).

Results

Population dynamics

Southampton Island herd

The caribou population on Southampton Island grew from 48 (38 one-year-old or older caribou) in 1967, the re-introduction year, to 13 700 ± 1580 (0.31 km^{-2}) one-year-old or older caribou in 1991 (see Fig. 1). The corresponding annual finite rate of growth was 1.27, with no indication of any decline in the rate of growth as population density increased.

Survival rate has not been quantified. However, a population balance model, using known fertility rate, indicated that, assuming 100 % survival of individuals older than calves, calf survival must have been at least 72 % to achieve the observed rate of growth (Heard & Ouellet, 1994). Conversely, if calf survival was 100 % then adult survival must have been at least 92 %. Female (excluding calves) pregnancy rate was near 100 % (all 23 month old females

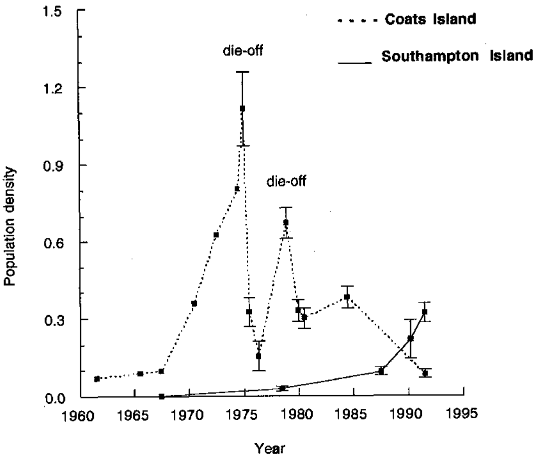

Fig. 1. Trend in caribou population density (number of one-year-old and older animals per km^{-2}) on Coats Island from 1961 and Southampton Island from 1967 (re-introduction) to 1991. Vertical bars represent one standard error of the estimated density. Data source: Coats Island estimates from 1961 to 1974 (unpub. N.W.T. Government files), 1975 to 1984 (Adamczewski *et al.*, 1986b), and 1991 (this study); Southampton Island estimates (Heard & Ouellet, 1994).

examined over a four year period were pregnant [n=21]) (Ouellet, 1992).

Hunting did not play an important role into the population dynamics of this herd because quotas were low relative to the population size (i.e. less than 1 %). Hunting quotas increased gradually from 25 males per year beginning in 1977-78 to 300 males and 100 females in 1990-91 (Heard & Ouellet, 1994).

Coats Island herd

The origin of this population is not known, but caribou have been on the island at least since the early part of the century (Gates *et al.*, 1986b). Over the last three decades the dynamics of this herd was characterized by rapid population increases and occasional substantial winter die-offs (Fig. 1). Substantial winter mortality occurred at least twice between 1961 and 1991. In spring 1975, over two carcasses were observed for every live caribou seen within the transects indicating that over-winter mortality was about 70 %. About 50 % of the caribou apparently died during the winter of 1978-1979 based on a decline in population size from 4200 in November 1978 to 1700 in June 1980. The crash unlikely occurred during the winter 1979-1980 because only about 200 carcasses were estimated in June 1980. Other die-offs could also have occurred during other winters and gone undetected. Except for the fall of 1974, density was always under 1 km^{-2}.

Juveniles were particularly affected by over-winter mortalities (Gates *et al.*, 1986b). In June 1975, following the winter die-off, not a single one-year-old caribou was seen. Among older individuals, it appears that adult males were more vulnerable than females. The sex ratio during aerial censuses were strongly female biased (Gates *et al.*, 1986b). For example, during the 1984 survey only 1.6 % of caribou older than one-year-old were obvious mature bulls. There is no doubt that many bulls were not identified during the censuses, nevertheless it suggests a biased sex ratio towards females. Ground surveys (Gates *et al.*, 1986b) also support this claim because males never exceeded 20 % of the adults. Hunting may have also partly contributed to the observed pattern because males apparently predominated in the kill (Gates *et al.*, 1986b). Most mature females (4 years old and older) were pregnant (30 out of 32). Pregnancy rate in younger females was not determined.

Although precise data are not available, it appears that the kill increased in the 1970's to reach a maximum of about 13 % (i.e. about 280 caribou; 177 males and 113 females) of the adult population (i.e. excluding calves) by mid-1980's. Therefore, in the 1980's considering the size of the population, hunting could have been an important limiting factor. Since then, likely because hunting quotas increased on Southampton Island (see above), the kill has decreased gradually in absolute and in relative terms and was possibly no more than 50 individuals by the end of the last decade (i.e. less than 10 % of the population).

Range quality

In the early 1980's, although the vegetation was low in biomass and diversity, the summer range was considered adequate relative to the population size (Adamczewski *et al.*, 1987b; Adamczewski *et al.*, 1988). Peak ruminal nitrogen in summer was comparable to values found for other caribou populations (Adamczewski *et al.*, 1988). The summer range has also been adequate on Southampton since reintroduction (Parker, 1975; Ouellet, 1992). Summer forage was of high quality and comparable to other arctic sites (Ouellet *et al.*, 1994). The diet of caribou on these two islands during summer was comparable and largely dominated by willows (Ouellet *et al.*, 1994; Adamczewski *et al.*, 1988). Annual production per unit area of sedges, grasses, and willows was high on these islands relative to population size (Table 1). Based on forage annual net primary production and plant consumption, Parker (1975; tables 14 and 15, p.53) suggested that the summer range on Southampton Island can support a density of about 6 km^{-2} (i.e. 260 000 caribou). The same model applied to Coats Island suggests that the summer range could support a density of 3.2 km^{-2} (i.e. 18 000 caribou). Insect harassment which can reduce foraging time (Klein, 1992) appears to be low, probably because the two islands are characterized by strong winds. All of these reasons support the argument that the summer range, relative to the population size (see Fig. 1), has been adequate on both islands.

However, the winter range is likely of better quality on Southampton Island. Typical feeding sites used in winter (i.e. sites with topographic relief and shallow snow) are overgrazed on Coats Island (Adamczewski *et al.*, 1988), whereas on Southampton Island only a small fraction of these sites are overgrazed (Ouellet *et al.*, 1993). Further, Southampton Island is characterized by a higher lichen standing crop, at least since the late seventies early eighties (Table 1). This difference in lichen standing crop was reflected by a larger proportion of lichens in the diet in the fall and in the winter of caribou on Southampton Island, relative to those on Coats Island (fall: 67 % vs 36 %; winter: 46-49 % vs 2-12 %; Gates *et al.*, 1986a). Based on lichen standing crop Parker (1975) suggested that Southampton Island can support a density of about

1km². This model applied to Coats Island suggests a population density of 0.3 km^{-2} (i.e. 1600 caribou). A better winter range on Southampton Island is also indirectly supported by the observation that body reserves (fat and muscle) in the spring are much lower on females from Coats Island (Adamczewski *et al.*, 1987b; Ouellet, 1992).

Discussion

The Coats Island herd showed marked fluctuations in abundance over the last three decades in response to a limited supply of winter food and high inter-annual variation in weather conditions affecting its accessibility. However, animals released on Southampton Island in 1967 were clearly not limited by winter food and as a result numbers increased rapidly and steadily throughout the same period. Therefore the comparison between these two genetic related populations is instructive because they represent both ends of a continuum from population growth occurring near the intrinsic rate of growth (i.e. Southampton Island herd) to the relative stability of a population regulated by competition for food (i.e. Coats Island population).

Fast population growth on Southampton Island

Rapid population growth on Southampton Island resulted from high fecundity and over-winter survival rates, relative to other predator-free populations, and appears to be a consequence of the high overall quality of its range, particularly the winter range. A similar conclusion was reached by Klein (1968) who documented the eruption of the reindeer population on St Matthew.

High fecundity was recorded on Southampton Island because females reproduced early in life. Early investment in reproduction was possible because females grew rapidly (Ouellet, 1992; Leader-Williams, 1988). Physical growth was rapid relative to Coats Island animals probably because the better quality of the winter range on Southampton Island resulted in 1) animals in excellent body condition in the spring thus reducing requirements to replenish their fat and muscle during summer and 2) not needing to accumulate as much fat in preparation to winter (Ouellet, 1992). Because Southampton Island mothers were in excellent body condition in the spring fetal growth during the late pregnancy period and calf growth

Table 1. Lichen standing crop and annual net primary production of sedges, grasses, and willows in the dominant range types found on Coats Island and Southampton Island, Northwest Territories.

Range types	Area (km^2)	Lichen standing crop (g DM m^{-2})	Annual production[3] (g DM m^{-2})
Coats Island[1]			
Dryas-lichen	590	29.9	7.8
Meadows	1 922	9.3	26.0
Polygons	133	4.3	4.3
Total/weighted means	2645	13.6	20.8
Southampton Island[2]			
Raised-lichen-Dryas sedge	5 745	58.0	21.0
Lichen-heath felsenmeer plateau	7 345	85.7	b
Lichen-heath felsenmeer lowland	3 789	99.7	b
Polygons	4 840	20.7	34.5
Sedge willow meadow	5 957	a	60.0
Sedge-heath transition	5 353	a	38.0
Total/weighted means	33 029	43.6	38.8

[1] data from Adamczewski *et al.*, 1988; 2, data from Parker, 1975; 3, annual production of sedges, grasses, and willows; a, lichens are not abundant in these range types; b, not available.

through lactation may have been consistently high. Fetal weight was related to maternal condition on Coats Island (Adamczewski *et al.*, 1987b) and therefore may be related to winter feeding conditions.

Population regulation on Coats Island

The major die-offs recorded on Coats Island took place at high population density relative to the other estimates and the fraction of animals dying was related to density (Fig. 1). Therefore, even though these die-offs were likely related to adverse snow conditions, mortality was in part density dependent, not solely density independent as suggested by Gates *et al.* (1986b). This conclusion is also supported by the observation that whereas high mortality was recorded on Coats Island, mortality must have been low on the neighbouring Southampton Island considering the rapid and steady rate of growth of the herd since re-introduction (Heard & Ouellet, 1994).

The pregnancy rate of yearlings and the over-winter survival of juveniles and adult males (see above) are likely the demographic features affected most by food shortage in winter as has been shown in other food limited ungulate populations (e.g. Leader-Williams, 1988; Clutton-Brock *et al.*, 1991; Tyler, 1987). Although Coats Island and Southampton Island populations were at two different densities, pregnancy rates of adults (3 years old and older at calving) were similar which confirms the low variability in adult pregnancy rates of caribou (Bergerud, 1983). However, extreme adverse climatic conditions may reduce pregnancy rate substantially (see Thomas, 1982). Unfortunately no data are available on pregnancy rate of yearling females (i.e. 2 years old at calving) from Coats Island. But, relative to other populations (see Leader-Williams, 1988) females on Southampton first reproduce early in life as all yearlings sampled were pregnant (see above). Therefore, age at first reproduction may in part be density dependent (Ouellet, 1992). Coats Island juveniles and adult males were more vulnerable to over-winter mortality and the sex ratio was female biased. Female biased sex ratios are the rule in ungulates (*Rangifer:* Klein, 1968; Skogland, 1985; Leader-Williams, 1988; Roe deer *Capreolus capreolus* L.: Gaillard *et al.*, 1993) but favourable conditions may prevent this situation because on Southampton Island the sex ratio was close to 50:50 (see Heard & Ouellet, 1994).

It was impossible to quantify the impact of weather conditions on the population dynamics of Coats Island herd as there is no weather station on Coats Island. Based on snow data from Southampton Island there was no obvious link between the calculated index of winter severity and the dynamics of Coats Island herd (Table 2). For example, the 1974-75 winter was not particularly severe based on this index although a major crash took place that year. On the other hand, snow accumulation on the ground began very early that year because there was 10 cm of snow on the ground at the end of September 1974 relative to the long term mean of 3 cm. We need to be cautious when extrapolating climatic conditions from one location to another. Ouellet *et al.* (1993) showed on Southampton Island some variation in snow condition from one site to the another suggesting that the use of climatic data form one site is possibly of little value in depicting the climatic conditions over a large area. Further, such index of winter severity is possibly too simplistic to reflect the real nature of the relationship between winter climatic conditions and caribou population dynamics (Gunn *et al.*, 1989; Tyler, 1987)

Table 2. Relative winter severity index based on snowfall, Coral Harbour, Southampton Island, Northwest Territories.

Winter	Total snowfall (cm)	Overall relative severity index
1971-72	158.1	30
1972-73	118.0	-38
1973-74	71.9	-136
1974-75	104.4	-71
1975-76	128.6	-8
1976-77	137.1	3
1977-78	115.9	-54
1978-79	80.9	-122
1979-80	------	-15[a]
1980-81	94.8	-62
1981-82	118.9	-19
1982-83	149.4	33
1983-84	116.9	-18
1984-85	126.2	-10
1985-86	142.4	30
1986-87	149.9	60
1987-88	124.3	-24
1988-89	145.7	-4
1989-90	163.0	73
1990-91	201.9	167
Mean	132.1	
C.V.	33.2	

[a] for the winter 1979-1980 the index was calculated excluding the fall period because snowfall data were missing.

The dramatic declines observed in two reindeer populations, on two islands off the coast of Alaska, were attributed to adverse climatic conditions following overgrazing of the lichens (Klein, 1968; Scheffer, 1951). Important over-winter mortalities were also related to adverse snow conditions on other islands (high Arctic Islands: Gunn *et al.*, 1981, St Matthew: Klein, 1968; Svalbard: Tyler, 1987). In some environments, the impact of weather conditions is so obvious that some authors have argued that adverse snow conditions might contain numbers below KCC (sensu McNab, 1985) indefinitely (for review see Tyler, 1987). However, high forage availability may partly act as a buffer against inclement weather (Skogland, 1985). The suggestion that the detrimental effects of snow conditions increased under resource limitation is supported by the observation that while important over-winter mortalities took place on Coats Island no such die-offs occurred on neighbouring Southampton Island. Although, we must recognize the impact of density-independent factors on the dynamics of insular predator-free herds, it is fundamental to specify that these populations are not totally at the mercy of such fluctuating environment because the feedback loop comprising more forage, more individuals, less forage, fewer individuals imposes a centripetality upon the system (Caughley, 1987).

Winter food is influenced not only by snow conditions but also by the summer plant growth response and grazing (i.e. plant consumption) throughout the year. The plant growth response is the rate of increase of edible plant biomass per unit area as a function of its standing density and environmental attributes such as temperature and soil moisture (Caughley & Gunn, 1993). Variability in climatic condition in summer could therefore also explain the inter-annual variation in abundance of caribou, but its effect appeared relatively unimportant (but see below) because animals were consistently in excellent body condition in the fall and the adult pregnancy rate was high on both islands.

Fluctuations recorded on Coats Island may also partly reflect the impact of hunting. Hunting mortality was high enough to curtail most increase in good years and possibly precipitate the decline in years with harsh winters. Further, population estimates presented were derived from aerial censuses, that were not corrected for visibility bias which could have been different from one census to another. Nevertheless, the magnitude of the fluctuations documented cannot be accounted solely on the basis of the impact of hunting or variation in sampling bias.

Density achieved

Population density on Coats Island, except for one census (i.e. 1975) remained under 1 km^{-2}, which is lower than the density (>2 km^{-2}) suggested by Bergerud (1980) and Seip (1992); the population density on Southampton Island was under 1 km^{-2} but the population is still increasing. This is particularly low relative to other predator-free populations (see Bergerud, 1980; Leader-Williams, 1988). For example, the population on South Georgia reached 23 km^{-2}. Why then is density attained on Coats Island so low? Low density on Coats Island is primarily related to the low net primary production. There is a good relationship between the standing crop of vegetation and *Rangifer* biomass-density (Skogland, 1980) (Fig. 2). However, other factors could also influence population density (e.g. plant composition, duration and severity of winter, island size and predation) but even if those factors may determine population size, in the case of predatorfree populations it is competition for food that regulates population size.

Modelling population dynamics and the future of Southampton Island herd

The eruption model has been used to describe the dynamics of predator-free *Rangifer* populations (e.g.

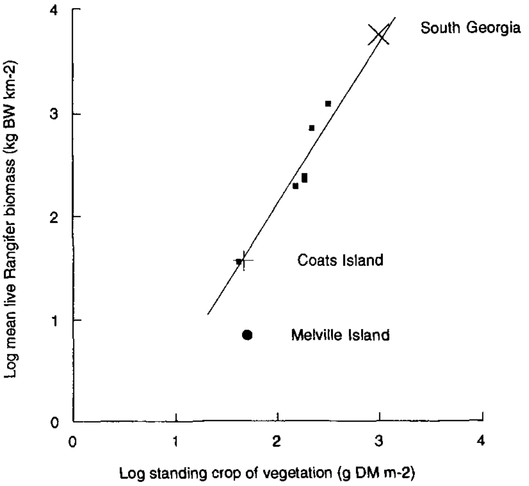

Fig. 2. *Rangifer* biomass in relation to standing crop of the vegetation for various Arctic regions (based on Skogland, 1980), South Georgia (from Leader-Williams, 1988), Coats Island (195 224 800 kg DM of available green biomass over 4152 km2 [Adamczewski *et al.*, 1988]; 2 000 caribou [see Fig. 1] with a mean body weight of 78 kg which is the mean body weight of adult females [Adamczewski *et al.* 1987b]) and Melville Island (mean above-ground biomass [51.8 g DM m-2] of the various range types [Thomas & Edmonds, 1984]; mean of 4 700 caribou [Miller, 1990] over 42 220 km2 with a mean body weight of 54.3 kg which is the mean body weight of adult females [Thomas *et al.*, 1977].

Leader-Williams, 1988). Caughley (1970) defined operationally an eruption fluctuation as an increase in numbers over at least two generations, followed by a marked decline. An eruption comprise a sequence of four stages (Caughley, 1970): 1) the initial increase stage covers the period between the population establishment and the attainment of the initial peak which exceed the KCC, 2) initial stabilization stage continues until the population commences a significant decline, 3) decline stage covers the period of this decline, 4) postdecline stage refers to the period thereafter. These four stages imply corresponding changes in reproduction (i.e. age at first reproduction and pregnancy rate) and winter survival in response to competition for food. The initiation of an eruption is a response to a change in conditions of life, favouring positive population growth (e.g. introduction of a population in a new habitat, cessation of heavy hunting), and is terminated by a modification of habitat (i.e. change in standing crop and plant composition) by the animals themselves. This model can apply to established or to newly introduced populations.

The dynamics of the Southampton Island herd do not provide evidence to support or invalidate the eruption model (Caughley, 1970) because the population is still increasing. However, the population could be in the initial stage of the model. It is also difficult to assess whether or not the Coats Island population conformed to the eruptive model (see Fig. 1). Based on previous estimates, the population should have stabilized around 0.5 caribou km^{-2}. Therefore, we could reject the model based on the basis on the 1991 population estimate. However, it is possible that external factors such as severe winters (i.e. snow conditions) may have acted to affect the predicted relationships between the caribou and its environment and promote the observed pattern. In other words, frequent impact of density independent factors on the dynamics of such insular predator-free northern populations have the potential to frequently reset the dynamics of a population to the initial stage of the model. On the other hand, differences in reproduction, physical growth, body condition, and survival between the increasing Southampton Island population and food limited populations, including Coats Island, are consistent with the model.

Based on the eruption model and the review conducted by Leader-Williams (1988) summarizing results of introductions of caribou and reindeer populations, we expect that the Southampton Island population will overshoot the KCC. A dramatic population crash may occur following a substantial depletion of lichens. Similar events occurred on other predator-free islands (e.g. St Paul, Scheffer, 1951; St Matthew, Klein, 1968). This situation can be modelled by a simple logistic growth model which incorporates a time delay between food availability and food limitation on the population (Messier *et al.*, 1988). How far the population exceeds the KCC and the importance of the crash that follows is a direct function of the duration of the time delay and the initial rate of growth of the population. The model indicates that populations relying on lichens are more likely to overshoot the KCC and crash because the slow recovery rate of lichens following grazing results in a longer time delay in the model. This conclusion is supported by the dramatic crash observed on St Matthew and St Paul, two populations relying heavily on lichens and growing at a fast rate, and the smooth stabilization of the abundance of the population on Barff Island, a population growing at a slower rate and exploiting graminoids (Leader-Williams, 1988). The model also indicates that the above prediction is valid only if the harvest level remains low relative to population size. Peak density should be influenced by the lichen standing crop and on environmental conditions. Obviously, harsh weather conditions in winter may precipitate the decline by reducing forage accessibility.

So far, we have considered that only winter forage drives the dynamics of insular northern predator-free caribou populations. However, it is possible that forage availability in summer may play a role at the end of the stage 1 of the model (i.e. overshooting of the KCC) when the population density will be unusually high. Observations made on St Matthew by Klein (1968) support this suggestion because before the crash, reindeer were in relatively poor body condition entering winter due to competition to high quality forage in summer (Klein, 1968).

Once the eruption has reached the post-decline stages (see above), the vegetation will be altered irreversibly (Caughley, 1970). At this stage, we suggest that lichens will not remain the key winter forage on Southampton Island. This is supported by the low incidence of lichens in the diet of caribou on Coats island (Adamczewski *et al.*, 1988) and their low abundance on St Matthew following the population crash (Klein, 1968); lichen standing crop remained low even two decades after the crash (Klein, 1987). In that regard, the dynamics of insular predator-free populations may be related to island size. On smaller islands, populations have the potential to reach KCC within a short period of time (e.g. within two decades). Within such a short period of time lichens do not have the ability to grow back (Ouellet *et al.*, 1993; Klein, 1987) because the rate of lichen utilization can exceed their rate of growth. For populations using a larger range, such as large migratory populations, it will take a much longer period of time to reach KCC following a decline. For example, the George River Herd increased during 40 to 70 years (Crête *et al.*, this issue) which is sufficiently long to allow lichens to grow substantially. Predation can also slow down the rate of increase of large migratory populations allowing more time for lichens recovery. Island size may also influence caribou population dynamics if larger islands have greater topographical and climatic variations. On large islands, like Southampton Island, snow conditions can be variable (Ouellet *et al.*, 1993) so even during harsh snow conditions caribou may be able to find some areas where food is still accessible. On smaller islands, like Coats Island, snow conditions are likely less variable and harsh snow conditions may reduce forage accessibility almost equally over the entire island.

With the predicted marked reduction in lichen abundance on Southampton Island, the abundance of deciduous shrubs, mainly *Salix* spp., and graminoids will play a more important role in the dynamics of caribou on Southampton Island. Because these plant types are more resilient to browsing and grazing (Ouellet *et al.*, 1994), we expect that following the first eruption the duration of the time delay to be shorter, hence a tighter relationships between caribou number and forage abundance. However, due to the impact of frequent density independent factors the population should be loosely regulated by food at low population density (i.e. possibly under 1 km^{-2}). The dynamics of Southampton and Coats Island herds will likely be comparable at this stage. Pregnancy rate in yearlings will drop dramatically and population recovery will be slower than the present rate of growth of the Southampton Island herd. Over a longer period of time the influence of larger scale changes in climatic conditions (Meldgaard, 1986) will certainly affect the dynamics of these two populations.

Conclusion

This review provided an opportunity to examine some basic assumptions relevant to the ecology of ungulates and the general model proposed (Bergerud, 1980; Seip, 1992) to explain the ecology of caribou populations. Our review supports the suggestion that isolated predator-free populations are ultimately regulated by competition for food. However, populations possibly do not attain a stable equilibrium primarily because variation in weather conditions affects forage accessibility in winter. Density achieved by these populations are variable and may be under 2 km^{-2}. Low population densities on Coats Island result primarily from low primary production. This review also emphasizes the importance of distinguishing between limiting factors that determine absolute population density and variation in density among years (in our case probably net primary production and winter weather which influences forage accessibility) from regulatory factors, processes that stop population increase (competition for winter food leading a delay in puberty and increased mortality from starvation) when examining population dynamics (Chitty, 1960; Messier, 1991). Finally, to better understand the ecology of predator-free caribou populations further investigations should be conducted on Southampton Island in the near future. Caribou abundance, fall and spring body condition (including pregnancy rate), and the vegetation should be monitored. Further understanding will also require a quantification of the impact of weather on the plant growth and the numerical and feeding responses of caribou to changes in plant biomass and species composition under various snow conditions.

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Relative contribution of decreased productivity and survival to recent changes in the demographic trend of the Rivière George Caribou Herd

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Abstract: The Rivière George caribou herd (RGCH) was numerically low during the middle part of the century but apparently erupted in the sixties and the seventies. Puberty was early and pregnancy rate was high among RGCH females from 1973 until the mid-eighties when fecundity decreased significantly, in particular among sub-adults; productivity remained low in 1992. Autumn calf female ratios reflected this trend in pregnancy, exceeding 50 calves: 100 cows between 1973 and 1983, but dropping thereafter progressively to a low of 24 in 1992. In 1993, this ratio rebounded back to 42. Annual adult survival rate of radio-collared females was high (0.95) at the beginning of the monitoring in 1984, but exhibited a variable but declining trend until 1992. Simulations were conducted to estimate the demographic trend of the RGCH between 1984 and 1992, using annual survival rates of radio-collared animals and annual autumn calf female ratios to estimate calf production. Age structure played a minor role in estimating the finite rate of increase (λ). According to the simulations, the RGCH increased in size until 1987, and showed a slight decrease thereafter. The herd should have decreased by 12-15% between 1988 and 1993, according to the simulations. Productivity first caused a decline in λ, but in recent years decreased survival contributed slightly more than productivity to the reduction in λ. Estimation of the herd size by means of aerial censuses in 1976, 1984, 1988 and 1993 suggested a similar pattern in demographic trend, differences being statistically meaningless. We speculated on the future of the RGCH, that could have erupted after many decades of unfavourable weather. The herd will exhibit a rapid descent to low numbers if wolves show a numerical response to current caribou abundance, or if lichen availability on the winter range decreases due to competition with the adjacent and increasing Rivière aux Feuilles herd; otherwise it will exhibit dampened oscillations, whose amplitude will depend on the time-lag of vegetation reaction to decrease grazing pressure on the summer range.

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Introduction

Demography of caribou and reindeer (*Rangifer tarandus*) for island populations, as well for continental ones, has often been characterized by huge numerical fluctuations. Changes have occurred on short time frames but also over centuries. The eruption and crash of the introduced reindeer population on St Matthew island in Alaska covered less than 2 decades (Klein, 1968), while the disappearance of a subspecies of small caribou in Greenland and its replacement by a larger one took place over millennia (Meldgaard, 1986). Periodic fluctuations at 65-115-year intervals were also documented during the last centuries in Greenland (Meldgaard, 1986). Large migratory herds of North-American caribou also fluctuated widely in number during the historical period. Most herds declined substantially during the first half of the current century, but have been increasing for the last decade (Williams & Heard, 1986; Klein, 1991).

When attempting to generalize about population dynamics of caribou, one must consider where studied populations are located with respect to the species range. Peripherical populations are generally more susceptible to density-independent limiting factors (sensu Messier, 1991). At the southern limit of their distribution, some caribou populations were recently reported to suffer from heavy predation that threatened their existence, e.g., the Quesnel Lake population in British Columbia preyed upon by wolves (*Canis lupus*) (Seip, 1992), and the Gaspésie Park population in Québec, affected by coyote (*Canis latrans*) predation (Crête & Desrosiers, 1995). At the northern limit of their range, Peary caribou on Banks Island have recently been declining dramatically, but the causes remain obscure (Miller, 1991). On the other hand, population dynamics of central Alaskan caribou may be unique due to the richness in large mammal populations encountered.

Population regulation, i.e. feedback mechanisms by which populations tend to come back to the carrying capacity (KCC: MacNab, 1985) when displaced from it (sensu Messier, 1991), should be easier to detect in caribou populations of the core of the species distribution. Caribou reach highest densities at tree-line where they form large migratory herds. They generally gather on the tundra in spring and stay until winter when they commonly move into the forest-tundra and the boreal forest (Williams & Heard, 1986). Strong regulation would result in a quick return to KCC, while weak regulation resulting from a time lag in density-dependance could result in cyclic populations. The model developed by Caughley (1976) to describe the relationships between large ungulate populations and their forage allows for both outcomes.

Some authors proposed that population dynamics of migratory caribou could be cyclic because of their dependence on lichens as winter forage (e.g. Messier *et al.*, 1988). Lichens carry a risk of instability because of their slow growth and their capacity to accumulate the annual production of decades, that can be consumed rapidly by an expanding caribou population (Messier *et al.*, 1988). Caribou expansions could lead to overgrazing of lichens, followed by a crash until lichens recover. After forest fires, lichen species important to caribou feeding in the Québec-Labrador peninsula take ≈30-40 years to recolonize the ground and to become large enough to be edible (Morneau & Payette, 1989). This recovery time is probably longer on the tundra. Messier *et al.* (1988) explored the possible consequences of such time lag in lichen recovery on the demography of RGCH.

It is important to distinguish between cycles and fluctuations in population dynamics because the causes and the mechanisms involved can be different, and can lead to different predictions and management practices. Cycles are characterized by a period (time span between 2 identical states) and an amplitude (difference between maximum and minimum population size); they can be described mathematically by a trigonometric function (sine or cosine). Cycles should normally be driven by endogenous causes to the system (e.g. lichen overgrazing and recovery, predation), but could also result from exogenous causes like cyclic climates (Schlesinger & Ramankutty, 1994). Changes in population level that do not have a regular periodicity, cannot be considered cyclic, although they form a sequence of peaks and troughs when plotted over time. Long term fluctuations in caribou numbers could result from changes in KCC, for instance because of varying snowfalls resulting from climatic changes (Crête & Payette, 1990). If migratory caribou herds are cyclic, the period of cycles certainly cover many decades (Messier *et al.*, 1988). Because it is very difficult to estimate precisely and accurately the size of migratory caribou herds (Crête *et al.*, 1991), and data covering long periods are not available, it is then impossible to determine if some or all migratory herds of caribou in North America exhibit cycles. To further complicate the demography of caribou, Caughley & Gunn (1993) showed that pseudocycles with a periodicity of a few decades could be generated from annual random fluctuations in precipitation.

Historical information on the Rivière (River) George Caribou Herd (RGCH) suggests that animals were abundant and followed the same migratory patterns during the second half of the 18th century as they do now (Taylor, 1969). At that time, lichens were probably abundant at the head of the Fraser Canyon since the Inuit used them to cook food and boil water (Taylor, 1969). Animals appeared rare by 1920, a situation that persisted until 1950 (Banfield & Tener, 1958; Bergerud, 1967), but the herd increased rapidly thereafter to peak by the end of the eighties (Couturier *et al.*, 1988, 1989; Messier *et al.*, 1988; Crête *et al.*, 1989; Hearn *et al.*, 1990). Forage availability on the calving and summer range, located on tundra plateaux bordering Rivière George, is apparently responsible for regulation of RGCH (Couturier *et al.*, 1988, 1989; Crête *et al.*, 1990a). Parturient and lactating females have had to compensate for the rarity of lichens before the green-up, and of leaves of deciduous shrubs thereafter, by consuming less preferred forage, in particular graminoids (Crête *et al.*, 1990a). Sub-optimal nutrition has affected body reserves of dams, with females exhausting their fat store during the first month of lactation (Crête & Huot, 1993). Lactation also appears to have been affected as RGCH calves have grown at a slower rate than calves of the adjacent Rivière aux Feuilles

Herd (RFH), or RGCH calves born and raised in captivity (Crête & Huot, 1993; Crête *et al.*, 1993).

The first sign of change in the demographic trend of RGCH showed up in 1984, when the autumn calf female ratio dropped from 52 calves per 100 cows, the average of the previous decade, to 38. This ratio remained around 40 for the next 2 years, but decreased thereafter (Couturier *et al.*, 1990). Annual survival rate of adult females was high at the beginning of telemetry studies in 1983, but also progressively declined until 1987 (Hearn *et al.*, 1990).

The objectives of this paper are to update the information on productivity and survival of the RGCH up to 1993, to evaluate the relative contribution of these factors to changes in the finite rate of increase (λ: Caughley, 1976: 51) during the last decade, to compare aerial censuses versus survival and productivity data, to estimate population trends, i.e. observed rate of increase ($\bar{r}$) versus the survival-fecundity rate of increase (r_s) (Caughley, 1976: 53-54), and to speculate on the future of the herd.

Study area

Parturient females of the RGCH gather on the tundra plateaux bordering the Rivière George to calve, and spend the first month of lactation in this habitat (Fig. 1). Female density in the most productive tundra habitat, below 600 m asl, slightly exceeded 10 individuals·km^{-2} in June and July, 1988 (Crête & Huot, 1993). Males used to join females along the Rivière George until the beginning of the eighties, and stay with them until September. More recently, males have stayed further west in the forest-tundra during the snow-free period. For the rest of the year, the RGCH migrates south and west and utilizes most of the Québec-Labrador peninsula north of the 52° N latitude; total range of the RGCH expanded in the early eighties and now covers ≈700 000 km^2 (Messier *et al.*, 1988; Hearn *et al.*, 1990). Lichens prevail in the winter food of the RGCH (Gauthier *et al.*, 1989), being relatively abundant (1223 kg·ha^{-1} over the total range) and seemingly lightly used (<1%: Crête *et al.*, 1990b). During the growing season, leaves of deciduous shrubs and graminoids dominate caribou diet, while lichens become progressively more important during the autumn (Gauthier *et al.*, 1989).

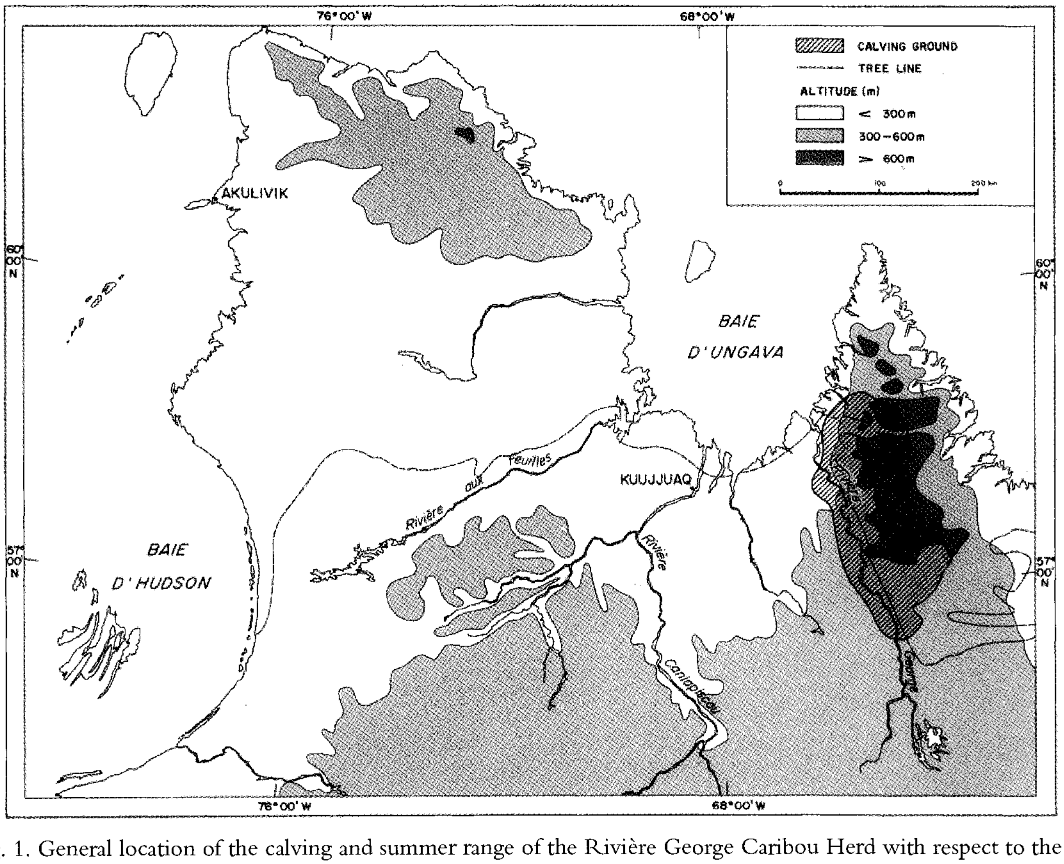

Fig. 1. General location of the calving and summer range of the Rivière George Caribou Herd with respect to the tree line and the altitude in the north of the Québec-Labrador peninsula.

The adjacent RFH is increasing in size, and was estimated at ≈260 000 individuals in 1991 (S. Couturier, unpubl. rep.). During calving and summer, the RGCH and the RFH are separated, but their ranges slightly overlap during the rest of the year (S. Couturier, unpubl. telemetry data). Wolves and, to a lesser extend, black bears (*Ursus americanus*) prey on the RGCH, but predation was a minor limiting factor in the eighties (Hearn *et al.*, 1990). Subsistence, sport and commercial hunting also affect the RGCH, and total kill has approached 30 000 animals in some years during the last decade (Crête *et al.*, 1990c).

Methods

Pregnancy rates were determined in March 1992 from a sample of 70 RGCH females collected near Kuujjuaq by Inuit hunters. Animals were aged as yearling, 2-year old or mature, based on tooth replacement and wearing. Comparisons were made with samples collected in 1976, 1980 and 1986-1987 (Bergerud, 1980; Parker, 1981; Couturier *et al.*, 1990).

Autumn composition counts for the RGCH have been carried out annually in late October and early November since 1973. Sampling techniques varied over time, particularly due to the inaccessibility of the range and to the large area used by caribou in some years. Calf:female ratios were generally estimated by ratio sampling (Cochran, 1977:150), observers counting animals per categories (calf, female, male) for a fixed amount of time per sampling point. Many thousands of caribou have been classified each autumn (see Messier *et al.*, 1988).

Animals from the RGCH have been monitored by telemetry since 1983, but radio-tagging was strongly biased in favour of adult females. At the beginning, only conventional VHF radios were used, but satellite telemetry has been used in conjunction with VHF radios since 1986. Between 30 and 115 female caribou were monitored annually by telemetry. Animals marked with VHF radio-collars were monitored irregularly from fixed-wing aircraft or helicopter. Radios were recovered when in mortality mode, often many months after death, and cause of death was determined whenever possible (Hearn *et al.*, 1990). Here we report only on the annual survival rate of females, estimated with the computer program Micromort (Heisey & Fuller, 1985). Seasonal and cause-specific mortality rates are not analyzed. We assumed that there were equal chances of detecting dead or living animals when transmitter batteries became exhausted, rather than computing also minimum survival rates, assuming that all censored observations resulted from animal death (Hearn *et al.*, 1990).

The size of the RGCH was derived using aerial census by estimating the number of females on the calving ground and by extrapolating to the total herd size with the autumn composition counts. The method used to determine the number of adult females on the calving ground changed over time: visual counts from a helicopter before 1984, black and white vertical air photographs in 1984 and 1988, and vertical colour slides taken from a helicopter in 1993. Visual counts in helicopter were biased in earlier censuses and later corrected (Crête *et al.,* 1989), and the sampling plans were progressively improved (Crête *et al.*, 1991; Couturier *et al.*, 1996).

The finite rate of increase (λ: Caughley, 1977: 51) of the RGCH was estimated in 2 ways: by calculating the survival-fecundity rate of increase (r_S: the rate of growth given current age-specific survival and fecundity (Caughley, 1977: 54)), and by calculating the observed rate of increase ($\bar{r}$) derived from aerial censuses. λ is the natural log (ln) of r or r_S (Eberhardt & Simmons, 1992). Fecundity was not estimated through pregnancy rates but rather with autumn calf:female ratios applied to all females (yearlings and older ones) because gestation rates were available for few years only, because they were based on relatively small sample sizes, and because summer survival rate of calves was not measured adequately. Calves were then assumed to be produced in autumn with balanced sex ratios, after perinatal and summer mortality occurred. In utero sex ratios are balanced in the RGCH (B. Hearn *et al.,*, unpubl.). All calf and adult mortality was assumed to occur in winter and it was estimated using annual survival rates of radio-tagged animals. Adult survival rates, available annually, were used also for calves and yearlings because of their similarity and better precision (Hearn *et al.,* 1990; unpubl.); similar survival for calves, yearlings and older females was reported for the Delta Herd in Alaska (Davis *et al.,* 1988).

λ derived from survival and productivity was computed in 2 ways, to take into account the possible influence of age structure. In both cases, the smoothed age structure computed by Messier *et al.*, (1988) for the RGCH served as the starting age distribution for a population of 1000 yearlings and adult females. We assumed a longevity of 16 years, survival rate being 0 for the last age class. Males were not included in the analysis because of a lack of information on their survival and because the dynamics of cervids rests mostly on females (Nelson & Peek, 1982). We first modelled continuous time from 1984 to 1993, by annually computing birth from the total number of females, then calculating the annual survival rate, and finally increasing each age class by 1 year. In the second case, we used the deterministic computer model SIMCON (C.E. Walters, Univ. British Columbia, modified by F. Messier, Univ. Saskatchewan and R. Courtois, Min. Environnement et Faune du Québec), assuming no density-dependence. For each year, we ran the program with the corresponding figures on productivity and survival until a stable and stationary age structure was attained, which occurred before 40 generations. Annual λ was computed for both approaches by comparing actual female population (N_t) with N_{t+1}. Population estimates (in autumn, including calves) derived from aerial censuses in 1976 (215 000), 1984 (644 000), 1988 (682 000)(Crête *et al.,* 1989) and 1993 (734 000) (Couturier *et al.,* 1996; Russell *et al.*, 1996) were used to calculate the observed rate of increase ($\bar{r}$).

The relative contribution of productivity and survival to the decrease of λ from the period of rapid increase (calf female ratio in autumn = 0.52; winter survival of calves and annual survival of older females = 0.95; λ = 1.18) was estimated with the simulation program SIMCON. Productivity was held constant at 0.52 calf female (0.26 female calf), while current annual survival, estimated from telemetry between 1984 and 1993, was entered in the simulation. Each run lasted 40 years, to allow stabilization of the age structure. Relative contribution of decreased productivity and survival to annual change in λ was determined by comparison of estimates with constant and observed productivity.

Results

Pregnancy rates decreased for all age groups after 1980, but remained relatively stable between 1986-87 and 1992 (Table 1). In recent years, fecundity of yearlings and 2.5-year olds was very low while the pregnancy rate among older animals (76-79%) was far from being maximal (e.g. Ouellet, 1992). Decreased fecundity, and possibly lower summer survival rate of calves, affected the autumn calf female ratios (Fig. 2). The latter was relatively stable and high between 1973 and 1983, and diminished progressively afterward. The 1993 composition count showed a reversal in the trend, reaching a value unobserved since 1986-1987.

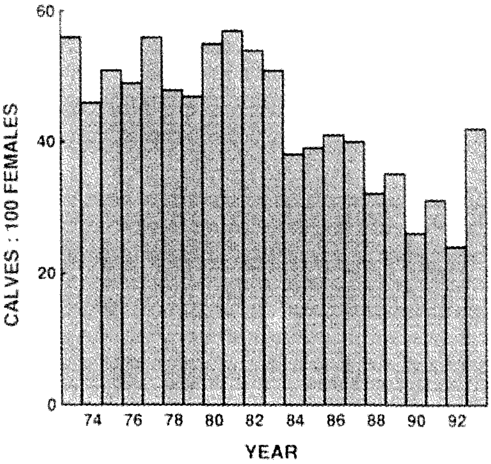

Fig. 2. Autumn (Oct-Nov) calf female ratios for the Rivière George Caribou Herd, 1973-1993, as estimated with ratio sampling. In general, many thousands of animals were classified each autumn as calves, older females and older males.

Annual survival rate of adult females exhibited an irregular but decreasing trend between 1984 and 1992 (Table 2). Data on annual survival of yearlings and calves were scantier than those on adults, and estimates were more variable due to a smaller number of animals being monitored. Annual survival rates of yearlings and winter survival rate of calves showed no tendency to be lower than adult rates.

The 2 approaches used to estimate λ ($\ln(r_s)$) with productivity and survival rates (simulation with time in continue or until stabilization of the age structure) showed relatively close agreement (Table 3). Age structure had only a minor influence on demographic changes. According to the simulations, the RGCH population growth rate progressively declined to zero by 1987-1989. There was a slight decreasing trend thereafter, and the herd

Table 1. Age-specific pregnancy rate (N) for Rivière George caribou, 1976-1992.

	Age (years) during the breeding season				Source
Period	1.5	2.5	≥3.5	Overall[a]	
1976	100 (1)	100 (6)	100 (15)	100	Bergerud (1980)
1980	43 (21)	90 (20)	95 (83)	89	Parker (1981)
1986-1987	0 (5)	67 (30)	76 (83)	67	Couturier *et al.* (1990)
1992	33 (6)	33 (6)	79 (58)	69	This study

[a] weighted according to the smoothed age distribution of Messier *et al.* (1988).

Table 2. Winter survival rate (November - May) of female calves and annual survival rate of yearling and older female caribou of the RGCH, as estimated from radio-collared animals between 1983 and 1993. Computations made with the computer program MICROMORT (Heisey & Fuller, 1985). Period 1983-1987, after Hearn *et al.* (1990).

Year[a]	≥ 2-year-olds	Yearlings	Calves
1983	---	0.95 (4 078)	---
1984	0.95 (15 190[b])	0.89 (5 773)	---
1985	0.92 (28 091)	---	---
1986	0.91 (28 622)	0.66 (2 508)	---
1987	0.84 (16 281)	---	1.00 (1 065)
1988	0.87 (13 388)	1.00 (1 825)	---
1989	0.93 (20 405)	0.84 (2 123)	---
1990	0.84 (23 779)	---	0.85 (1 317)
1991	0.81 (23 654)	0.83 (1 933)	---
1992	0.83 (25 033)	0.88 2 872)	0.79 (924)

[a] Beginning one June 1 i.e. 1983-1984 etc.

[b] Total radio-transmitter days.

Table 3. Finite annual rate of increase (λ) of RGCH females, as estimated with the annual survival rate of radio-collared animals and the autumn calf female ratio. In one case, λ was estimated with a simulation program until stabilization of the age structure; in the other, the 1984-1992 period was simulated with time in continue.

Year	Stabilization	In continue
1984	1.11	1.13
1985	1.08	1.10
1986	1.08	1.08
1987	0.99	0.96
1988	0.99	1.00
1989	1.07	1.03
1990	0.92	0.95
1991	0.92	0.89
1992	0.99	0.98

Table 4. Relative contribution (%) of productivity and survival in the decrease of λ for the females of the RGCH during the period 1984-1992, in comparison to 1983, when λ = 1.18.

Year	λ	Contribution (%)	
		Productivity	Survival
1984	1.11	100	0
1985	1.08	60	40
1986	1.08	50	50
1987	0.99	28	72
1988	0.99	50	50
1989	1.07	79	21
1990	0.92	48	52
1991	0.92	35	65
1992	0.99	22	78

diminished by 12-15% between 1988 and 1993 according to the simulations. Based on census estimates, λ averaged 1.15, 1.01 and 1.01 for the periods 1976-1984, 1984-1988 and 1988-1993, respectively; comparative figures for the last 2 periods were 1.06 and 0.97 when λ was estimated from survival and productivity data, i.e. r_S.

During the first 2 years λ decreased, productivity was most responsible for the diminishing demographic vigour (Table 4). After 1986, annual survival had a slightly greater influence on reducing λ than productivity.

Discussion

Probable demographic trend in 1993

One might question the validity of simulations using the same annual survival rate for yearlings and adults, and of estimating winter survival of calves with the same value. The comparisons that we could make for the 2 youngest age classes with adults, taking into account sample sizes (Table 2), indicated that survival rates were relatively similar. Moreover, as adults always dominated in the population, overestimation of calf and yearling survival would have resulted in only a slight positive bias in λ. Another positive bias in estimating λ could result from the way we used censored telemetry data, assuming equal chances of detecting living and dead animals at the end of transmitter life.

The 2 independent approaches used to estimate the demographic trend of the RGCH (λ) during the last decade show some disagreement: 1.06 vs 1.01 for the 1984-1988 period, and 0.97 vs 1.01 for 1988-1993 interval. However we cannot conclude that the disagreement between the 2 trend estimates is statistically significant because the confidence interval for the 1988 population estimate was ±36% (α=0.10)(Crête *et al.*, 1991). Therefore it would be impossible to detect a 28% increase for the first period, or a 12-15% decrease for the second one, even if real. The precision of the combined 1993 population estimate improved (±13%; α=0.10: Couturier *et al.*, 1996), so that detection of demographic trends with aerial censuses could be easier in the future. Nevertheless, the use of survival and fecundity rates (r_S) may possess some advantages over aerial censuses in detecting demographic trends. Survival/fecundity rates appear to exhibit less variability than population estimates, although deterministic simulations do not take into account the precision of such rates. In addition, λ could estimated annually with fecundity/survival rates between 1984 and 1992, but only 2 times during the same period from populations estimates. Moreover the 2 estimates of λ derived from aerial censuses were related because they both relied on the 1988 census, which was imprecise. The disagree-ment between our 2 estimates of demographic trend would be significantly reduced if the 1988 census were an underestimate, a possibility considering the large confidence interval associated with this census.

It is likely that the RGCH decreased slightly between 1987 and 1993 because the trend in autumn calffemale ratios and adult survival rates between 1984 and 1992 was clearly declining (Fig. 2; Table 2). Recruitment improved in 1993, but adult survival would also have to increase for the demographic trend of RGCH to reverse. There must be 52 calves per 100 females in autumn in a caribou population for balancing mortality when annual survival of yearlings and adults reaches 0.80; the autumn ratio must be 39 when annual survival is 0.85. The high calffemale ratio observed in 1993 can be explained by the low 1992 recruitment, which resulted in a high proportion of barren females that were more likely to produce a calf in 1993 due to superior body reserves during the previous breeding season (Crête & Huot, 1993). Moreover the 1993 spring was particularly early, which may have contributed to diminishing perinatal mortality. The poor physical condition of lactating females (Huot, 1989; Crête & Huot, 1993; unpubl.) and the overgrazed summer range (Crête *et al.*, 1990a; M. Manseau & C. Morneau, in prep.) suggest that the RGCH should continue to decline in the near future.

Relative contribution of decreased productivity and survival

Reproduction appears to be the first demographic parameter to have been affected when competition for forage on the summer range became significant at the beginning of the eighties. It continued to decrease afterward but survival also diminished simultaneously. In recent years, the importance of survival slightly exceeded that of reproduction in depressing λ. The first consequence of sub-optimal foraging condition in summer was then decreasing pregnancy and possibly increasing perinatal mortality. With time, deficient nutrition of females in late gestation and during peak lactation resulted in decreasing life expectancy. This could be the result either of cumulative impact of poor physical condition or of selection for a life strategy adapted to high competition for forage (Skogland, 1990).

The future of the RGCH

The biogeography of caribou does not differ much from that of other boreal cervids, highest densities being observed in the core of the species range, with peripheral populations at low density. This pattern suggests that there exists some adjustment between caribou numbers and range quality, and that the concept of KCC should be applicable to caribou. Oksanen (1988) hypothesized that food chains would be limited to 2 trophic levels in unproductive landscapes like the tundra, and that herbivores would be regulated by forage, imposing much pressure on the vegetation. The diversity of mammals is low in northern Québec, and wolves have almost no alternate preys besides caribou (Crête & Manseau, 1996). The observation that migration is a good life strategy to escape predation (Bergerud & Page, 1987; Fryxell *et al.*, 1988; Heard & Williams, 1992) also suggests that the RGCH should be regulated by forage. Available data indicate that it is the case (Crête & Huot, 1993).

Seip (1992) suggested that population dynamics of RGCH, regulated at high density by forage, contrasted with that of other North American migratory herds, regulated at lower density by the combined impact of wolf predation and forage. However this suggestion is speculative as no regulation mechanisms have been described yet for migratory herds in the Northwest Territories, Yukon or Alaska. Relative stability in size of many herds may have complicated the detection of density-dependance.

Annual variation in summer climate affects forage quality and growth of boreal cervids (e.g. Saether, 1985; Crête, 1988), while snow condition in winter can result in malnutrition and death (e.g. Crête, 1976; Gates *et al.*, 1986). Climate may then influence caribou demography in drastic, but also in very subtle ways. Besides profound climatic changes that occur at a geological scale and that are caused by astronomical, tectonic, cryogenic and oceanic effects (Harrington, 1987), the climate exhibited subtle changes since the last glaciation. The period of warmest temperature (Climatic optimum) happened between 6 000 and 2 500 years B.C. (Lamb, 1977:378) and it was followed by a cooling, culminating with the Little Ice Age, between 1500 and 1650 A.D.(Lamb, 1977:461). For instance, this cooling modified the composition of the mixed forests of the Great Lakes-St. Lawrence region (Campbell & McAndrews, 1993). Afterward, the climate improved, with the first half of the XXth century being particularly warm (Lamb, 1977:478).

Among the factors proposed to explain caribou rarity in the Québec-Labrador peninsula during the first half of the XXth century (predation, hunting, destruction of winter range by fire or by overgrazing of lichens, climate), a high incidence of wet and snowy winters during consecutive decades (Crête & Payette, 1990) appear the most plausible explanation. Archaeological observations suggest that period of warm and wet climate also coincided with rarity of reindeer in Europe (Luoto, 1993). Conceptually, the first half of the century in the Québec-Labrador peninsula could be viewed as a period with decreased KCC, or a period with prolonged negative demographic balance, when a limiting factor became very important. In the absence of significant grazing, vegetation, in particular lichens, became luxuriant. When the climate became more favourable in the fifties, the RGCH erupted.

The RGCH increased during 3 or 4 decades, peaking by the end of the eighties, and most probably slightly declining since 1987. Two future outcomes which are extreme ends of a continuum, are possible: a rapid descent to low numbers (< 100 000 individuals) or oscillation around KCC (roughly within the bracket 400 000-800 000). In the first case, the demographic model would be that of a cyclic population; in the second, Caughley's (1976) herbivore/vegetation model with dampened oscillations. Assuming constant climate, the RGCH will exhibit cycles if wolves show a numerical response with time lag to caribou. This is possible as the RGCH now spends most of its time in the forest-tundra and the forest, where it could be more vulnerable to predation. Wolves would precipitate a caribou decline, in the same manner as lynx (*Lynx lynx*) does for cyclic snowshoe hare (*Lepus americanus*) populations (Keith *et al.*, 1984). It is much less likely that lichens provoke cycles because they have been overgrazed on the summer range, where animals can compensate by other food sources (Crête & Huot, 1993). The scenario could be different if lichen availability decreased substantially on the winter range, due to intense competition with the increasing RFH. Otherwise, the RGCH will exhibit dampened oscillations, with the amplitude of oscillations dependant on the time of reaction of the vegetation on the summer range to decreasing grazing pressure. First indications suggest the latter is slow on the tundra (M. Manseau & M. Crête, unpubl.), and that adjustment to KCC will not be rapid.

Managers can actually have very limited influences on the RGCH as it has been naturally regulated by forage on the summer range. However their task will be to forecast the future of the herd in order to advise the users in the best possible way. The elements most susceptible to influence drastically the demographic trend of the RGCH in the near future are: recovery rate of the vegetation on the summer range, predation rate by wolves and ease of access to forage in winter. Permanent plots should be established in the most critical summer habitat types, and monitored every 5 years to measure changes in the vegetation. Similarly, cause-specific mortality rates of radio-collared caribou should continue to be investigated, in order to detect any increase in wolf predation. Finally winter feeding ecology should deserve some research.

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The relationship between food intake and predation risk in migratory caribou and implications to caribou and wolf population dynamics

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Abstract: We examined the hypothesis that spring migration in barren-ground caribou (*Rangifer tarandus*) enhances access to high quality food, reduces predation risks or both. We related our findings to the hypothesis that one of the consequences of migration is that prey populations cannot be regulated by predation because predators are unable to respond numerically to changes in abundance of migratory prey. In the Northwest Territories, migration to calving grounds by pregnant cows reduced the risk of predation on neonates. Wolf (*Canis lupus*) densities on calving grounds averaged only 22 % of winter range densities because most wolves denned near tree line. The quality and quantity of food that was available to cows that migrated to calving grounds was lower than for bulls and other caribou that lagged far behind the pregnant cows during spring migration. Fecal nitrogen levels were higher in bulls than in cows in late May and early June but there were no differences in mid or late June. Areas occupied by bulls in late May had a greater biomass of live sedges than on the calving ground in early June. It appears that although food in July is abundant and nutritious, insect harassment prevents efficient feeding. Body fat reserves in both sexes declined to almost zero by mid-July, the lowest level of the year. Insect numbers declined in August and body fat levels increased to the highest level of the year by early September. Because the timing of caribou's return to the hunting ranges of tree line denning wolves was related to caribou density, our data were inconsistent with the suggested consequence of migration. Tree line denning by wolves and density-dependent changes in caribou migration suggests a mechanism for population regulation in caribou and wolves. We suggest that the process is as follows; when caribou numbers increase, some density-dependent factor causes range expansion in August (e.g., competition for food) causing caribou to return earlier to the hunting ranges of tree line denning wolves, more denning wolves have access to caribou, wolf pup survival increases and wolf numbers increase. The effect on caribou population growth will depend on the timing and magnitude of the wolf numerical response.

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Introduction

Migration in large herbivores has probably been shaped by selection to reduce predation risk, to enhance access to high quality food or both (Fryxell & Sinclair; 1988, Fryxell *et al.*, 1988). Where migration reduces predation risk because predators are unable to follow migrants, predators may not be able to respond numerically to changes in prey abundance and migrants will more likely be regulated at relatively high densities by competition for food rather than by predation.

The causes and consequences of the migration of barren-ground caribou (*Rangifer tarandus*) to calving grounds have been debated for some time. Klein (1970, 1992) and Whitten & Cameron (1980) stated that caribou move to track seasonal changes in plant nutrient content and digestibility. Kuropat & Bryant (1980) suggested that by migrating to calving grounds Western Arctic herd cows were following an optimal foraging strategy and Eastland *et al.* (1989) argued that nutrient levels and digestibility were probably higher on the Porcupine caribou herd's calving ground during calving than in completely snow free areas further south. Conversely, Whitten & Cameron (1980), Skogland (1989, 1990) and Cameron *et al.* (1992) found that plant phenology was later and that plant biomass was lower on calving grounds during calving than in the more southerly areas occupied by bulls. Food quality (Bergerud, 1990), digestibility and biomass (Russell *et al.*, 1993) were found to be lower on calving grounds during calving than in the more southerly areas occupied by bulls. A simulation model indicated that pregnant cows would have an energetic advantage if they migrate with the bulls rather than migrating to calving grounds (Russell *et al.*, 1993).

Wolves (*Canis lupus*) and other predators are relatively rare on caribou calving grounds during calving (Whitten & Cameron, 1980; Heard & Calef, 1986; Bergerud, 1988; Fancy & Whitten, 1991; Cameron *et al.*, 1992; Heard & Williams, 1992). Messier *et al.* (1988) reasoned that because caribou migrate beyond the reach of denning wolves, whose movements are largely confined to the vicinity of their dens, then wolves could not show a numerical response to increased caribou numbers. Bergerud (1980), Heard & Calef (1986) and Heard & Williams (1992) suggested that wolves could show a numerical response to changing caribou densities because caribou show density - dependent range expansion and contraction. At high caribou densities more caribou return earlier to areas near tree line where most wolves den. If this results in higher wolf pup survival then wolves may show a numerical response to changing caribou densities. The timing and magnitude of the numerical response would determine when, or if, predation is inversely density-dependent (depensatory) or regulatory (see Messier, 1994).

In this paper we present data relating to the proposed causes and consequences of the migration of barren-ground caribou to calving grounds. Data were collected primarily on the Bathurst caribou herd, but also from 3 of the other large herds of migratory barren-ground caribou in the Northwest Territories; the Bluenose, Beverly and Qamanirjuaq (previously spelled Kaminuriak; see Williams & Heard, 1986)

Methods

In May and June 1990, 1991 and 1992 we documented the general movements of bulls and pregnant cows in the Bathurst herd during unsystematic flights in Cessna 185 and Bell 206B aircraft. In May and June 1990 we collected feces from the surface of the snow both on the calving ground and from areas occupied by bulls. In 1991 and 1992 we shot about 10 bulls and 10 cows in each of 3 seasons; May-June (28 May for cows in 1991, 29-30 May for cows in 1991, 3-6 June for bulls in 1991, 25-26 May for bulls in 1992), late July (27-29 July in both years), and early September (4-6 Sept in 1991 and 3-8 Sept in 1992). Total fat was estimated from backfat depth and weight of all fat adhering to both kidneys and total muscle was estimated from gastrocnemius weight based on the relationships in Adamczewski *et al.* (1987). Fat and muscle weights were divided by metatarsus weight to adjust for variation in body size. Diet was inferred from the analysis of plant fragments, collected from the rumen and feces of the shot animals, that were identified by microhistological analysis at the AAFAB Composition Analysis Laboratory, Fort Collins, Colorado, USA. The concentration of nitrogen in the feces was determined using the micro kjeldahl technique and was used as an index of nitrogen in the diet.

Vegetation was sampled in both upland and lowland habitat. Biomass was determined by removing all vegetation, except mosses, from 10 2000 cm^2 sampling plots placed at random in each habitat type in areas occupied by bulls and cows in late May and early June, July and September 1990. Cut vegetation was immediately sorted into the following categories; lichen, live sedge and other monocots, dead sedge and other monocots, live forbs, live woody vegetation and other dead vegetation.

We estimated the magnitude and causes of neonatal mortality on the Beverly herd's calving ground between 11 and 16 June 1993. The sex, age and reproductive condition of all caribou observed were recorded from a helicopter while flying along lines systematically spaced across the calving ground. The helicopter was flown about 50 m above the ground at 100 kmhr^{-1} although speed and altitude varied. Caribou were classified as neonates, yearlings, two year old or older males, and two year old or older females. Breeding females (pregnant or post-partum) were identified by the presence of a distended udder or hard antlers. Females without hard antlers and without a calf at heel but with a distended udder were assumed to have given birth and the calf had died. Barren cows had neither udders nor hard antlers but they carried about 10-15 cm of new antler growth. Field necropsies were carried out on all dead calves found during those flights. Calves with appropriately spaced puncture wounds and associated subcutaneous haemorrhaging were considered to have died from wolf predation.

Relative wolf densities were based on wolf sighting rates collected during calving ground surveys conducted between 1963 and 1993 and from spring composition surveys 1976 - 1994.

Results

Distribution and Movements

Spring and summer movements of both bulls and cows in the Bathurst herd were similar in 1990, 1991 and 1992. In late May and early June of 1990, 1991 and 1992, all pregnant cows were on the calving ground near Bathurst Inlet (no neonates were seen anywhere else) while the only place we found bulls was near treeline between 200 and 300 km further south (Figs. 1 and 2). Because our sampling for caribou distribution was not systematic we cannot rule out the possibility that there were no bulls elsewhere on the tundra or still within the boreal

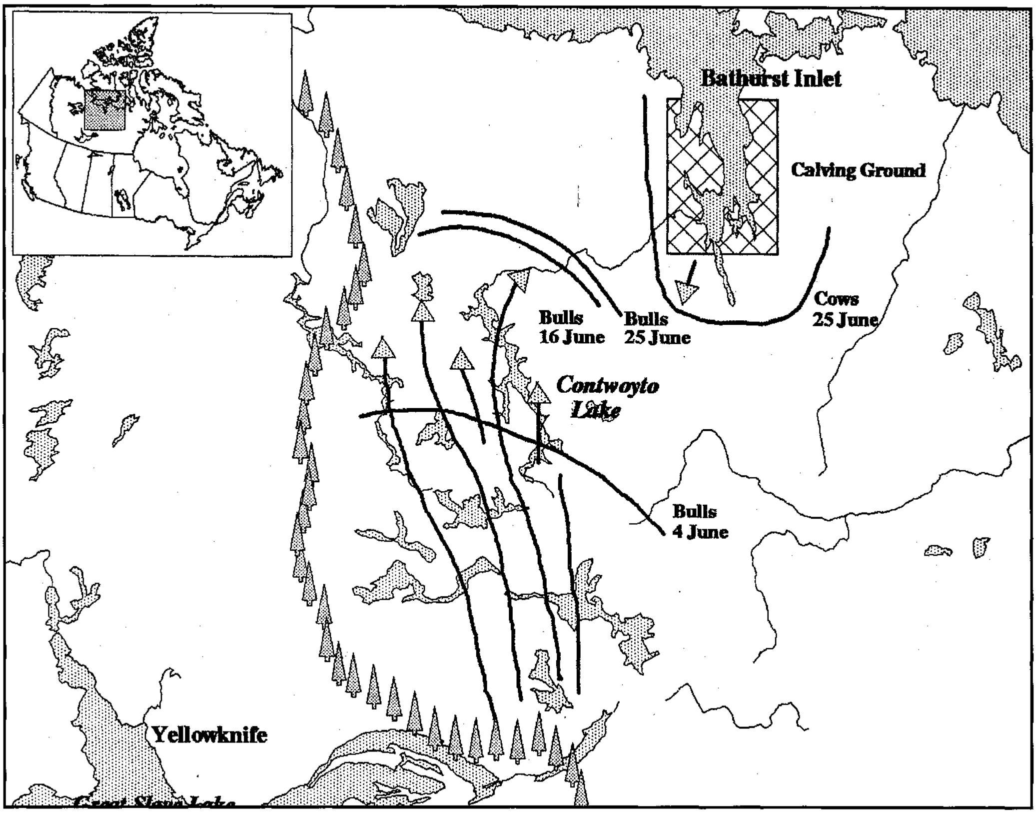

Fig. 1. Distribution of bulls and cows in the Bathurst caribou herd in June 1990. Concentric lines indicate the location of the most northerly bulls on June 4, June 16 and June 25, the location occupied by calving cows between 4 and 16 June and the location of the most southerly of the cows and neonates on 25 June.

forest but bulls typically make up only about one per cent of the animals on calving grounds e.g., 1.3% (23/1778) of the one year old or older animals classified on the calving ground of the Bathurst herd in 1986, 0.65% (17/2597) in 1990 and 0.49% (22/4533) and 0.59% (20/3408) on the Beverly herd's calving ground in 1988 and 1993 respectively. After calving, cows moved southwest and by 25 June 1990, the front of the cow distribution had almost met with the most northerly bulls which had moved north during that period. The sexes occupied the same general areas in July and September (Fig. 2).

Plant Biomass

Sedges (*Carex* and *Eriophorum* spp.) are the first plants to produce new spring growth after snowmelt and they were either the first or second most common food item in the diet of both sexes in late May and early June. The biomass of live sedges in lowland habitats was higher within the areas occupied by bulls than the biomass of live sedges in lowland habitats on the calving grounds (Table 1; Mann-Whitney U-test, U=7, $n_1=n_2=10$, $P<0.01$). Biomass of live sedges was highest in July.

Diet quality

Between 1 and 4 June 1990, nitrogen in feces collected from areas occupied primarily by bulls was greater than nitrogen in feces collected on the calving ground (Fig. 2; t=4.77, df=32, P=0.0001) There were no nitrogen concentration differences in feces collected from areas occupied by bulls and cows on 13-15 June 1990 (t=0.29, df=19, P=0.78) or 25-26 June 1990 (t=0.49, df=34, P=0.62). Similarly, in late May and early June of both 1991 and 1992, fecal nitrogen from bulls shot near treeline was significantly higher than in cows collected on the calving ground (Fig. 3; F=16.99, P=0.0002), but there were no differences between the sexes in July of either year when they occupied the same area. We shot one cow that was with the bulls in June 1991. Plant fragment analysis of fecal and rumen samples indicated that her diet was more similar to the bulls collected in the same area than it was to the diet of cows on the calving grounds. Nitrogen in the feces of that cow (2.05%) was also more similar to the fecal nitrogen of bulls collected in the same area ($\bar{x}$=2.08%) than it was to the fecal nitrogen of cows on the calving grounds ($\bar{x}$=1.76%).

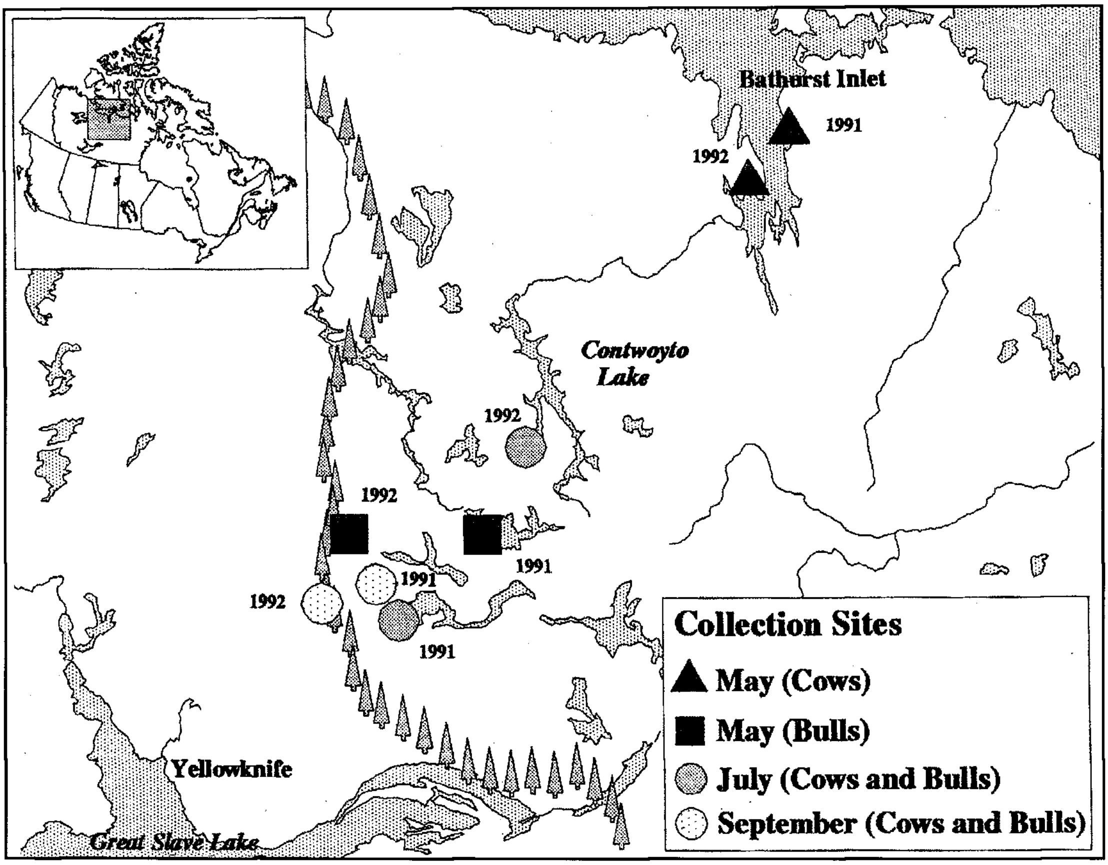

Fig. 2. Locations where we collected caribou from the Bathurst herd in 1991 and 1992. May collection sites were in different places for bulls and cows. Because the sexes occupied the same general areas in July and September both bulls and cows could be collected at the same site.

Body condition

Body fat and muscle decreased in both sexes from May to July and increased from July to September in both years (Table 2). Seasonal differences in fat weights were significant for both sexes when years were combined (cows, F=28.13, P=0.0001; bulls, F=29.92, P=0.0001). When years were combined, seasonal differences in muscle weights were significant for cows, but not for bulls where the sample size was small (cows, F=23.13, P=0.0001; bulls, F=2.72, P=0.08). Both sexes had significantly more fat in July 1992 than in July 1991 (F=120.31, P=0.0001) but years did not differ in May or September (May, F=0.92, P=0.34; September, F=3.5, P=0.07).

Wolf density and predation on neonates

Wolf densities on calving grounds during calving, as

Table 1. Mean biomass (SE) of lichen and live sedges within 10 2000 cm^2 sampling plots on the Bathurst caribou herd's range in 1990.

Sampling location	Lichen biomass (g/m^2) Upland	Lichen biomass (g/m^2) Lowland	Live sedge biomass (g/m^2) Upland	Live sedge biomass (g/m^2) Lowland
Bull distribution, May-June	21 (7.3)	0.2 (0.11)	0.1 (0.07)	6.6 (2.78)
Cow distribution, May-June	13 (1.6)	0.3 (0.30)	0.0 (0.0)	1.5 (0.66)
Distribution of both, July	12 (3.1)	3.3 (1.35)	1.0 (0.36)	12.8 (2.62)
Distribution of both, September	390 (69)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)

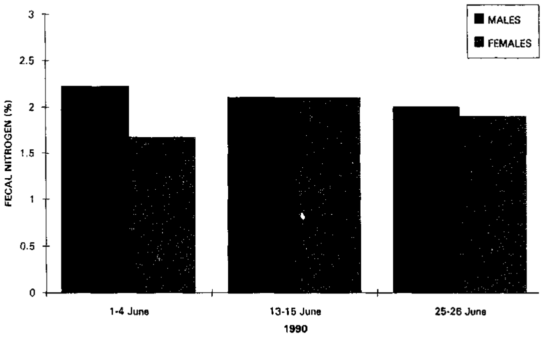

Fig. 3. Fecal nitrogen concentrations from areas occupied by bulls and cows in the Bathurst caribou herd in 1990.

indexed by the wolf sighting rate, averaged only 22% of densities on caribou winter and spring ranges, i.e., in March and April. This trend was the same for all 4 herds (Table 3). On the Beverly herd's calving ground in 1993 we saw 16 wolves in 64.2 h of flying (24.9 wolves/100 h) and wolf predation accounted for 70% of neonatal deaths (23 of 33 calves examined). By 1 week after the peak of calving 11.4% (4,310 of 37,654 parturient cows) of neonatal calves had died. Based on the proportion of necropsied calves that had died from wolf predation, 8% were killed by wolves (0.70 x 11.4) and 3.4% died of other causes.

Discussion

Our data suggest that by migrating to calving grounds, cows sacrificed foraging benefits which would have been available to them had they migrated as the bulls did. The differences between the sexes, in March to July movements, were similar to other migratory barren-ground caribou herds (e.g., Parker, 1972; Fancy *et al.*, 1989) and other researchers have also noted that plant phenology is later and that plant biomass is lower on calving grounds, than in the more southerly areas occupied by bulls (Whitten & Cameron, 1980; Russell *et al.*, 1993). However, even though food biomass on calving grounds was low, it is possible that biomass was high enough for calving cows to obtain foraging benefits, when coupled with the increased digestibility of new plant growth. Our data on fecal nitrogen

Table 2. Seasonal changes in fat and muscle weights of bulls and cows in the Bathurst caribou herd in 1991 and 1992.

Sex/ Collection period	Fat index						Muscle index					
	1991			1992			1991			1992		
	Mean	sd	n	Mean	sd	n	Mean	sd	n	Mean	sd	n
Cows												
May-June	4.6	2.2	11	6.2	3.7	10	0.19	0.02	11	0.20	0.02	10
July	-1.4	0.37	10	1.4	0.6	8	0.15	0.02	10	0.15	0.02	9
September	22.4	12.8	8	7.0	6.8	9	0.20	0.03	8	0.18	0.02	9
Bulls												
May-June	5.3	3.7	9	5.5	2.0	10	0.18	0.04	9	0.19	0.02	10
July	1.1	4.6	8	2.3	1.4	10	0.16	0.03	10	0.17	0.02	9
September	18.4	12.3	11	14.5	8.8	10	0.16	-	1	0.20	0.02	4

Table 3. The number of wolves seen per 100 hours when flying over caribou in March and April and on the calving grounds during calving in June (number of years of data; number of flying hours).

	Bluenose	Bathurst	Beverly	Kaminuriak
March and April	38 (11;507)	100 (11;483)	106 (15;655)	70 (6;589)
June calving ground	1 (4;200)	8 (11;531)	45 (8;414)	6 (8;400)
Weighted means:	March and April = 80 Calving ground = 17			

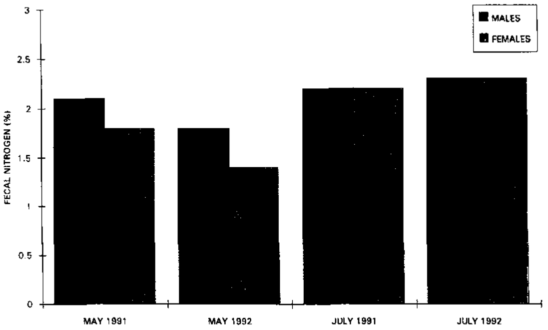

Fig. 4. Fecal nitrogen concentrations from bulls and cows collected from the Bathurst caribou herd in May and July of 1991 and 1992.

concentration show that this was not the case. Nitrogen intake by cows on the calving ground, as determined from fecal nitrogen, was lower than nitrogen intake by bulls. The difference in food quality between the sexes was probably important ecologically because comparatively small differences in food quality or protein intake can markedly influence weight gain and survival in ungulates (Albon & Langvatn, 1992). Moreover the greatest differences may have occurred in late April and throughout May, before our collections began, not in late May and early June. Although green vegetation was rare in early June on calving grounds, before that it was entirely absent. The general phenology of the environment suggests that bulls would have had green food available to them much earlier than cows. Differences in fecal nitrogen were unlikely the result of differential foraging between the sexes at that time of year because fecal nitrogen did not differ between sexes when they occupied the same area. Fecal nitrogen from the one cow we collected in June 1991 was similar to that of the bulls with which she was associating and fecal nitrogen did not differ between the sexes in late May in caribou on Southampton Island, where both sexes occupy the same area (Heard & Ouellet, 1994),

The advantage of migrating to calving grounds appeared to be a lower predation risk for neonates. Bergerud (1988, 1990), Fancy & Whitten (1991) and Cameron *et al.* (1992) also made this argument but our paper provides data on relative wolf abundance, based on wolf sighting rates, to support that conclusion. There are fewer wolves on caribou calving grounds because most wolves den near tree line often hundreds of kilometres away (Heard & Williams, 1992). Relatively more wolves den near the Beverly herd's calving ground and sighting rates are correspondingly higher. We suggest that our estimate of 8% wolf predation mortality of all neonates by one week after the peak of calving, in a year when wolf abundance was close to our long term average, represents strong selection for cows to attempt to reduce predation risks. Our estimate of 70% of all neonatal mortality from wolf predation was similar to the mean wolf predation mortality for the Beverly herd in, 1981,, 1982 and, 1983 of 68.5% (Miller *et al.* 1988).

We suggest that changes in body fat and muscle over the summer is primarily related to the level of insect harassment which affects time spent feeding (Klein, 1992; Russell *et al.*, 1993). Caribou aggregate into dense groups and body fat reserves decline in July when insect harassment is greatest. When insect numbers decline in August, the large aggregations break up and caribou amass large amounts of fat even though plants are senescing. Because the time period of fat assimilation is so short, we suggest that caribou attempt to reduce competition for food by spacing out as widely as possible. This could explain the density-dependent range expansion and contraction observed in migratory caribou populations (Simmons *et al.*, 1979; Bergerud *et al.*, 1984; Heard & Calef, 1986; Valkenburg & Davis, 1986; Messier *et al*, 1988; Couturier *et al.*, 1990) even at the cost of increased predation risk.

The potential exists for wolves to show a numerical response to changing caribou densities because wolf pup survival appears to be related to caribou availability (Williams & Heard, unpubl. data). We suggest that when caribou numbers increase and caribou expand their summer range, more caribou come earlier within the hunting ranges of tree line denning wolves, pup survival increases and wolf numbers increase (Heard & Williams, 1992). There is little variation possible in the wolf functional response because their diet is almost exclusively caribou throughout the year (Williams & Heard, unpubl. data). The effect of the resulting change in predation rate on caribou numbers will depend primarily on the timing and magnitude of the numerical response.

Our understanding of caribou population dynamics would increase if we knew more about the trade-off between food intake (or some other density-dependent cause of range use changes) and predation risk in August. A test of our hypothesis requires that predation rate be measured and evaluated as being either independent of density, depensatory (inversely density-dependent) or density-dependent and of sufficient magnitude to stop herd growth (Messier, 1994). The dynamics of the George River herd (Couturier *et al.*, 1990) represents a potential test of our hypothesis. As the size of the George River herd has increased, competition for summer food has increased, as indexed by reduced fall fat and pregnancy rates (Couturier *et al.*, 1990), caribou are expanding their summer range, caribou are arriving earlier at tree line (John Russell pers comm.), and wolf numbers are increasing (Toby Anderson and other Nain hunters, pers comm.). Herd size may still be increasing (see Couturier these proceedings). Those observations are consistent with our hypothesis but the effect of wolf predation cannot be determined until population growth stops.

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Ecology of the Porcupine caribou herd

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Abstract: Researchers have described general patterns of population regulation that fit most caribou (*Rangifer tarandus*) herds. Nevertheless, specific factors operating on particular populations vary greatly, and efforts to categorize herds according to the general patterns often lead to confusion. It is difficult for biologists to attempt to describe population dynamics in terms of density relationships for wide-ranging arctic caribou such as the Porcupine Herd. In these herds density varies as a function of dispersal and erratic movement patterns and is not simply the number of caribou divided by a fixed range area. Density is also a poor surrogate for resource availability per individual caribou because climatic factors affect forage and/or access to forage independendy of caribou numbers. Thus classic signs of nutritional stress such as delayed puberty, reduced productivity, and winter starvation can occur when a population is small as well as large and do not necessarily denote food competition brought on by high density, *per se*. Nutritional stress and exacerbated predation due to adverse weather conditions occasionally cause the Porcupine Herd to decline, and limiting factors such as poor nutrition, predation, harvest, accidents, and disease act in combination to keep herd growth rates low during periods of good weather. Adverse weather setbacks occur frequently, and the herd remains within a fairly restricted range of densities over long time periods. There is no true density dependent regulation and no equilibrium in this system.

Key words: caribou, density, limitation, population dynamics, regulation, *Rangifer tarandus*

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Introduction

Numerous biologists have attempted to identify the factors that determine caribou population dynamics. The Porcupine Herd was put forth as an example of a population regulated by predation when it was stable during the 1970s (Bergerud, 1980). The herd then increased during a period of predominantly mild weather from the late 1970s until about 1989, but rate of increase between censuses declined as the population approached its peak (Table 1). Physiological condition of females declined and the herd is now decreasing, causing some biologists to proclaim regulation by competition for food (Allaye-Chan & White, 1992). In this paper I will present some basic natural history data for the Porcupine Herd and try to point out ways in which it does and does not fit these and other hypotheses for population regulation.

The Porcupine Herd and its environment

The Porcupine Herd has numbered between about 100,000 and 180,000 animals over the past 30 years. It is well known for its spectacular aggregations on the arctic coastal plain and its importance to subsistence hunters, and it has been the subject of intensive research for many years.The herd has always occupied the same general area, but annual movements and range use patterns are complex. Generally, the herd winters south of tree line, although much of the winter range is actually alpine tundra, and in some years much of the herd remains on arctic tundra all year. In spring the caribou migrate north to calve and spend the summer on arctic tundra, where they may remain for only a few weeks, or for several months. Mountain habitats are used extensively, and irregular mid-summer movements south to the edge of the taiga occur nearly every year. The herd often penetrates deep into traditional winter ranges during August, only to return north again before making its final fall migration in late September or October.

The Porcupine Herd shares its range with 3 other large ungulate species. Moose (*Alces alces*) occur throughout the Porcupine Herd's range, but average density is low (ca. 0.1/km^2; Gasaway *et al.*, 1993). Dall sheep (*Ovis dalli*) are abundant in some mountain ranges but scarce or absent in others. About 500 muskoxen (*Ovibos moschatus*) occur on the arctic coastal plain in Alaska and another 150 in the northern Yukon.

Table 1. Population size and rates of increase of the Porcupine caribou herd, 1972-92.

Year	Population		Increase rate between censuses	
1972	100,000			
1977	105,000	(+28,000)	1972-79 = STABLE	
1979	105,000		r = 0.058	
1982	125,000		r = 0.077	
1983	135,000			
			r = 0.050	INCREASING 1979-89 r = 0.053
1987	165,000		r = 0.038	
1989	178,000			
			r = -0.036	1 DECREASING
1992	160,000			

Several large predators capable of taking adult caribou or their calves also inhabit the range of the Porcupine Herd. Wolf (*Canis lupus*) distribution and den site locations are not limited at tree line as reported for the Canadian barren grounds (Weiler & Garner, 1987; Heard & Williams, 1991), and wolves prey on caribou throughout the year. Hibernating brown (*Ursus arctos*) and black bears (*U. americanus*) have no affect on the Porcupine Herd on winter range, but brown bears are effective predators on summer range. Golden eagles (*Aquila chryseatos*) are relatively common near the primary calving areas and are adept at taking young calves (Whitten *et al.*, 1992a). Wolverines (*Gulo gulo*) and lynx (*Lynx canadensis*) occur widely but have little effect on Porcupine caribou. Mountain lions (*Felis concolor*) have shown up on Porcupine Herd range recently, but their predation on caribou is insignificant.

Clearly, the Porcupine Herd shares some characteristics with other large migratory populations, but there are also important differences. For example, the large Canadian herds tend to have far fewer alternate prey options for predators, and they also tend to have fewer effective predator species. The Porcupine Herd occupies primarily montane habitats, while the barren-ground herds inhabit much gentler terrain. As we search for common links in the ecology of caribou herds, we should not forget that their environmental conditions are often quite different.

Population dynamics of the Porcupine Herd

Limiting factors

By definition, limiting factors reduce the rate of increase of a population. Nutrition certainly limits the Porcupine Herd. Forage production and quality vary both geographically, due to general environmental conditions, and *in situ*, due to annual variation in meteorological conditions that affect plant growth (Jorgenson & Udevitz, 1992). Presumably this contributes to the variability in body condition of adult females after the summer foraging season that occurs both within and between years (Fig. 1). Evidence for relative shortages of forage (i.e., inaccessibility due to deep snow) is also compelling, and caribou are generally in poor shape after severe winters. Poor condition of adult females in the adjacent Central Arctic Herd has been linked to decreased reproductive performance (Cameron *et al.*, 1993). Perinatal calf mortality (occurring within 48 hr of birth) is common in the Porcupine Herd and derives mostly from causes that are consistent with poor nutrition (Roffe, 1990; Whitten *et al.*, 1992a).

Predation also limits the Porcupine Herd. Most of the nonperinatal mortality of calves during the

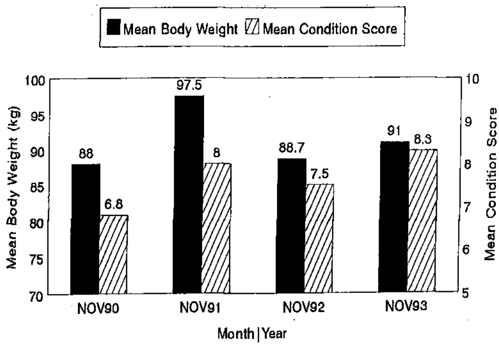

Fig. 1. Mean fall body weight and condition score of Porcupine Herd cows, 1990-93. Condition score is an index of the amount of soft tissue covering bone (5 being high, 1 low) summed for 3 sites: withers, ribs, and hips (Gerhart *et al.*, 1992)

first month after birth is caused by eagles, brown bears, and wolves. Nonperinatal mortality is higher when calving is displaced into foothill and mountain areas than when calving occurs primarily on the coastal plain where predators are scarce (Table 2; Whitten *et al.,* 1992a,b). Predation is also involved in a high proportion of adult deaths.

Human harvest is a minor limiting factor. Hunter kill is typically about 1,000-5,000 caribou and seldom exceeds about 3% of the herd. Subsistence harvest by rural residents within the range of the herd is already essentially *ad libitum*, and significantly increasing nonlocal harvest is not politically feasible. Accidents, disease, and parasites take their toll. Insects and weather cause little direct mortality, but have profound effects on caribou through their influence on habitat use and feeding, which in turn influence nutrition and predation.

Potential regulating factors

Of all these limiting factors, only nutrition and predation have been suggested as regulating the size of the Porcupine Herd. Regulating factors are defined as acting in a density dependent manner to keep a population within normal density ranges (Davis & Valkenburg, 1991; Messier, 1991). Unfortunately, because it is defined as number of animals divided by area used, density becomes a confusing parameter in a large migratory caribou herd.

The problem is that range size of a caribou herd is difficult to quantify objectively. Range use varies seasonally and even within seasons. Density is conventionally based on year-round range, but the same areas are not used every year. Most published accounts list range area for the Porcupine Herd at about 250,000 km^2 (Bergerud, 1980; Garner & Reynolds, 1986; Russell et al., 1993). Total year-round range actually occupied during the past 15 years is closer to 340,000 km^2 (Valkenburg *et al.*, this workshop). Maximum extent of range use occurred in the 1970s and early 1980s when the herd numbered about 100,000 and used virtually all its known range at a density of about 0.3/km^2. As the population increased, the herd did not expand its range and maintain a constant density. Nor did density increase in proportion to population size, as would have occurred if range size were fixed. Density reached as high as 1.1/km^2 during several years in the late 1980s when the herd was near its peak population of 180,000 but used only about half the historic range. Thus, density did increase as the population grew, but its peak value resulted as much or more from range restriction as from population growth.

Recent declines in caribou body condition and in yearling recruitment occurred at a time when caribou density was highest. However, other signs of nutritional stress such as delayed puberty and perinatal calf mortality occurred throughout the period of population increase (Tables 2 & 3). There was relatively poor recruitment in the early 1970s when the herd was at relatively low density (Davis, 1977; Fancy *et al.*, 1992), yet recruitment was consistently good during the mid-1980s when the herd was growing and density increasing (Fancy *et al.*,

Table 2. First month calf mortality in the Porcupine caribou herd, 1983-90.

Year	Perinatal Mortality[a] (%)	Nonperinatal Mortality[b] (%)	
1983	21.5	13.5	
1984	7.5	8.5	
1985	21.2	13.8	
1986	--	--	
1987	9.0	21.0	Displaced by snow
1988	12.2	16.8	
1989	15.0	9.0	
1990	10.0	0.0	

[a] Occurring within 48 hr of birth and deriving mostly from nutritional causes (Whitten *et al.*, 1992*a*).

[b] Occurring >48 hr after birth and caused primarily by predation.

1992). Cows captured and collared in the early 1980s were smaller than those caught a few years later, rather than larger, as would be expected if caribou numbers affected access to food resources in a strictly density dependent manner (Alaska Dep. Fish and Game, unpubl. files). Thus, it is not at all clear that lowered body condition or other signs of nutritional stress in the Porcupine Herd have been caused by increased caribou density. Furthermore, Porcupine Herd density has never approached the K-carrying capacities calculated for other herds (5-14/km^2) or at which other herds experienced food related die-offs (19/km^2; Bergerud, 1980).

Density dependence has also been suggested for the relationship between caribou and predators. Bergerud (1980) argued that caribou need space to avoid wolves, and he predicted that at densities exceeding about 0.4/km^2 caribou would encounter wolves frequently and predation rates would rise to stabilize the caribou population. Seip (1991) set the level at which wolf/caribou equilibrium occurs in migratory arctic herds at about 0.6-1.1/km^2. The Porcupine Herd in recent years has covered this range of densities. Messier (1991) stated that Bergerud's predation regulation hypothesis poses two testable predictions: 1) that predation rate increases with caribou density, and 2) that wolf predation becomes sufficient to stabilize a caribou population before it is stressed by poor nutrition.

The few published accounts of wolf populations on Porcupine Herd range indicate stable numbers (Weiler & Garner, 1987; Stephenson, 1991). Caribou density did not stabilize at 0.4/km^2, as predicted by Bergerud (1980). Neither early calf mortality nor adult mortality increased measurably even during severe winters at peak population/density levels. Overwinter calf mortality finally did increase in the early 1990s, but only when there was also food stress (Fancy *et al.*, in press). Thus the predation hypothesis did not stand up to Messier's tests.

Effects of adverse weather on population dynamics

Many biologists have suspected density dependent population regulation in the Porcupine Herd because it has remained within a fairly restricted realm of densities. Yet we've seen that evidence for regulation by either predation or nutrition is weak. If density dependent regulation is not occurring, what does keep the Porcupine Herd within bounds?

In theory, density dependent population regulation occurs through negative feedback loops between animals and their environment. That is, the number of animals per unit area affects other environmental components, and vice versa. The major problem with density theory and arctic caribou is that many factors other than caribou density profoundly affect the environment.

Caughley & Gunn (1993) recently pointed out that important relationships between herbivores and their forage can be missed by focusing on herbivore density alone because forage availability varies with weather and can change independently of herbivore numbers or density. We know there was adverse weather on the Porcupine Herd range in the early 1970s and again in the early 1990s. I believe that nutritional stress occurred then because, even at relatively low caribou densities, adverse weather reduced the availability of forage resources. Functionally, the result was the same as if density suddenly jumped to a much higher level. But the system was not density dependent, it was resource dependent. Caughley & Gunn (1993) suggested that the proper parameters to compare in such weather-driven systems are rate of increase in the animal population and density of forage biomass. For

Table 3. Age-specific parturition of known-age Porcupine caribou herd females.

	Age (Years)						
Cohort[a]	2	3	4	5	6	7	8
1981	0/5[b]	3/5	5/5	2/2	2/2	2/2	2/2
1982	0/28	18/25	7/14	8/8	7/8	5/5	2/2
1983	1/9	5/6	0/1				
1984	1/9	4/8	1/2	1/1			
1981-1984	2/51	30/44	13/22	11/11	9/10	7/7	4/4
	4%	68%	59%	100%	90%	100%	100%

[a] Birth year. 1981 females were 22 months at capture. All others were <10 months.
[b] Number parturient/total captured.

migratory caribou I think we need to get stop thinking of caribou/km^2, and think instead of available resources per caribou.

Unfortunately, it is not a simple task to merely change the label on an x-axis and plot recruitment versus available forage per caribou. The influence of weather is extremely difficult to measure because it can affect resource availability in many ways. Snow can make forage unavailable, or less available, and it affects the energy costs of foraging so that the net nutritional value of forage is variable, and never the same as the gross energy indicated by a bomb calorimeter. Summer weather affects both primary productivity and accumulation of key nutrients. Superimposed on all this are potential feedback loops between caribou and forage. If snowcover concentrates caribou onto small areas, there may be intense grazing pressure and a strong negative effect on forage. In contrast, if crusted snow generally restricts access to all forage, there may be less grazing pressure when food is limited, rather than more. Finally, equivalent weather events can have different effects on forage (i.e., the second year of drought can have a worse effect on plants than the first), and equivalent availability of forage can have different effects on caribou (i.e., a moderate winter after a severe one can have a greater effect on spring body condition than a single moderate winter after a series of mild winters). We should at least try to consider these complicating effects of weather when we investigate interactions between caribou and their range.

The role of predation in a weather-driven system

Weather induced nutritional stress stops population growth in the Porcupine Herd. This does not mean that predation is unimportant in the ecology and population dynamics of the herd. Caribou and wolves affect each other profoundly and the same adverse weather that reduces nutrition can also exacerbate predation, as when deep snow impedes caribou movements, or weakens them to the point where they are more vulnerable to wolves.

Most wolves the Porcupine Herd encounters are in resident packs on year-round range. These wolves thrive when caribou use their territories. Packs from some distance around may converge on a caribou concentration, and well fed wolves may experience a short-term boost in pup production. But when caribou move on they don't just become scarce, they virtually disappear. Caribou shift areas seasonally, but they also abandon parts of their range for years at a time. Whenever caribou shift away from an area, resident wolves must adjust back to resident prey availability. The longer the caribou stay away, the greater the adjustment wolves must make.

The Porcupine Herd calving and early summer range includes extensive areas of coastal tundra where sedentary ungulate prey are rare. Wolves using these areas must depend on caribou, but on most of the calving grounds caribou do not linger more than a few weeks. Few wolves can raise pups on the coastal plain, and no wolves den in the core calving area in Alaska (Weiler & Garner, 1987). Wolves, brown bears, and golden eagles all hunt primarily the fringes of the calving area.

Thus, the Porcupine Herd spaces away from predators effectively on its calving area. Bergerud's (1980) argument that wolves would stabilize the Porcupine Herd was based on the assumption that resident packs would thrive at times of high caribou density and produce surplus pups. Young migrant wolves would then move to the calving grounds and kill many calves. A few wolves not associated with established packs have indeed been captured near the core calving area, but such wolves did not become more abundant as the herd increased. More importantly, early calf mortality did not increase (Fancy *et al.*, in press). I believe that regular shifts in seasonal distribution of caribou and erratic changes in annual distribution effectively limit the long-term numerical response of predators to the Porcupine Herd.

Summary

Periodic adverse weather temporarily changes forage availability in the range of the Porcupine Herd, and caribou decline because of nutritional stress and the additive effects of predation, harvest, and other limiting factors. Adverse weather may also exacerbate predation. Declines can be rapid because nutritional stress affects the population from both ends–it lowers natality and raises mortality, and there are no biological restraints on mortality (Caughley & Gunn, 1993). Recovery has constraints because calves can only be born and recruited so fast, and predation never goes away.

The Porcupine Herd has effective predator avoidance options, and predation is not regulating. Nevertheless, predation remains a major limiting factor. Net recruitment during the period of mild weather, normal predation, and normal harvest that persisted through most of the 1980s resulted in an increase rate of only about 5% annually and a doubling time of about 14 years. The population would take 28 years to quadruple, which is a very long time to go without experiencing an adverse weather setback in the Arctic. The Porcupine Herd undergoes population fluctuations of variable amplitude and period because weather setbacks come at irregular intervals. Recovery rates under normally prevailing conditions are slow enough and weather setbacks occur frequently enough that the population tends to stay within a fairly narrow range of densities and seldom, if ever, reaches levels where there would be population regulation through food competition if access to forage were never restricted. There is no true equilibrium in this system, and synergism in stochastic events can drive it out of the range we normally see, but that's a rare occurrence.

The mechanism for population regulation I've suggested for the Porcupine Herd differs from what Bergerud (1980) proposed. It also differs from Seip's (1991) model for migratory arctic caribou, because I see no indication that predation or density dependent competition for food, either singly or in combination, stop growth of the herd in the absence of adverse weather. My model incorporates most of what Caughley & Gunn (1993) proposed for kangaroos and caribou in "desert" environments. It also reaches much the same conclusion as Valkenburg *et al.,* (this workshop) and Adams *et al.,* (in press) have for interior Alaska caribou.

This model is essentially a "plurality of factors" approach. In a practical sense, it holds that there is no single, ultimate regulating factor that alone explains the population dynamics of migratory arctic caribou over the range of densities and environmental conditions we normally experience. Finally, we must acknowledge that, although the same functional components may operate on many different caribou populations, those components will differ in magnitude in different times and different places and, therefore, do not inevitably lead to the same results. All caribou herds are not the same. The ecological situation of each is unique, and attempts to categorize herds into types usually lead to confusion (Davis & Valkenburg, 1991). In our search for common ground, we should examine processes. I see no reason to suspect that any single factor regulates all populations, or that any single explanation of population dynamics applies to all herds, or even to all herds of a certain type.

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Population decline in the Delta caribou herd with reference to other Alaskan herds

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Abstract: After growing continuously for nearly 15 years, the Delta caribou herd began to decline in 1989. Most other Interior Alaskan herds also began declining. In the Delta herd, and in other herds, the declines were caused primarily by high summer mortality of calves and increased natural mortality of adult females. Other minor causes included increased winter mortality of calves, and reduced parturition rates of 3-year-old and older females. The decline in the Delta herd also coincided with increased wolf (*Canis lupus*) numbers, winters with deeper than normal snow, and warm summers. Mean body weight of annual samples of 10-month-old female calves was consistently low during the decline. Except in some of the smallest Interior Alaskan herds, we conclude that evidence for population regulation in Alaskan caribou is weak, and that herds are likely to fluctuate within a wide range of densities due to complex interactions of predation and weather. Unless wolf numbers are influenced by man, the size of a caribou herd in a given year is likely to be largely a function of its size during the previous population low and the number of years of favorable weather in the interim.

Key words: rainfall, *Rangifer*, snow, temperature, weather, wolves

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Introduction

Caribou herds in Alaska and elsewhere have fluctuated in size over time, and the factors involved in these fluctuations have been widely debated (Leopold & Darling, 1953; Skoog, 1968; Van Ballenberghe, 1985; Messier *et al.,* 1988; Bergerud & Ballard, 1989; Seip, 1991; Eberhardt & Pitcher, 1992; Bergerud, 1993). Several caribou herds in Alaska were intensively studied during late 1970s and 1980s when herds were generally increasing (Davis *et al.*, 1991; Cameron *et al.*, 1993; Adams *et al.*, 1994; Whitten, 1994). This paper reports results of a continuing study of limiting and regulating factors in the Delta caribou herd, during the period of population decline from 1979 to 1993 and compares more limited data from other Alaskan herds.

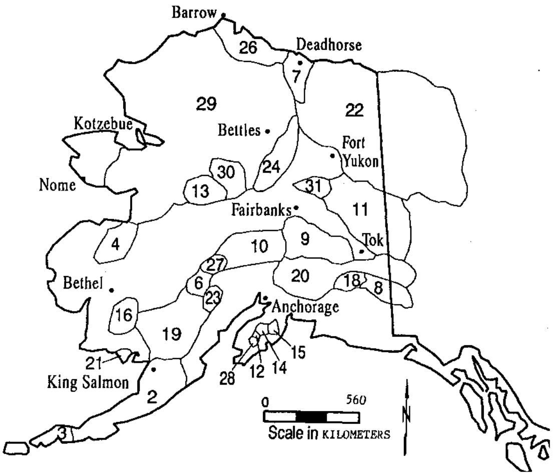

Fig. 1. Distribution of 31 caribou herds in Alaska.

Study area and population

The Delta caribou herd is one of 31 herds composing a total population of about 880,000 caribou in Alaska (Table 1, ADF&G files). About 750,000 of these caribou occur in the 3 largest herds: Western Arctic (29), Porcupine (22), and Mulchatna (19) (Numbers correspond to herd numbers in Fig. 1 and Table 1). Most of the other herds occur in the mountainous areas of Interior Alaska and range in size from a few hundred to about 40,000 caribou. The Delta herd (9) occupies an area of about

Table 1. Estimated size and crude density of Alaskan caribou herds.

Herd no.[a]	Herd name	1993 population estimate	Total range size (km^2)	Crude density caribou/km^2	Population trend since 1989
1	Adak (western Aleutians)[b]	750	376	2.0	up
2	Ak. Peninsula (north)	18,000	33,500	0.5	down
3	Ak. Peninsula (south)	2,500	4,900	0.5	stable
4	Andreafsky	<50	unknown	—	unknown
5	Beaver Mountains	649	6,000	0.1	unknown
6	Big River	750	11,500	<0.1	unknown
7	Central Arctic	23,444[c]	54,000	0.4	stable
8	Chisana	850	9,000	<0.1	down
9	Delta	3,661	12,500	0.5	down
10	Denali	1,890	10,000	0.2	down
11	Fortymile	21,884[c]	50,000	0.4	down
12	Fox River	75	500	0.2	up
13	Galena Mountain	275	10,500	<0.1	up
14	Kenai Lowlands	100	1,500	<0.1	stable
15	Kenai Mountains	300	1,000	0.3	stable
16	Kilbuck Mountains	2,500	10,000	0.3	up
17	Macomb	500	3,500	0.1	down
18	Mentasta	880	25,000	<0.1	down
19	Mulchatna	110,000	103,000	1.1	up
20	Nelchina	40,361	75,000	0.5	stable
21	Nushugak Peninsula	750	2,000	0.4	up
22	Porcupine	165,000	335,000	0.5	stable
23	Rainy Pass	500-1,000	9,000	0.1	unknown
24	Ray Mountains	700	17,000	<0.1	up
25	Sunshine Mountains	800	8,000	0.1	unknown
26	Teshekpuk	27,630	24,000	0.9	up
27	Tonzona	800	6,500	0.1	down
28	Killey River	100	500	0.2	up
29	Western Arctic	450,000	350,000	1.5	up
30	Wolf Mountain	650	8,500	<0.1	stable
31	White Mountains	1,000	8,000	0.1	up
TOTAL (approximate)		880,000			

[a] Numbers shown on fig. 1.

[b] Not shown on fig. 1.

[c] 1992 estimate.

[d] Stablilized through harvest.

12,000 km^2 of the northcentral Alaska Range. Its calving, summer, and autumn ranges are alpine tundra and its winter range is alpine tundra, muskeg, lowland black spruce (*Picea mariana*) and white spruce (*Picea qlauca*) forest. Adjacent herds include the Macomb herd (17) to the east, Denali herd (10) to the west, White Mountains herd (31) to the north, and Nelchina herd (20) to the south.

Until the early 1970s the Delta herd was considered one of many rather insignificant groups of caribou in Alaska. It was relatively small in size, had an inaccessible range, and management and research efforts were concentrated on the larger, road-accessible Fortymile and Nelchina herds. However, after the decline of the Fortymile and Nelchina herds in the early 1970s, the Delta herd received more attention from hunters, and consequently, from the Alaska Department of Fish and Game (ADF&G). Efforts to determine population identity and recruitment had begun in the late 1960s, but the first systematic census was not done until 1973. In 1979 ADF&G identified the need for a long-term population dynamics study of an Interior caribou herd, and began intensive research on the Delta herd. Initial studies were to determine the causes of low calf production and/or survival prevalent in the herd from 1971 to 1974. However, after a wolf control program primarily to benefit moose (*Alces alces*), the Delta herd increased rapidly (Gasaway *et al.*, 1983), and data collected through 1989 was representative of a growing population.

From 1979 to 1989 the Delta herd grew continuously from 4,191 to 10,690 (Davis *et al.*, 1991). From 1979 to 1982 the herd grew rapidly (λ = 1.20), because harvest was light, adult female mortality was low, and natality and calf survival were high (Davis & Valkenburg, 1985). From 1982 to 1985 the herd grew slowly from 7,335 to 8,083 caribou (λ = 1.03) because it was limited primarily by harvest, but also by increased adult mortality from wolf predation, and decreased calf survival (Davis *et al.*, 1987). From 1985 to 1989 the herd grew at a moderate rate (λ = 1.07) primarily because of high natural mortality of adult females and high calf mortality (Davis *et al.*, 1991). Since 1989 the Delta herd has been in a rapid decline. In this paper we review recent data on the Delta herd and other Interior herds in the light of current models of population regulation and limitation in caribou. We consider the influence of the following factors in caribou population declines: general density dependence, nutrition, predation, weather, harvest, immigration, and habitat loss.

Methods

We annually estimated population size, recruitment of calves to autumn, and age-specific natality rates of females in the Delta herd. In most years we also collected data on weights of 10-month-old female calves, and mortality rates and causes of death of radiocollared females older than 10 months. Starting in 1991 we also began weighing and collaring 4-month-old females. Movements and distribution of radiocollared caribou in the Delta herd and surrounding herds were monitored to detect immigration or emigration.

Population censuses (total counts) were conducted during mid June to mid July each year and followed techniques described by Davis *et al.* (1979) and Valkenburg *et al.* (1985). We estimated calf recruitment to September/October and April with helicopter surveys. Allocation of sampling effort was based on the distribution of radiocollared females. Natality rates of radiocollared females were estimated by looking for distended udders, hard antlers, or calves at heel from a Piper Super Cub or Bellanca Scout aircraft during the calving period (15 May 1 Jun) (Bergerud, 1964; Davis *et al.*, 1991). Weights

Table 2. Harvest, adult natural mortality, natality and recruitment in the Delta caribou herd, 1976-1993.

	Estimated harvest		Mortality[a] of females >1 year	Natality[a] rate of females >2 years		
Year	M	F	% dying (n)	% parturient (n)	Sept.-Oct. calf:cow (n)	April calf:cow (n)
1976	0	0	–	–	45 (258/572)	–
1977	0	0	–	–	42 (319/756)	–
1978	0	0	–	–	39 (126/324)	–
1979	0	0	0 (11)	–	65 (115/177)	–
1980	104	0	0 (29)	–	49 (288/585)	–
1981	268	73	0 (39)	77 (13)	41 (319/776)	–
1982	274	77	7 (47)	70 (10)	37 (318/860)	29 (205/708)
1983	1,302	234	4 (55)	77 (22)	46 (307/665)	49 (194/396)
1984	507	191	4 (50)	90 (31)	36 (222/613)	51 (256/499)
1985	614	117	22 (48)	93 (41)	36 (232/629)	44 (302/694)
1986	841	183	10 (39)	83 (40)	29 (329/1141)	–
1987	644	38	10 (43)	89 (28)	31 (320/1026)	29 (285/976)
1988	555	22	15 (46)	88 (32)	35 (631/1802)	21 (161/774)
1989	681	18	11 (48)	83 (30)	36 (432/1218)	16 (84/651)
1990	552	83	15 (40)	72 (39)	17 (265/1567)	9 (97/1082)
1991	456	22	23 (40)	71 (35)	8 (102/1245)	–
1992	0	0	20 (30)	96 (28)	11 (99/918)	–
1993	0	9	47	30 (23)	4 (46/1113)	–

[a] Data from radiocollared females.

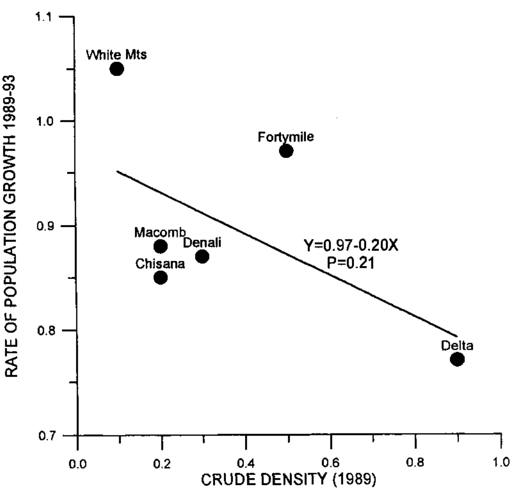

Fig. 2. Linear regression of crude caribou density versus annual average population growth rate (λ).

of 4- and 10-month-old female calves were sampled by immobilizing 9-15 animals from a helicopter in October or April, respectively. Mortality rates of female caribou were estimated with radiocollared individuals. When a mortality was detected, we used a helicopter or ground transportation to investigate the cause of death.

Because weather data were not available within the range of the Delta herd, we used a method of spatial interpolation (universal block kriging; Cressie, 1991:155) to calculate 3 weather variables (snow depth on 1 Mar and 1 Apr, mean Jun, Jul and Aug temperature, and total rainfall during 15 Jun-15 Aug) for the range of the Delta herd using surrounding climate and snow stations (National Oceanic and Atmospheric Administration, Climatological Data--Alaska; U.S. Dept. Agric., Soil Conservation Service--Alaska Snow Surveys). These weather variables were plotted and compared with data on caribou parturition (natality) rates and September/October calf:cow ratios.

Results and discussion

Immediate causes of the decline in the Delta *herd*

The proximate or immediate causes of decline of the Delta herd from 1989 to 1993 are clear. In order of importance they were: 1) high natural mortality of calves from birth to late September during 1990-1993, 2) high natural mortality of females older than calves primarily from wolf predation, 3) high mortality of radiocollared calves from September/October to April during 1991-1993, and 4) relatively low natality rates of adult females during 1990, 1991, and 1993 (Table 2).

Density-dependent resource limitation

Evidence for density-dependent resource limitation in the Delta and other Interior Alaskan herds was ambiguous. Although there was a weak relationship between density and population growth rate between 1989 and 1993 (Fig. 2). Some low density herds (e.g., Denali and Mentasta) declined, while others that had as high or even higher densities than the Delta herd did not decline (Table 3). However, the greatest decline occurred in the Delta herd which also had the highest density of caribou.

Table 3. Recruitment (fall calf:100 cow ratio) in 7 Interior Alaska caribou herds from 1980 to 1993.

	Herd calf:100 cow ratio in fall						
Year	Chisana	Denali	Fortymile	Macomb	Mentasta	Nelchina	White Mtns.
1980	23[a]		61[b]	13	42	42	–
1981	–	–	31	33	40	43	–
1982	21	–	27	26	39	54	–
1983	–	–	33	24	28	27	31
1984	–	41	–	40	29	34	–
1985	–	28	36	31	46	46	31
1986	33	38	28	–	–	42	–
1987	28	37	37	–	12	51	–
1988	31	33	30	32	18	48	33
1989	15[a]	30	24	34	15	39	36
1990	11	17	29	17	–	33	–
1991	1	7	16	9	2	45	13
1992	0	16	30	14	6	40	23
1993	2	6	28	18	4	24	22

[a] Fixed wing count only.

[b] Count probably not representative of herd.

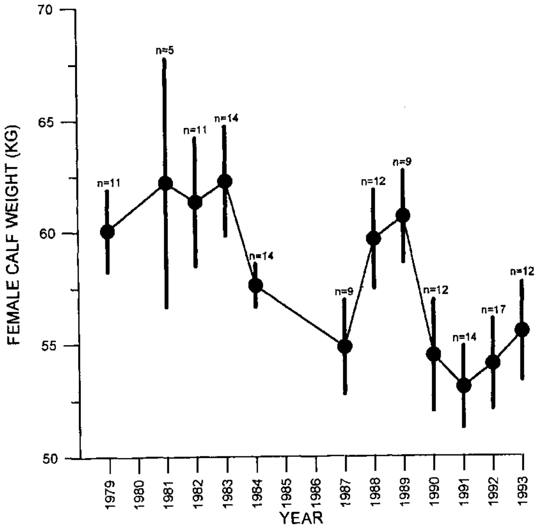

Fig. 3. Mean weight and standard error bars of samples of female calves weighed in April 1979-1993.

Nutrition as a limiting factor
Nutrition in the Delta herd apparently was poorer from 1990 to 1993 than in most prior years. However, it is not clear how decreased nutrition may have contributed to reduced population performance. Body weights of 10-month-old Delta calves have generally been lower since 1989 (Fig. 3), and the parturition rate of females was significantly lower in 1990 and 1991 than from 1984 through 1989 (χ^2 = 9.99, $P < 0.01$) (Table 2). In 1993 natality was very low. Since 1979 body weight of 10-month-old calves (which presumably reflects overall body condition in the Delta herd) has been a reasonably good predictor of calf survival to autumn (Fig. 4). This correlation may reflect increased vulnerability of calves to mortality factors during their first summer of life in years when overall herd nutrition is suboptimal prior to calving (Adams *et al.*, 1994). Poor survival of offspring in populations of animals with suboptimal nutrition has been widely reported (Skogland, 1985).

It is tempting to conclude that the reduced natality rate in the Delta herd in 1993, and perhaps in 1990 and 1991, contributed to the caribou decline. However, in 1993 natality rates in the adjacent Denali herd and in the Chisana herd were at least twice as high as in the Delta herd, and autumn calf cow ratios were similar (6:100 in the Denali, 4:100 in the Delta, and 2:100 in the Chisana) (Adams, pers. commun.; Valkenburg, 1993). In addition, in 1992 natality in the Delta herd was the highest recorded, and the autumn calf:cow ratio was among the lowest recorded (Table 2).

The cause of the low natality in the Delta herd in 1993 is unknown, however, weather in May and September 1992 was unusual and the growing season was short. Persistent cold and snow in May resulted in the latest leaf out ever recorded in Fairbanks (25 May), and *Eriophorum* flowers were not available to caribou in the Alaska Range until after 15 May. Subsequently, on 11 September an arctic storm system moved into Interior Alaska from the northwest and by 15 September there was over 60 cm of heavy, wet snow on the ground throughout the range of the Delta herd. The Delta herd left the Alaska Range en masse, and together with many hundreds of caribou from the Denali herd, they arrived near Fairbanks about 27 September. Many of these caribou wintered north of the normal range of the Delta herd in black spruce forest immediately adjacent to Eielson Air Force Base and in areas north of Fairbanks. During winter 1992-1993 many Delta and some Denali caribou were mixed with White Mountains caribou in the White Mountains north of Fairbanks and with Nelchina caribou in the Chulitna Mountains southeast of Cantwell. In late April and May, caribou from these 4 herds began separating and by mid June all radio-collared caribou had returned to their respective herds. Natality rates of the Delta, Denali, and Nelchina herds were all lower than normal, but natality in the White Mountains herd remained high (Valkenburg, 1993). Snow conditions were severe in all autumn and winter ranges from September through December. After December snow remained deep in the forested winter ranges north of the Alaska Range, but was reduced by wind and warm temperatures in the Alaska Range

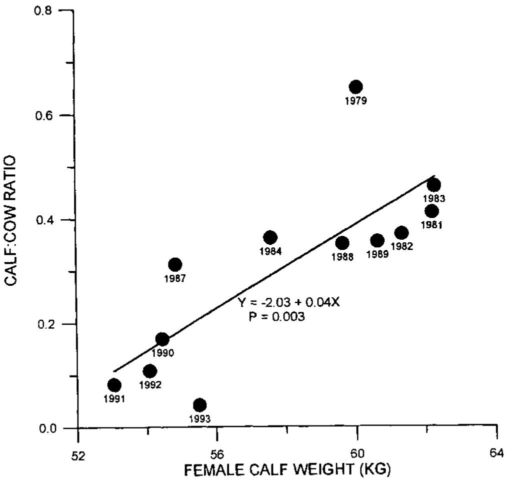

Fig. 4. Linear regression of female calf weight in April on September-October calf:cow ratio (data from Table 2).

where most of the Denali herd and about half of the Delta herd wintered.

Predation

There is compelling evidence that predation by wolves has been a major influence on the Delta herd over time. After wolf control in the mid-1970s the Delta herd became the most rapidly growing caribou herd in the state (Davis *et al.*, 1983; Gasaway *et al.*, 1983). In the mid-1980s, as wolf density approached precontrol levels, recruitment of caribou calves decreased and mortality of adults increased (Table 2). During 1983-1993 in the Delta herd, wolves were implicated in 23 out of 26 cases where the cause of death of adult radiocollared female caribou could be determined. In 26 additional cases, the precise cause of death could not be determined primarily because many of these caribou died during summer. In summer it was difficult to find evidence of hemorrhaging, so even if the kill site had been visited by bears or wolves, it was not possible to determine if the predators were scavenging or whether they killed the caribou. Long bones were recovered at about 50% of the winter kill sites, and in no case was malnutrition (as indicated by marrow fat content of less than 20%) documented as a possible contributing or direct cause of death.

In the recent decline, we did not determine causes of neonatal calf mortality. However, in the adjacent Denali herd (10) and the nearby Mentasta herd (18), wolf and grizzly bear predation were the major causes of high calf mortality (Adams, pers. comm.; Jenkins, pers. comm.). Grizzly bear densities are lower and wolf densities are higher in the range of the Delta herd than in the Denali herd (Dean, 1987; Mech *et al.*, 1991; Boertje, 1993; Reynolds, 1993) and it therefore appears probable that wolves are more important as predators of calves in the Delta herd than in the Denali herd.

Prior to summer 1989 our data suggests that moose were the primary prey of wolves, but shortly thereafter, wolves switched to eating caribou. In February-March 1989, just prior to the caribou decline, we investigated prey selection in 4 wolf packs in the Delta herd's range-by tracking collared individuals 2-3 times daily. Caribou and moose were abundant within the ranges of all packs. By weight, moose comprised two-thirds and caribou one-third of the wolves' diet (assuming 1 average moose = 3 average caribou). During the 30-day period, the 4 wolf packs studied killed 16 moose, 23 caribou, and 2 sheep. The small wolf packs killed as many caribou as the larger ones. At that time caribou and moose were both increasing (McNay, 1990; Boertje, 1993). Subsequently, coincident with severe winter weather, wolves increased, caribou declined and moose continued to increase until 1992 (Boertje, 1993). Comparative data from radiocesium (CS-137) concentrations in wolves corroborated this behavioral switch in prey selection over time (Boertje *et al.*, 1992). In addition, Mech *et al.* (1994) presented evidence that wolves included a higher proportion of caribou in their diet after 1989 in the range of the Denali herd.

Because much of the evidence for wolf predation as the main limiting factor in the Delta herd is circumstantial, we cannot be absolutely certain that the Delta herd would not have declined if wolf numbers had been substantially lower. If wolves are effectively removed from the calving and summer ranges of the Delta herd during the ongoing control program (winters 1993-1994 and 1994-1995) and the herd fails to recover, we will accept this as strong evidence that wolves were not the cause of the high calf mortality.

Another important question is whether wolves could have caused a decline in caribou without the presence of adverse weather. From 1985 on, wolves were an important limiting factor. The April 1988 and 1989 calf:cow ratios suggested increased overwinter mortality of calves prior to the onset of severe winters. However this probable decrease in recruitment, prior to the onset of severe weather, was insufficient to cause the herd to decline. In addition, wolves did not show a concurrent numerical response--wolf numbers remained relatively stable from 1985 to 1989 prior to the onset of bad weather (Boertje, 1993).

Wolf predation as a density dependent limiting factor

Bergerud (1993) proposed a conceptual model of population regulation in woodland caribou where wolf predation acts in a density dependent way and maintains caribou density at low levels (i.e., $<0.1/km^2$) because caribou lose the ability to effectively 'space out' from wolves at higher density. Although this model may fit some of the smallest Alaskan herds, clearly there are many herds which survive for long periods at moderate densities and neither 'space out' nor 'space away' from wolves. Furthermore, we found no clear relationship between caribou:wolf ratio or caribou equivalents:wolf ratio and caribou growth rate (Table 4, Figs. 5 and 6). It appears that Interior Alaskan caribou herds undergo extended periods of slow growth punctuated by short periods of rapid decline. Superficially, this may appear to be density-dependent predation, but growth rate of caribou may be more sensitive to influence of stochastic environmental factors rather than caribou density.

Table 4. Characteristics of 6 Interior Alaska caribou herds, 1980-1993.

Herd (Herd No., Fig. 1)	Crude density caribou/km^2 1989, 1993	Size in 1989 relative to existing historical estimates	Mean annual population growth 1980-89(λ)	Mean annual population growth 1989-93(λ)	1989 fall caribou:wolf ratio	1989 fall caribou equiv.:wolf	1989 caribou population size
Chisana (8)	0.2, 0.1	mod	1.07	0.85	unknown	unknown	1,540
Delta (9)	0.9, 0.3	high	1.11[a]	0.77	56:1	230:1	10,690
Denali (10)	0.3, 0.2	low	1.09	0.87[b]	20:1	55:1	3,250
Fortymile (11)	0.5, 0.5	low	1.09	0.97	85:1	150:1	22,766[h]
Macomb (17)	0.2, 0.1	mod	1.04	0.88	27:1	120:1	686[i]
Mentasta (18)	0.2, 0.1	mod	1.00[e]	0.77	34:1[f]	62:1[g]	2,687
Nelchina (20)	0.8, 0.8	mod	1.09[a]	1.03[a]	73:1	235:1	40,317
White Mtns. (31)	0.1, 0.1	n. a.[c]	1.10[d]	1.05	18:1	76:1	930

[a] Growth rate reduced by harvest.

[b] The population peak actually occurred in 1990.

[c] This area was formerly considered part of the range of the Fortymile herd, the herd was first recognized in the late 1970s.

[d] Growth rate is approximate because the 1980 population estimate was poor.

[e] Population estimates during the period ranged from 2,393 to 2,697 but no trend was apparent.

[f] Assuming a fall population of 80 wolves within the range of the herd (data from Tobey, 1991).

[g] Assuming about 750 moose within the caribou range (data from Tobey, 1990).

[h] 1990 population estimate.

[i] Interpolated between 1988 and 1990 estimates.

Weather as a cause of declines

Because the declines of Interior Alaskan caribou herds were nearly simultaneous, and because there appeared to be a nutritional link in the Delta and Denali herds (i.e., reduced body weight and reduced natality rate), it appeared likely that a widespread factor such as weather was involved in the declines. We examined 3 weather variables: winter snow depth as a contributing factor to adult mortality and summer calf survival, and summer temperature and rainfall as factors contributing to lower natality (presumably through reduced body condition during

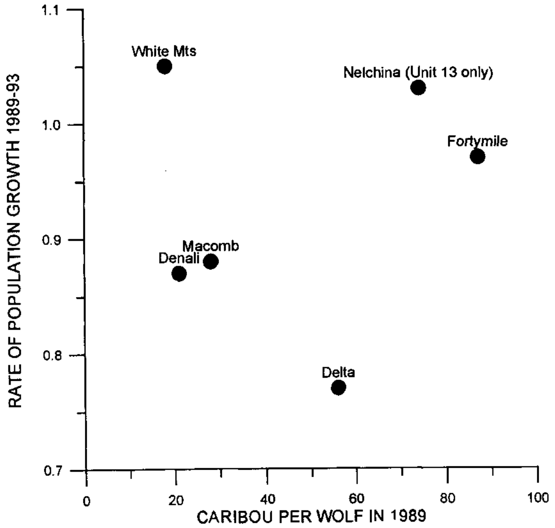

Fig. 5. Scatter plot of annual average population growth rate (λ) versus caribou:wolf ratio for 6 Interior Alaska caribou herds.

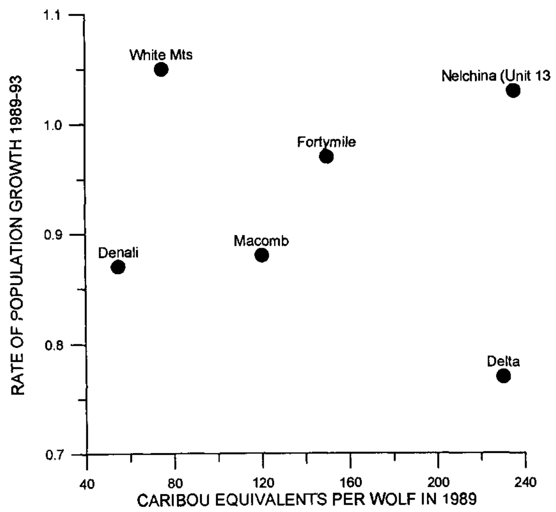

Fig. 6. Scatter plot of annual average population growth rate (λ) versus caribou equivalents:wolf ratio for 6 Interior Alaska caribou herds.

the rut) and decreased calf survival the following summer (through reduced body condition of calves at birth). The caribou decline in the Delta herd was coincident with 4 of the most severe winters since 1972 and followed 3 warm summers (Fig. 7). This was probably also true for the Macomb and Denali herds where weather was similar. However, in east central Alaska on the winter ranges of the Chisana, Mentasta, and Nelchina herds only the winter of 1989-1990 was severe, and snow depth barely exceeded 70 cm (snow data from Northway). The Chisana and Mentasta herds declined rapidly (Table 3) but the Nelchina herd continued to grow even though both wintered in contiguous and overlapping areas.

Harvest, emigration, and habitat destruction

Harvest, emigration, and destruction of winter range by fire and industrial development were potential factors that were either proposed as previous or potential causes or documented as contributing factors in previous declines of Alaskan or other caribou (Leopold & Darling, 1953; Skoog, 1968; Bergerud, 1974). These factors can be completely ruled out as factors in the current declines of the Delta and other Interior herds. In some herds (Denali and Macomb) harvest did not occur during the decline. In other herds, harvest was restricted to low levels and primarily to bulls (Chisana, Delta, Mentasta, Fortymile). Despite the inclusion of about 200 radiocollars in Interior caribou herds annually during the 1980s and 1990s and the occurrence of intermingling on winter ranges during 1989-1993, only 2 10-month-old collared females were documented as dispersing (both dispersed from the Macomb herd; 1 to the Nelchina herd and 1 to the Fortymile herd). From 1980 to 1993 no major fires occurred on Interior caribou winter ranges, and some low density herds declined. Large-scale human developments have not occurred on Interior caribou ranges in Alaska. Two herds, Nelchina and Central Arctic, have had their ranges bisected by the Trans-Alaska Pipeline. Central Arctic caribou have been displaced from their former calving areas (Whitten & Cameron, 1985); however, population consequences of this displacement have not been clearly documented. The Nelchina herd crosses the pipeline each spring and autumn without incident.

Conclusion

Evidence gathered during the current declines of the Delta and other Interior herds has led us to conclude that changed weather patterns increased vulnerability of caribou to predation and resulted in a numerical and behavioral response in wolves which in turn resulted in declines in many caribou herds. We therefore propose a conceptual model for Interior Alaskan herds that incorporates stochastic weather events that interact with predation and nutrition to limit herd size within a wide range of densities. The upper and lower bounds of population size would be a function of the amount of suitable habitat, the length of good or bad climatic periods, and interactions between predators and alternate prey. Only in rare circumstances would absolute food shortage become a major limiting factor. Food availability could be a limiting factor in some cases and may have a strong relationship with weather and predation because weather could make food unavailable and wolves could prevent caribou from foraging optimally. Vulnerability of caribou to predation would vary largely independent of density, and the size of a particular herd at a given time would primarily be a function of the size to which it was reduced during the last decline and the number of intervening years with favorable weather. Additional stochasticity could result from, as yet, largely unpredictable behavioral responses of wolves to numbers and vulnerability of all major prey species. In the recent Alaskan declines, there were no clear relationships between the rate of population

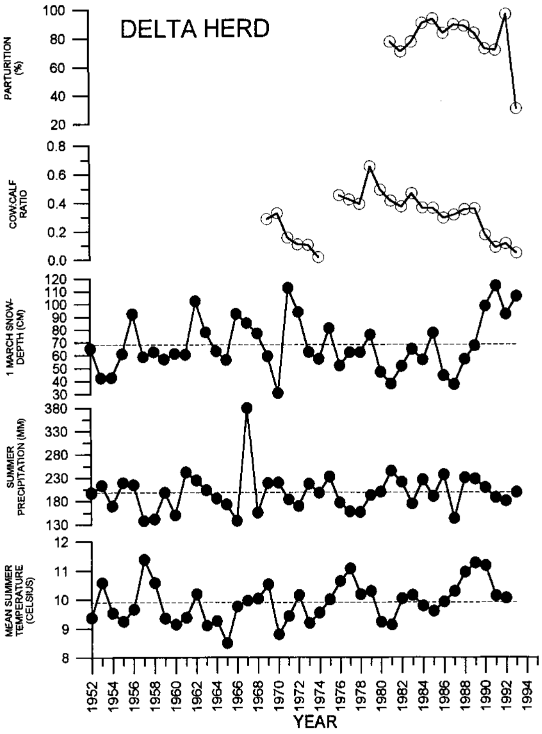

Fig. 7. Plot of parturition rate and autumn calf:cow ratio in relation to snow depth, summer precipitation, and summer temperature in the range of the Delta herd.

decline, density, and numbers of alternate prey (Figs. 2, 5, and 6; Table 4).

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Population ecology of two woodland caribou herds in the southern Yukon

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

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

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Introduction

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

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

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

Study area

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

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

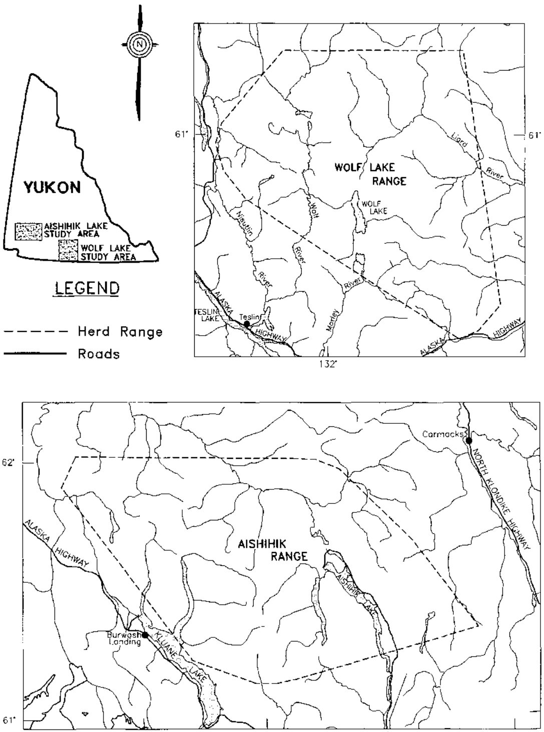

Fig. 1. Ranges of the Wolf Lake and Aishihik caribou herds.

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

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

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

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

Methods

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

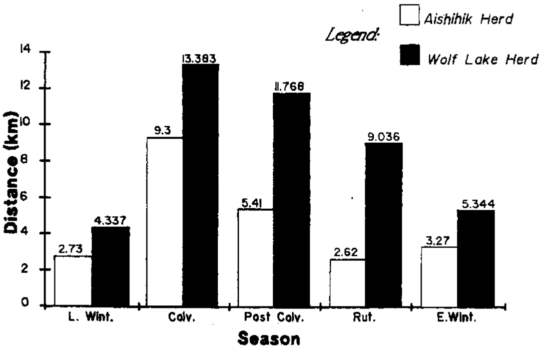

Fig. 2. Average distances between radio-collared caribou against season, for the Aishihik and Wolf Lake caribou herds.

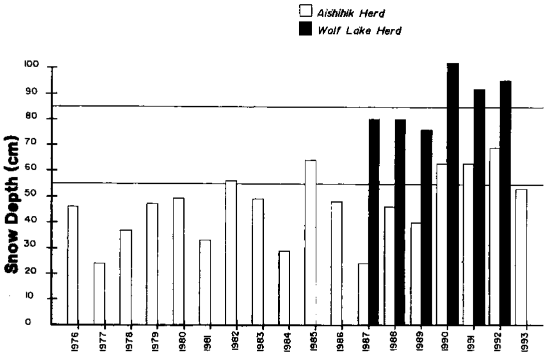

Fig. 3. Snow depths on 1 March on the Aishihik and Wolf Lake caribou winter ranges. The horizontal reference lines at snow depths of 55 and 85 cm represent the depths at which feeding and mobility, respectively, are adversely affected (Russell & Martell, 1984).

Results

Aishihik herd

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

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

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

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

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

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

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

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

Wolf Lake herd

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

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

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

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

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

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

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

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

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

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

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

Discussion

Demographic similarities between the two herds

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

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

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

Demographic differences between the two herds.

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

Ecological implications

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Conclusions

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

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

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

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Population Ecology of Caribou in British Columbia

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

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

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Caribou ecotypes in British Colombia

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

Population declines during the 1900's

The current population of caribou in British Columbia is estimated at 14,000 - 17,000 animals (BCMOE in press). Although there are no reliable estimates of historic populations, the current population is generally believed to be substantially reduced from historic numbers (Bergerud, 1978). Caribou have been eliminated from about 15% of their historic range, especially in the southeastern and central parts of the province (Fig. 1), and some currently occupied habitats have experienced population declines (Edwards, 1956; Bergerud, 1978; Stevenson & Hatler, 1985; Seip, 1992a).

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

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

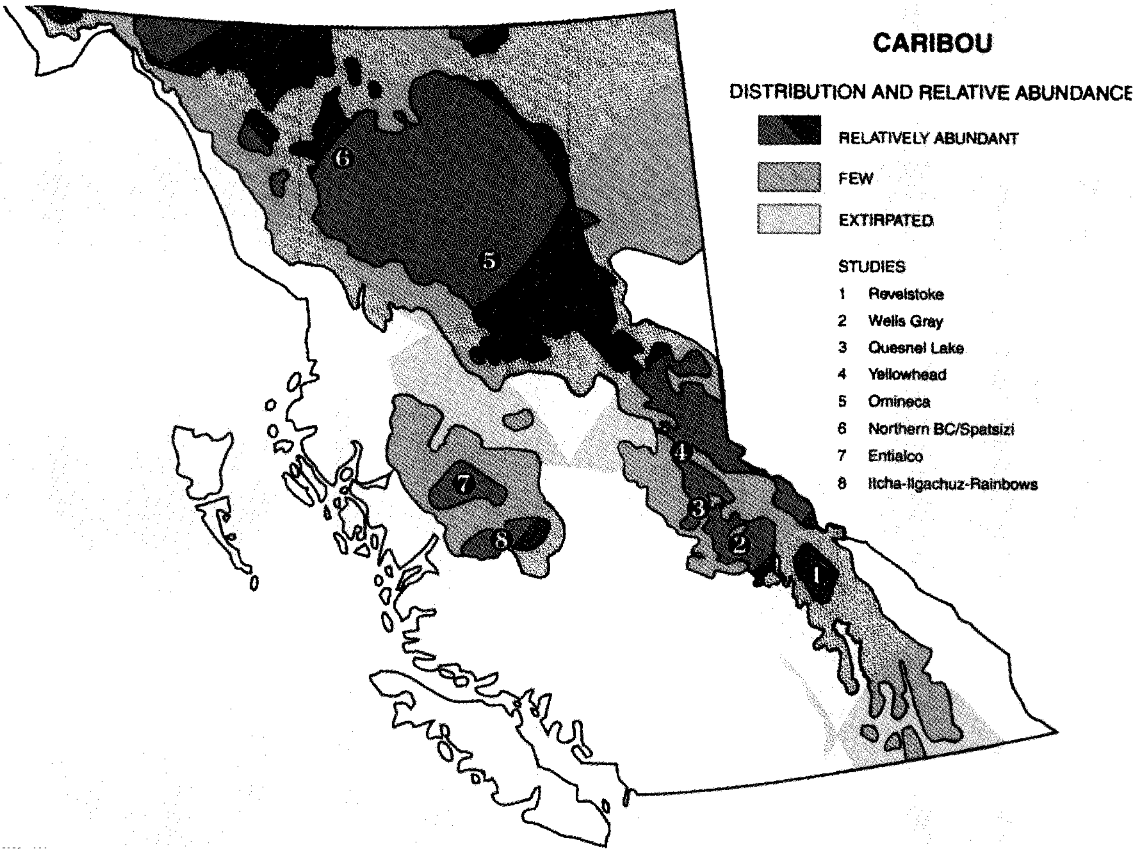

Fig. 1. Current and historic distribution of caribou in British Columbia (Bergerud, 1978, BCMOE, 1979), and the location of recent caribou research projects.

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

In summary, the general pattern throughout most of this century appears to be a population decline and range reduction of caribou in B.C.. Overhunting in accessible areas, and increased wolf predation resulting from increased moose populations, were likely the major factors contributing to those declines. In addition, some historic habitats have been abandoned due to habitat destruction or disturbance (Stevenson & Hatler, 1985).

Current population status

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

Pregnacy rate

Several studies have determined the pregnancy rate of adult female caribou by measuring plasma progesterone levels in winter. These studies reported that about 94% of adult females (≥ 2 years) were pregnant (Table 2). Bergerud & Elliot (1986) reported 84% of adult female caribou (≥ 2 years) in northern B.C. were pregnant, based on the presence of distended udders during the calving period. The lower value based on distended udder counts probably occurs because those counts would include non-parous 2 year olds that would have been classed as yearlings (1.5 years old) the previous winter when progesterone levels are sampled.

Neonatal survival

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

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

Calf survival through the summer

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

Wolf predation appeared to be a major cause of caribou calf mortality after the initial neonatal period. Seip (1992a) reported that when wolves were present and uncontrolled at Quesnel Lake during the mid-1980's, calf/cow ratios in October were only 2.5 calves/100 adult females, compared to 39 calves/100 adult females when wolves were absent or reduced by wolf control. Bergerud & Elliot (1986) reported 15.1% calves in the fall for northern B.C. herds when wolf numbers were low compared to 7.5% calves when wolves were more abundant. The major

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

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

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

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

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

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

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

Adult survival

The only reliable estimates of adult mortality rates have come from monitoring the survival of radio-collared caribou. Annual adult mortality rates varied from 0-29% among studies in B.C. (Table 5). Most studies found that the major period of mortality occured between May and October, especially during periods when caribou were migrating between winter and summer ranges. Adult caribou experienced a higher mortality rate at low elevations than at high elevations (Seip, 1992a; Cichowski, unpubl. data; Watts; unpubl. data; Wood, unpubl. data). Several of the studies were unable to determine the primary causes of mortality because dead caribou were not visited immediately after death. However, when cause of death was determined, wolf and bear (*Ursus* spp.) predation were the primary causes of adult mortalities. Avalanches were a major cause of adult mortality in the Revelstoke studies (Simpson, 1987a; B. McLellan, pers. comm.), an area of steep rugged terrain and very high snowfall and avalanche hazard.

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

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

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

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

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

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

Population trend

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

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

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

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

[1] λ=(1-M)(1-R) where M = adult mortality rate and R = calf recruitment rate (Bergerud & Elliott, 1986).

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

Anti-predator strategies and the density of caribou populations

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

In west-central B.C., radio-collared adult female caribou that calved on large alpine plateaus in the Itcha, Ilgachuz and Rainbow mountains had high calf survival through June (Table 7). In the adjacent Tweedsmuir-Entiako area, radio-collared caribou that calved in low elevation forested areas had very low calf survival, whereas caribou that calved in alpine and subalpine habitats had higher calf survival, similar to the Itcha-Illgachuz-Rainbows (Table 6). Two caribou that calved on islands, one of them over 3 successive years, also had high calf survival. Cumming & Beange (1987) also reported that caribou in Ontario calve on islands to avoid predators.

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

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

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

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

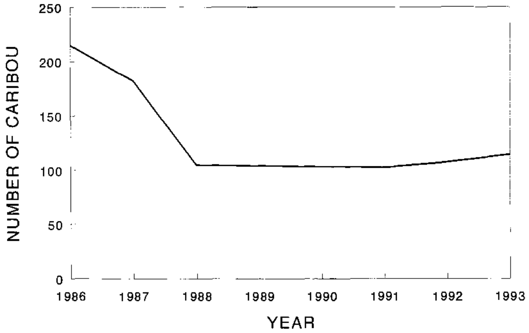

Fig. 2. Population trend of woodland caribou in the Quesnel Lake area, based on March counts corrected for sightability.

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

The Quesnel Lake caribou stabilized at a density of about 0.04 caribou/km^2 over the entire annual range. Densities on winter ranges were higher (0.2/km^2), but the density over the annual range best represents the density at which caribou were available to wolves through the year. Other B.C. caribou herds that space out in subalpine forests and alpine peaks in summer also occurred at a density of about 0.04/km^2 over the annual range (Table 8). In contrast, caribou herds that aggregated on large alpine plateaus in summer, ie. the Itcha-Ilgachuz-Rainbows herd and the Spatsizi herd, occurred at a density of about 0.1-0.2/km^2 over the annual range. That density is similar to caribou herds in Yukon and Alaska (0.15-0.3/km^2) that aggregate on alpine plateaus during summer (Farnell & McDonald, 1988, 1990; Adams & Mech in press).

Prior to the increase in moose abundance in B.C. during the 1900's, it is likely that higher densities of caribou were able to co-exist with wolves. However, when moose numbers increased, caribou that lived in close proximity to moose habitat were eliminated or greatly reduced, and the caribou remaining today represent animals that were more effective at spacing away from moose and wolves in summer. For example, in Wells Gray Park, most of the caribou that traditionally spent the summer in close proximity to moose habitat have disappeared and the current stable population represents caribou that migrate away from moose habitat in the summer (Seip, 1992a). Current stable caribou populations should be able to maintain their densities, as long as their predator avoidance strategy is not further disrupted by natural or human factors.

These results support the general model proposed by Seip (1991), that the abundance of caribou is primarily determined by the effectiveness of their anti-predator strategy. Caribou which aggregate on alpine plateaus for calving and summer range are fairly effective at avoiding predators and attain the highest caribou densities in B.C. Caribou that space out in subalpine forests during summer experience greater exposure to predation and are reduced to lower densities (Seip, 1992a). Caribou which live in boreal forests in northeastern B.C. have the fewest options to become spatially separated from predators and consequently occur at even lower densities (1 caribou/25-250 km^2; BCMOE, in press), similar to other areas of the boreal forest across Canada (Edmonds, 1991; Cumming & Beange, 1993).

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

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

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

Implications for caribou management

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

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

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

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

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Habitat partitioning between woodland caribou and moose in Ontario: the potential role of shared predation risk

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Abstract: This paper explores mechanisms of coexistence for woodland caribou (*Rangifer tarandus caribou*) and moose (*Alces alces*) preyed upon by gray wolves (*Canis lupus*) in northern Ontario. Autocorrelation analysis of winter track locations showed habitat partitioning by caribou and moose. Numbers of Delaunay link edges for moose-wolves did not differ significantly from what would be expected by random process, but those for caribou-wolves were significantly fewer. Thus, habitat partitioning provided implicit refuges that put greater distances between caribou and wolves, presumably decreasing predation on the caribou. Yet, direct competition cannot be ruled out; both apparent and direct competition may be involved in real-life situations. A synthesis including both explanations fits ecological theory, as well as current understanding about caribou ecology.

Key words: apparent competition, autocorrelation, competition, gray wolf, *Rangifer, Alces, Canis*

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Introduction

Knowledge in woodland caribou ecology, until recently, has lacked the maturity necessary for broad generalizations. But some attempts have been made. In Ontario, Devos & Peterson (1951) pointed out that caribou range continued to shrink, despite closure of legal hunting in 1929 (supported by Cringan, 1957). Simkin (1965) suggested that a caribou decline following moose immigration about 1900 was due to increased biomass supporting higher predator densities; similar to those later reported in British Columbia (Bergerud & Elliot, 1986). Bergerud (1974, 1985) hypothesized that all caribou in Ontario would need islands or shorelines as escape habitat for calving. Other studies supported this generalization (Simkin, 1965; Bergerud, 1985; Cumming & Beange, 1987; Bergerud *et al.*, 1990). Cumming & Beange (1987) concluded that caribou in the boreal forest show fidelity to wintering areas similar to that of white-tailed deer (*Odocoileus virginianus*, Halls, 1978). Cumming & Beange (1993) further showed that timber harvesting in portions of these wintering areas temporarily terminated their use by caribou, the non-use period lasting for at least 10 years; circumstantial evidence suggested that the displacement resulting from entire wintering areas being cut led to extinction of the local caribou band.

Elsewhere in North America, earliest hypotheses tended to be applied to all North American caribou, only incidentally including woodland caribou; even then, views sometimes appeared diametrically opposed (e.g. Scotter, 1972; Bergerud, 1974). Bergerud (1974, 1980) hypothesized that, across North America, predation sets caribou stocking limits at 0.4-0.8/km^2 or less, well below the levels that would be set by food availability. Support for the importance of predation came from subsequent studies: (Gauthier & Theberge, 1986; Edmonds, 1988; Elliott, 1985; Bergerud & Elliot, 1986; Elliott, 1989; Hayes *et al.*, 1989; Bergerud, 1992). Bergerud (1992) later revised his density figure downward for woodland caribou to 0.04/km^2. In line with this initial generalization, studies of predator avoidance by cows with calves have provided a catalogue of strategies used by woodland caribou to reduce predation during calving: to the use of islands and shorelines has been added dispersion in mountains (Bergerud *et al.*, 1984) and forest wet-land habitat (Paré & Huot, 1985; Brown *et al.*, 1986). Bergerud (1992) pointed out that, where special geographic features are not available, caribou can still reduce predation during calving by dispersing to create rareness.

Predation during the rest of the year has received less attention, sometimes for good reason. At Quesnel Lake, and Wells Gray Park, British Columbia, high elevations provided winter refuge (Seip, 1989; Seip, 1990) and, clearly, calf mortality was limiting the caribou population. Still, Bergerud & Elliot (1986) calculated adult mortality across North America at 18-21% (9% after predators were reduced), and other studies have shown the importance of winter mortality. Edmonds (1988) reported 22% adult mortality of woodland caribou in Alberta, all during winter and mostly due to wolves; fall recruitment of calves averaged 15%, a level high enough to have sustained the herd (Seip, 1990; Bergerud, 1992) if it had not been for the high adult mortality. In the Burwash area of the Yukon, Gauthier & Theberge (1986) found disproportionate consumption of caribou relative to available biomass during the rutting and winter periods, but not during calving. Hayes *et al.* (1989), in the Findlayson area of the Yukon, found low recruitment (10%) and high adult mortality (27%) before wolf control; wolves relied heavily on caribou for prey in the areas they occupied, but on moose in other areas. Lately, Seip (1985, 1989, 1992) hypothesized that wolf predation is the major cause of caribou population decline in southeastern British Columbia, that wolf populations are sustained primarily by moose, and that wolf predation on caribou is greater where caribou live in close proximity to the moose. The above studies suggest that this generalization might apply whether the proximity was during calving time or winter.

Yet, apart from populations theory (e.g. Eberhardt, 1991) and optimal foraging theory (Belovsky, 1991) little reference has been made in caribou literature to general ecological theory. In this paper, we present an initial attempt at relating caribou research findings with general theory; toward that end, we present as an example a study of habitat partitioning during winter in Ontario; and we introduce autocorrelation analysis, a statistical method not previously used to analyze caribou data.

Woodland caribou findings and ecological theory

Mathematical models have provided a body of theory in general ecology that seems useful for understanding caribou ecology in a wider context. Holt (1977) drew attention to the fact that although competition for resources is widely recognized, competition to avoid predation is not. He investigated the possibility with multiple models and found that a predator necessarily imposes "reciprocal equilibrial abundances" upon alternative prey species, even if these species are otherwise independent. Holt (1977) argues that, at equilibrium, the alternate prey species of most food-limited predators should exhibit this "apparent competition". In some cases, the less productive prey can be eliminated. Holt (1977) points out that to some extent, all species in the predator's diet will be to blame for the exclusion of one, and concludes that understanding the factors controlling a species' density requires examination of the entire community in which the species is embedded.

Holt (1984) then investigated requirements for co-existence when two prey species share a common predator. He observes that an influx of predators into a habitat should reduce prey density; however, if a predator can choose where to forage without interference from other predators, (at least) as many species of prey can coexist in the predator's diet as there are distinct patches discriminated by the predator. "Habitat partitioning can permit coexistence even when predation is intense, essentially because it allows the number of predators exploiting a given prey to be determined independently of the availability and productivity of alternative prey," (c.f. Seip, 1992).

Further models (Holt & Kotler, 1987) show that a rare prey species may benefit from co-occurring in patches with a more common prey species (particularly if the rarer prey is less preferred). Consumption of one prey species reduces time available for encountering and capturing the alternative prey; thus, predator selectivity may provide an "implicit refuge" for a low-quality prey. The predator should depart from a patch when its instantaneous rate of foraging decreases to the average rate of yield over the entire habitat in which the predator is foraging. From these results it is possible to plot "constant-yield isoclines". A predator might be expected to leave patches of prey that are unusually low in average foraging return compared with other patches.

On the basis of Seip's (1992) generalizations about woodland caribou and these aspects of ecological theory, we hypothesized that caribou in Ontario some 40-50 years after moose immigration was complete should be spatially separated from moose and wolves in winter. To test the hypothesis we flew transects over a selected study area during four winters (1981-84), plotting locations of tracks for woodland caribou, moose and wolves.

Methods

Study area

The study area encompassed 6 500 km^2 of boreal forest located 125 km north of Thunder Bay, Ontario. Centered on Wabakimi Lake, it lies on the eastern edge of glacial Lake Agassiz. Streams and highly divided lakes abound. Stony sand and till thinly cover the Archean granitic uplands, typical of the heavily glaciated Precambrian shield. The terrain displays a smoothly rolling surface into which lakes with gently sloping sides are set (Teller & Clayton, 1983). The surficial geology map shows 24% of the area classified as bedrock. Summer temperatures are cool (mean daily temperature 16°C), winters cold (mean daily January temperature -20°C). Total precipitation averages 750 mm/year. The maximum snow depth recorded during the 4 winters of the study at Flat Lake, an Ontario Ministry of Natural Resources snow station located in the southeast corner of the study area, was 95 cm. The number of weeks during January to March with snow depth over 50 cm were, by year, 2, 11, 4, 14; the numbers of weeks reporting heavy crusts were 1,0,3,5, usually in March. In addition, winter rains or brief thaws occasionally left thin skims of ice across the snow that would not have been recorded as crusts.

Wildfires have left a mosaic of stands, primarily black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*), but with a few mixed stands including trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*). Mosses, such as *Pleurozium schreberi* cover much of the forest floor, but patches of ground lichens (e.g., *Cladonia mitis*, *C. rangiferina,* and *C. alpestris*) grow under poorly stocked stands of jack pines on sand flats and under scattered spruce on rock outcrops (Antoniak, 1993). Tree lichens, e. g., *Usnea comosa* and *U. dasypoga,* are common but not especially abundant (Ahti & Hepburn, 1967).

No logging had taken place and no roads entered the study area. The few human activities were extensive in nature: canoe enthusiasts and fly-in anglers (using small boats with outboard motors) traversed major waterways in summer; tourist outfitters flew hunters into remote lakes during autumn; trappers, mostly native, crossed some parts of the area during winter. Tourist outpost camps, trappers' cabins, and some private cottages constituted the only permanent human dwellings. The southern boundary of the study area is approximated by the transcontinental line of the Canadian National Railway. North of the study area the forest stretched unbroken and undisturbed to the Hudson Bay Lowlands.

Data collection

We plotted tracks of woodland caribou, moose, and wolves on 1:126,720-scale maps during transects flown about 300 m above ground level at 3-km intervals during 4 winters (1980-84). Data from a subsequent survey in 1988 were analyzed but not included here because a thin layer of ice prevented location of wolf tracks. Transects oriented north-south in the southern 2/3 of the study area became east-west in the northern 1/3 to permit boundaries at least 2 transect widths beyond any caribou tracks on all sides, thus including all contiguous and close (i.e. within about 20 km) winter aggregations of caribou centered around Wabakimi Lake. We noticed no difference in observability of tracks due to direction. We recorded tracks wherever located, not only directly on the transect lines, and we turned aside from the transects to examine any tracks seen in the distance, or to follow individual track sets until the species was positively identified, using criteria described by Cumming & Beange (1987). The 3-km spacing of transects left an unexamined strip between transects, but due to the mobility of the animals, and our turning to look at tracks, we believe that we missed few tracks for this reason. Some tracks may have been missed in the northern quarter of the study area when fuel shortages curtailed circling.

Since densities of all species were low, track aggregates were not frequent. Because a letter representing a species covered about 0.05 km^2 at this scale, we made no effort to delineate track aggregates, but simply recorded presence of tracks wherever a transect crossed them, or allowed them to be located. We recorded wolf tracks by packs, rather than by individual animals. All flights took place during sunny days, at least 3 days after a snowfall, and between 10 AM and 3 PM. One complete survey required about 4 days. Flights were carried out during mid to late February, except for 1983-84 when the survey was delayed until early March.

We looked for tracks in snow rather than for animals because neither woodland caribou nor wolves can be located reliably in forested country. As snow cover was continuous each year from late November to early April, tracks provided records of animal locations from the day of the flight backward in time until at least the last previous snowfall, and sometimes up to a month or more before in the case of "old tracks". Although woodland caribou return to traditional areas each winter (Cumming & Beange, 1987), much like white-tailed deer, they are not so restricted by deep snow and do not congregate under heavy conifers the way deer do. Hence, although tracks in dense conifers are more difficult to locate than tracks in hardwoods or in the open, few animals of the species investigated would remain so sedentary under heavy conifers that their tracks could not be observed around the edges of these stands. Snow conditions probably affected track observability, especially the rare winter rains or thaws that formed icy crusts and made location of wolf tracks difficult. This factor may have contributed to the low number of wolf tracks recorded in the first 2 winters. The high number of wolf tracks recorded in 1984 may have been partly due to the heavy crust (but no ice) that made travel easy. Thus, although we might easily have missed predator prey interactions or their results, such as carcasses that become impossible to locate after a few weeks, we obtained reliable data on animal locations.

Estimates of animal numbers were difficult to obtain. Although track densities may imply relative animal densities, we made no effort to arrive at numbers of animals from this method. Rather we totaled numbers of caribou seen on the ice on a single day in March for a minimum estimate of caribou (Cumming & Beange, 1987), obtained moose densities from routine management aerial surveys, and calculated wolf densities from numbers of packs and size of the only pack in which the animals were seen.

Statistical analysis

The use of tracks rather than direct observations may have influenced the spatial data. Animals may have been more widely separated than the tracks indicated due to time considerations, i. e., a first animal may have been far away by the time a second left tracks near the same location. However, the reverse could not occur. Therefore all track data show minimum distances among individuals and species. Field data were analyzed using an (ARC/INFO) Geographic Information System (GIS) at the Center for the Application of Resources Information Systems, School of Forestry, Lakehead University. With this system, we easily, and with minimal error, transferred field maps to a computerized base map in layers by species and year. To establish computer cells with real reference, we used the distance between transects to determine cell size (approximately 3x3 km, actually 9.29 km^2). Cells were then located adjacent to each other centered on transect lines, totaling 697 cells for the entire study area. Due to the low densities of wolf tracks, the within-species dispersion of wolf packs could not be studied using statistical procedures similar to those for moose and caribou.

Chi-square tests

We compared frequency of repeated use of same computer cells from year to year (1-4 winters) for caribou and moose using χ^2, the null-hypothesis being that the frequency distributions were not significantly different among years.

Autocorrelation analysis

Traditional methods of examining space-related data have been criticized by Legendre & Fortin (1989) who advocate instead analysis of spatial autocorrelation, pioneered by Cliff & Ord (1973). A variable is said to be autocorrelated when values at some points in space can be predicted from known values at other known positions. The assumption of independence of observations underlying many traditional statistical methods is not met whenever spatial structure is present, since each new observation contributes an unknown proportion to 1 degree of freedom. We used a spatial autocorrelation analysis program called AUTOCORRELATION for Macintosh (Legendre & Vaudor, 1991) to calculate standard normal deviates (S.N.D.'s) for each distance class from which we plotted correlograms. The null hypothesis for S.N.D.'s is the randomization assumption in which the locations of the points are randomly distributed over the area. The theory behind these computations can be found in Sokal & Oden (1978), Cliff & Ord (1973) and Upton & Fingleton (1985). We plotted correlograms for all 3 species and cross-correlograms for pairs of species.

As recommended by Oden (1984), we used a Bonferroni correction to assess the significance of correlograms. The total level of significance for a correlogram was fixed at 0.05 which was divided by the number of distance classes (20) to test the S. N. D. coefficient value at every distance class.

Schoener's Index of overlap

Spatial overlap between species was examined by calculating Schoener's (1970) index (following McCullough *et al.*, 1989):

$$C_{ih}=1-1/2\sum|P_{(if)}-P_{(hf)}|,$$

where C_{ih} is the overlap of species *i* on species *h*, P_{ij} is the proportion of all observations of species *j* that occurred in grid cell *j*, $P_{(hj)}$ is the proportion of the other species (*h*) in the *j* grid cells. Ranges for *C* extend from zero (no overlap) to 1 (complete overlap). Multiplying *C* by 100 provides percentage overlap. This is the same as Whittaker's (1952) index of association for community studies.

Nearest neighbor analysis

To interpret some results from autocorrelation analysis, we tested presence of clumping using the Clark & Evan (1954) distance to nearest neighbor index. Although an older index, R_{CE} (Ward & Parker, 1989) continues to be widely used (e.g., Kenkel, 1988) and improved (e.g., Petrere, 1985). R_{CE} is the ratio between the observed mean distance to nearest neighbor and the expected nearest neighbor distance from an identical population randomly distributed on an infinite plane. Values <1 indicate clumped dispersion; values >1 indicate uniform dispersion, referred to the standard normal distribution. This index assumes a lack of interdependence that our data do not necessarily show, but errors from this source are relatively small (Donnelly, 1978). More important in many studies is the edge effect, for which Donnelly (1978) proposed a correction. However, a study area of 6 500 km^2 approaches the theoretical infinite plane closely enough to negate the necessity for such a correction (J. Jarvis, G. Bell, pers. comm.)

Expanded nearest neighbor analysis

Distance to nearest neighbor holds special significance for studies involving predation. Distance from prey to predator could be expected to be negatively correlated with predation risk because predators will require more time to find prey when individual prey animals are located at greater average distances (Cumming, 1975). We measured our distances directly with GIS and compared them with t-tests. We further analyzed the data using Delaunay triangulation (see Upton & Fingleton, 1985), which calculates the number of near neighbors rather than measuring their distances. A program called LINKS (Legendre & Vaudor, 1991) examined (x, y) coordinates of track sightings for each year, both within and among species. The program then used the Delaunay triangulation method to link each point in a plane to its nearest neighboring animals in any direction. Given any triplet of points, the triangle uniting these points was included in the triangulation if, and only if, the circle passing through the 3 points included no other point in the set of study. Thus the number of link edges indicated how many times an animal's neighbor was a caribou, moose or wolf.

We subdivided the resultant list of link edges by species for comparisons in contingency table analyses, followed, where significant χ^2 values warranted, by Bonferroni confidence intervals (Byers *et al.*, 1984). From Bonferroni's inequality (Neu *et al.*, 1974), a set of simultaneous confidence intervals was constructed such that "one can be at least 100(1 - α)% confident that the intervals contain their respective true proportions, *Pi:*

$$\bar{p}_i - Z_{\alpha/2k}\sqrt{\bar{p}_i(1-\bar{p}_i)/n} \le p_i \le \bar{p}_i + Z_{\alpha/2k}\sqrt{\bar{p}_i(1-\bar{p}_i)/n}$$

where $Z_{\alpha/2k}$ is the upper standard normal table value corresponding to a probability tail area of $\alpha/2k$; *k* is the number of categories tested" (Byers *et al.*, 1984. p. 1052). Where the expected proportion P_{io} does not lie within the interval, the expected and actual values differ significantly, in our case with the level of significance fixed at 0.05.

These exploratory tests of link edges may not be valid, because reference to a χ^2 table assumes the independence of the observations, a condition that is not met here. To improve confidence in our tests, we replaced observed data for each study year with animal codes randomly assigned to the available x, y coordinates, a method similar to some described by Manly (1991) and Crowley (1992). By maintaining identical numbers of caribou, moose, and wolf sightings, we could follow the same procedures as before to produce links between animals. Observed link counts were then entered into a contingency table, and the χ^2 statistic calculated for the random simulation data. By doing this we simulated a randomization hypothesis technique that does not require independence of observations (Murchison, pers. comm.). The species names become merely labels that could be rearranged in any combination. The random assignment of animal codes to existing points seemed preferable to random selection of new coordinates since the former procedure is in accordance with the autocorrelation hypothesis, and avoids the chance of choosing a location that does not make sense in the real world.

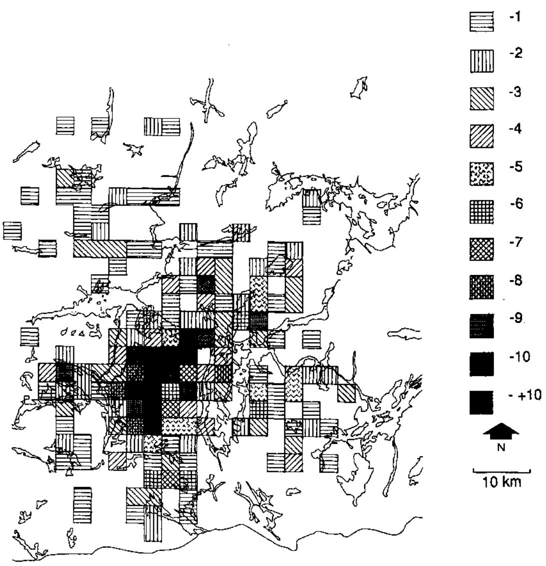

Fig. 1. Caribou track densities revealing a core area with 10+ tracks recorded during 4 winters (by 9.29 km^2 grid cells).

Results

How were caribou, moose and wolves dispersed?

Transects totaling 7 634 km during 4 winters revealed 557 caribou tracks, 631 moose tracks, and 157 wolf-pack tracks. Caribou tracks were located in 22% (1,422 km^2) of the study area cells (Fig. 1). These occupied cells showed a strong central ten-

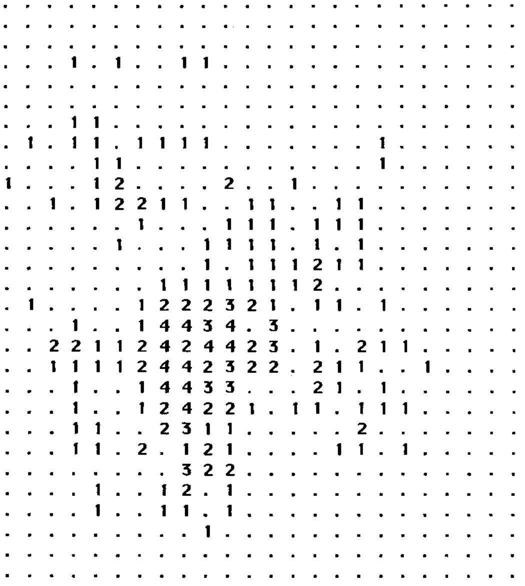

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Fig. 2. Numbers of years (out of 4) for which winter tracks of woodland caribou were found in 9.29-km² computer-generated grid cells. In each winter, a core area with tracks was surrounded by other areas used less consistently by caribou.

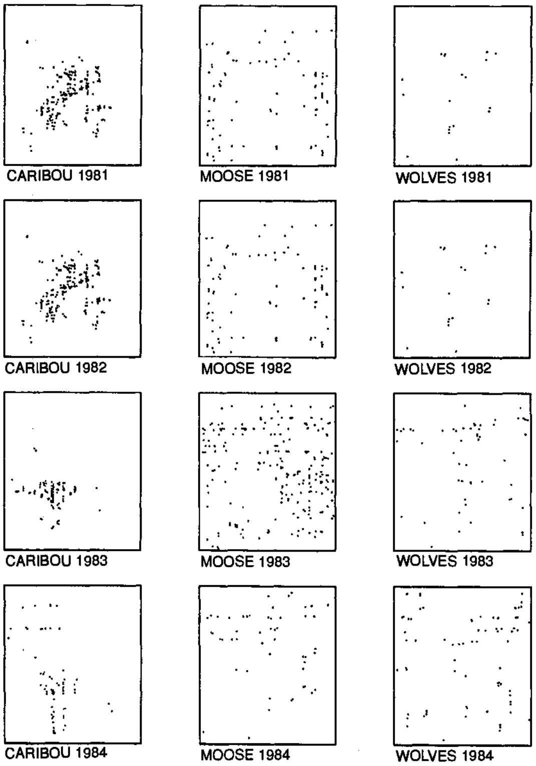


Fig. 3. Spatial patterns of woodland caribou, moose and wolf packs in northern Ontario based on tracks in snow during 4 winters.

dency: 10 of the 138 tracked cells, located centrally, showed >10 tracks during the 4 years; generally farther from the center, another 14 cells contained 4-10 tracks each; in the remaining cells at greater distances from the core, fewer than 4 tracks/cell were found (Fig. 1). The caribou showed more fidelity to this same central area than to the rest of their range, returning to a 99-km² central area each winter (Fig. 2), an additional 81 km² generally surrounding the core 3 of the 4 years, and another 288 km², for the most part farther from the core, 2 years; peripheral cells totaling 95 km² were used only one year. Moose tracks, on the other hand showed no such central tendency: few moose tracks were located in the area occupied by caribou; elsewhere, moose tracks were distributed without obvious pattern throughout the study area (Fig. 3). Out of 324 computer cells in which moose tracks were recorded, none totaled > 5 tracks/cell for the 4 years. The frequency with which moose repeated use of the same cells from year to year showed a highly significant difference from that of caribou (Table 1, χ^2=21.8, d.f=3, P=0.0001): moose used the same cell 1 or 2 years more frequently, while caribou used the same cell during 4 years more frequently. Thus space use by caribou was less homogeneous than that of moose.

Inspection of field maps suggested that wolves inhabited the entire study area, but perhaps at lower densities where caribou were located. Concentrations of tracks were most numerous in the northeast; fewest in the southwest. We identified from tracks about 5 wolf packs in the 6500 km² study area, or about 1 300 km² per pack, but we could not be certain all were present in the more difficult survey years. We saw only one pack of wolves, 8 in number.

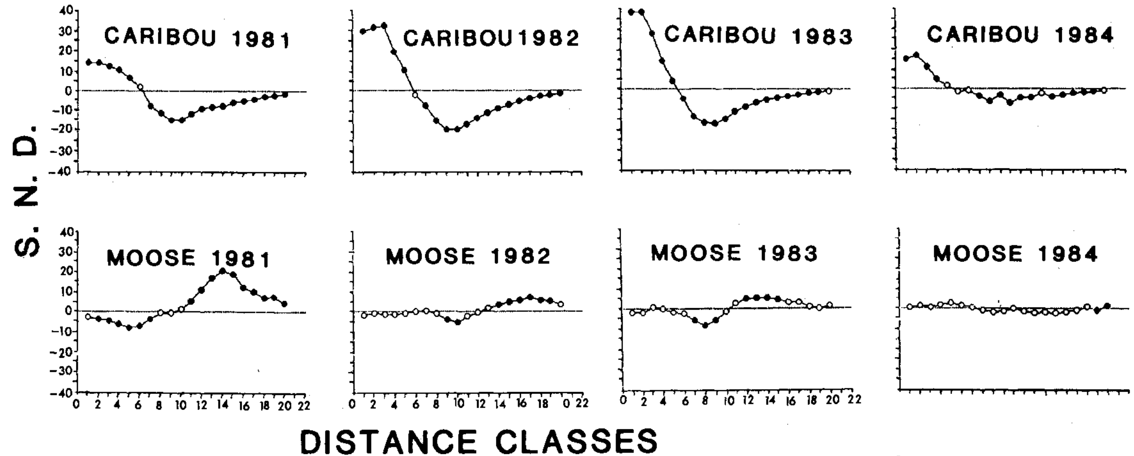
Were observations within species autocorrelated?

Correlograms plotted for caribou from standard normal deviates showed consistently significant

Table 1. Annually repeated occupation of same 9.29 km² computer-generated grid cells by caribou and moose from four years' observations of tracks in winter.

Number of Years' Use	Caribou	Moose
One year only	106	218
Two years	32	102
Three years	9	12
All four years	11	2

χ^2=21.8, d.f.=3, P=0.0001



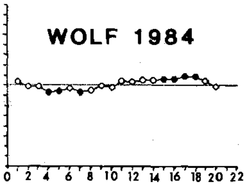


Fig. 4. Spatial correlograms based on standard normal deviates (SND) showed a tendency for caribou to be positively correlated with other members of its own kind at close distances. Negative correlations at longer distances indicated that an individual was not as likely to be found at distance from others of its kind as would be expected by chance. A similar patter was shown in only one year by moose, and in less than half the first 8 classes by wolves. Black squares represent significant values at the a=5% level; white squares are non-significant values. Distance classes were 3.8 km.

positive autocorrelation for short distance classes and significant negative autocorrelation for longer distance classes (Fig. 4). This correlogram pattern is typical of a single large patch (Legendre & Fortin, 1989). In these correlograms distances beyond about class 16 should not be considered because too few pairs of points are available for meaningful analysis.

In contrast, moose locations in 1981 were negatively autocorrelated for short distances and highly positively correlated for longer distances. Such a pattern can be explained as a "hole-effect" (Journel & Huijbregts, 1978) resulting from the "doughnut" type of dispersion shown by moose, to some extent each year, but especially in 1981. The more obvious "hole-effect" in 1981 was due to the greater number of observations along the western boundary of the study area completing the "doughnut" pattern. To confirm this diagnosis, we removed 46 (from 325) of the western records to destroy the doughnut pattern. The result was a correlogram showing no significant differences, similar to that for 1982, proving that the earlier result was, in fact, a hole-effect artifact, rather than real negative and positive autocorrelation. Moose tracks in all other years showed random distributions over the first 6 distance classes. This finding was unexpected since moose in northern Ontario are usually found in small groups of up to six animals during winter (Cumming, 1972). To further assess these distributions, we calculated Clark & Evans (1954) distance to nearest neighbor indices (R_{CE}) for each species (Table 2). The expec-

Table 2. Dispersion of caribou, moose and wolves in northern Ontario as measured by distances to nearest neighbor (Clark & Evans, 1954) from tracks in snow during 4 winters.

Species	Year	*n*	R_{CE}[a]	C[b]
Caribou	1981	217	0.33	-18.97
	1982	177	0.40	-15.38
	1983	99	0.28	-13.77
	1984	64	0.43	-8.68
Moose	1981	89	0.75	-4.54
	1982	270	0.82	-5.73
	1983	220	0.81	-3.57
	1984	52	0.74	-3.57
Wolves	1981	19	0.77	-1.90
	1982	9	1.00	0.001
	1983	54	0.78	-3.09
	1984	75	0.63	-6.13

[a] R_{CE} is the ratio between the observed mean distance to nearest neighbor and the expeced nearest neighbor distance, with values <1 indicting clumped dispersion ab values >1 indicating uniform dispersion.

[b] C is related to the normal curve, therefore any value exceeding ±1.96 differs significantly from a random dispersion at the 5 per cent level (Clark & Evans, 1954).

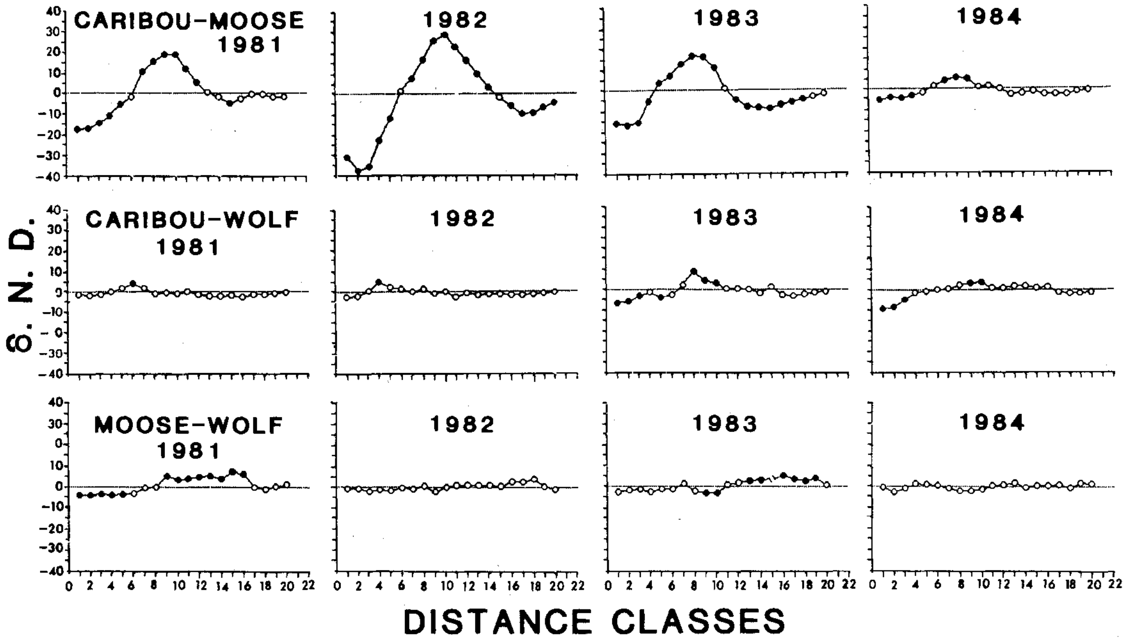


Fig. 5. Spatial cross-correlograms based on standard normal deviates (SND) for pairs of species show negative correlations at shorter distances, indicating that an individual is not as likely to be found near another species as would be expected by chance. Black squares represent significant values at the a=5% level; white squares are non-significant values. Distance classes were 3.8 km.

ted clumped dispersion for caribou was indicated by numbers well below one. A similar low index, but less pronounced, was shown for moose, confirming that moose also clumped together at least to some extent.

Due to relatively small numbers of wolf observations (Fig. 3), we prepared a wolf correlogram only for 1984 when most tracks were recorded. At lags 4, 5, and 7, the graph showed only slight evidence of the negative autocorrelation that would be expected from a territorial animal (Fig. 4). R_{CE} values (Clark & Evans, 1954) revealed no trend here, as they suggested slight clumping tendency for two years, and random dispersion for the other two (Table 2).

What was the autocorrelation structure between species? Correlograms for caribou-moose always showed strong negative cross-autocorrelations at short distance classes and positive cross-autocorrelations at longer distance classes, indicating negative spatial structure between these species (Fig. 5). Caribou and wolves showed no cross-autocorrelation during 1981, 1982, but the 1983 and 1984 cross-correlograms again showed negative cross-autocorrelation at short

Table 3. Overlapping use of habitat by woodland caribou and moose shown by use of 697 possible 9.29 km^2 grid cells each year during 4 winters.

Year	Number of cells with tracks			Cells with both caribou and moose tracks	Caribou cells with moose tracks in adjacent cells
	Caribou	Moose	Both	(%)	(%)
1981	80	66	4	5.0	26.3
1982	69	190	4	5.8	24.6
1983	39	159	1	2.6	41.0
1984	43	41	1	2.3	18.6
Total	231	456	10	4.3	26.8

Table 4. Schoener's Index of overlap for caribou, moose, and wolves in the Wabakimi Lake study area, based on tracks of each species per computer cell.

Comparison	1981	1982	1983	1984
Caribou/moose	0.071	0.046	0	0.091
Caribou/wolf	0.071	0	0	0.035
Moose/wolf	0.029	0.021	0.064	0.246

Note: Zeros indicate no occurrences of tracks by different species in the same cells.

distances and positive cross-autocorrelation at longer distances. We explain the lack of cross-autocorrelations in the first 2 years by the small number of wolf track observations. Thus, in years when numbers of wolf track observations were adequate, caribou and wolves also showed spatial separation. No pattern of cross-autocorrelation appeared for moose and wolves except in 1981, when the expected negative cross-autocorrelation at short distance classes was observed (although this result might also be explained in part by the same hole effect as for moose alone).

To what extent did areas occupied by the different species overlap?

The presence of negative cross-autocorrelation between species raised questions about the extent of overlap among areas used by these animals. Caribou and moose appeared not to associate with each other. Few computer cell grids (9.29 km^2) showed tracks of both species during any year of the study (Table 3). Of 835 cells for which tracks of one or the other of these 2 species were recorded, only 10 included tracks of both during the same year, and only 27% of cells with caribou tracks showed moose tracks even in adjoining cells (Table 3). Wolf tracks seemed to be more associated with the moose than with the caribou (Fig. 3). Values of Schoener's C index proved to be extremely low for all 3 species, the highest indicating <25% overlap between areas occupied by moose and wolves (Table 4). According to this index, the 3 species occupied distinctly different spaces.

Presumably, such separation could be accomplished by caribou and moose avoiding each other every winter, but only 13% of computer cells recording tracks of either species during the 4 year period showed tracks of both. A similar pattern was recorded once more during the 1988 survey. Thus the differing dispersions indicated habitat partitioning over time, not simply annual avoidance of each other.

Did caribou dispersion increase the distance to predators?

Since predation rates vary with distance between predator and prey (Cumming, 1975), the remoteness of alternative prey species from common predators should provide a measure of relative predation risks for those species. Using simple distance to nearest neighbor measures, mean distance from wolves to caribou over four winters was 15.6 km, significantly greater than that from wolves to moose at only 4.8 km (paired t=9.78, d.f.=156, P<0.001), but more sophisticated measures are available.

Delaunay nearest distance link edges were not independent for the three species (e.g., for 1981, χ^2 = 468, d.f. = 4, P=0.0001) during any year, and the

Table 5. Observed and expected proportions of Delaunay triangulation link edges showing Bonferroni 95% confidence intervals using 1981 data. Where the expected proportion does not lie within the interval, the expected and actual values are significantly different showing that the proportions are not independent. C=caribou, M=moose, P=predator (gray wolf).

	- 5 %	Observed proportion	+5 %	Expected proportion	Significance and direction
p C-C	0.565	0.594	0.623	0.462	* >
p M-M	0.160	0.183	0.206	0.070	* >
p P-P	0.008	0.015	0.022	0.003	* >
p C-M	0.487	0.063	0.077	0.180	* <
p P-M	0.010	0.018	0.026	0.015	
p P-C	0.014	0.023	0.032	0.038	* <

Note: no expected proportions lie near 5% limits (e.g., differences of expected proportions from 5% limits for C-C and P-C, the closest signficant proportions recorded, are 18% of those limits).

Table 6. Significance of Bonferroni 95% confidence intervals and direction of difference for caribou (C), moose (M), and wolf (P) paired associations during four winters.

	1981	1982	1983	1984
p C-C	★ >	★ >	★ >	★ >
p M-M	★ >	★ >	★ >	★ >
p P-P	★ >		★ >	★ >
p C-M	★ <	★ <	★ <	★ <
p P-M				
p P-C	★ <		★ <	★ <

Note: none of the significantly different expected proportions in years 1982-84 lay as close to 5% confidence levels as those recorded for 1981 in Table 5.

1988 data for caribou and moose showed continuation of this pattern. In contrast, data with randomly assigned animal codes showed independence for all comparisons in every year, increasing confidence that our data differed from random. Bonferroni confidence intervals for 1981 (Table 5) showed that caribou-caribou link edges, moose-moose link edges, and wolf-wolf link edges all occurred significantly more frequently than expected, indicating intraspecific clumping. Moose-wolf link edges did not differ significantly from what would be expected by random process, showing that these two species did not react to each other either positively or negatively. In contrast, caribou-moose and caribou-wolf link edges were significantly fewer than expected indicating that the caribou dispersion placed animals of this species at greater than expected distances from both moose and wolves. The importance of this finding was enhanced by the fact that the pattern remained the same each year throughout the study (Table 6), none of the relationships being reversed in any year.

Discussion

Strong negative cross-autocorrelations between caribou and moose, little overlap between occupied areas, and greater than expected (from chance) distance from caribou to the nearest moose all indicated that caribou and moose partitioned the habitat. Negative cross-autocorrelation between caribou and wolves for the only year with sufficient data, and greater than expected distances from caribou to the nearest wolf, suggested that caribou wintering areas constituted implicit refuges. Thus, in Ontario, caribou spaced away from wolves (Bergerud, 1992), thereby fitting the generalizations proposed by Seip (1992) and the theory of Holt (1977). This finding also supports Bergerud's (1985) contention that all "relic herds" in Ontario have escape habitats which enable them to persist in the face of wolf predation.

Moose showed no autocorrelation, even though Clark & Evans (1954) indices indicated a clumped dispersion, perhaps because the groupings by moose were small enough to be recorded as individual tracks, or on too small a scale for autocorrelation analysis to detect. Wolves failed to show the negative autocorrelation expected of territorial animals. Messier & Crête (1985) suggested that wolf packs would become "detached" at densities <0.23 moose/km^2; that is, due to severe food limitations, they could not fully colonize the area. If the 8 wolves seen in one pack were representative, the observed packs would total about 40 wolves, or 0.006 wolves/km^2, a density low enough for these packs to be detached. Wolf packs might also constitute one instance where tracks did not truly indicate the extent of spacing.

Why did wolves specialize on moose?

The observed association of moose and wolf tracks, rather than caribou and wolf tracks, raises a further question: why were wolves found with moose rather than caribou? The relationship may be even stronger than implied because of the added risk of injury to wolves that choose to prey on moose (Mech, 1966). Holleman & Stephenson (1981) working in Alaska concluded that wolves prey on caribou where abundant but will take moose when they are not. One would expect caribou as the smaller prey to be easier to kill; certainly moose are not highly preferred prey when other species of smaller ungulates are available (Murie, 1944; Pimlott *et al.*, 1969).

Three factors may be involved. Firstly, perhaps caribou in Ontario have better escape possibilities than moose, across frozen lakes and in their open-forested wintering areas (Antoniak, 1993). In contrast to the caribou, moose often try to stand (Mech, 1966) and thus may be easier to capture in deep snow. But no real evidence of caribou superiority in escaping wolves is available.

Secondly, the choice may be due to optimal foraging. None of the species could be censused accurately, but totaling the areas of the 9.29 km^2 cells occupied by caribou (520 km^2) and comparing that total with the approximately 100 caribou estimated for the wintering area by Cumming & Beange (1987), suggested a population density of 0.19 caribou/km^2 in the wintering area (0.015 in the entire study area). An estimate for 1989 using a different method came to 0.11 caribou/km^2 (Bergerud, 1989) in the portion of the study area that is now a park (Cumming, 1987a). Moose densities were estimated by the Ontario Ministry of Natural Resources at 0.15 moose/km^2. Since caribou weigh only about 100 kg, c.f. 400 kg for moose (Banfield, 1974), the biomass/km^2 provided by the caribou (19 kg/km^2) must have been only about 1/3 that provided by the moose (60 kg/km^2). Assuming equal vulnerability to wolves, optimal foraging theory suggests that wolves should choose moose because the expectation of yield (in biomass) is greater and, therefore, the moose would constitute the better item (MacArthur, 1972). Wolves should, indeed, pursue only moose since the time required for pursuit would, presumably, be less per unit biomass than for caribou, because the distance wolves had to travel to reach a caribou would be greater (MacArthur, 1972) - a consideration made even more likely by snow depths >50 cm (see Huggard, 1993, for effects of snow on wolf preying behavior).

Thirdly, prey selectivity may depend strictly on prey availability, as concluded by Holleman & Stephenson (1981). Messier & Crête (1985) reported 0.2 moose/km^2 to be the lowest threshold for supporting wolves. At 0.15 moose/km^2 even our moose density was well below that threshold. Possibly, caribou biomass, being lower still, was simply too low to support a population of wolves. Presumably, if the caribou population increased sufficiently (i.e. to about 3x their current density) the wolves would be able to switch their attention to the caribou and still survive, as Holt & Kotler (1987) suggested (see also Bergerud, 1983). Therefore, caribou survival may depend on locating places for wintering where moose and wolves are few. In such places they can sustain their populations, but only at low enough densities so that wolves could not specialize on them and survive (perhaps even <0.03/km^2, Seip, 1992).

Direct competition

But is this predation-related understanding of the results the only one possible? Ecological theorists might choose to ascribe results to direct competition. During winter, moose exploit shrubs and tree regeneration < 3 m in height (Cumming, 1987b). Woodland caribou in Ontario , on the other hand, winter in areas with substantial mats of ground lichens, but few shrubs (Antoniak, 1993). The simplest explanation for the observed habitat partitioning might be that caribou and moose occupy different niches in the boreal forest, partitioning habitat by niche differentiation in a patchy habitat, rather than by a more complicated set of interactions involving wolves. In this case, the simpler explanation should be accepted. However, this view would not explain why caribou numbers in Ontario remain far below food carrying capacity (Ahti & Hepburn, 1967). Presumably, if niche differentiation were the only explanation, each niche would be filled to capacity. Since they do not appear to be filled, predation may also be involved.

Apparent competition

Support for the idea that changes relate to predation rather than competition only is provided by densities of the three species reported for northern Ontario. The 40 wolves estimated in the study area represent a population density of about 0.006 wolves/km^2. Ontario Ministry of Natural Resouces surveys in the park portion of the study area during 1961 and 1989 reported two estimates of about 0.004 wolves/km^2. All three estimates are within the 0.004-0.008 wolves/km^2 range put forward for this part of Ontario by Kolenosky (1983). In comparison, Kolenosky (1983) suggests densities of 0.002-0.004 wolves/km^2 for areas farther north where continuous and stable (Darby *et al.*, 1989) caribou populations constitute the major support for wolves, moose being only "common" to "rare", and then mainly along riparian zones (Cumming, 1972). Thus current wolf densities are higher in areas where moose are common, as would be expected from Simkin's (1965) hypothesis.

Direct and apparent competition

But are explanations specifying habitat or predation as limiting factors on caribou populations really competitive, as many biologists in the long controversy over caribou limiting factors (Cumming, 1992) have assumed? Holt (1977) suggested that the realized patterns of abundance probably reflect both direct and apparent competition which may be complementary components (Holt, 1984). Holecamp & Sherman (1989) illustrated the possibility of multiple correct answers to questions of causality in behavioral biology. Could we, as they suggest, consider a synthesis? Enough is not known about woodland caribou to undertake Tinbergen's (1963) 4 levels of explanations, but we can attempt an analysis using Mayr's (1961) proximate and ultimate causes. The direct effect (Armstrong, 1990) of behavior producing the dispersions we observed in our study area was to increase the average distance from caribou to predators, but all these areas were also located in stands with ground lichens (Antoniak, 1993). Thus, the proximate limiting factor of woodland caribou populations in northern Ontario may be predation, but the ultimate limiting factor may be availability of predator-free lichen patches for winter habitat. Both direct competition and apparent competition may contribute to an explanation, as Holt (1977) suggested.

Generalized ecology for woodland caribou in boreal forests of Ontario.
The findings of this study complement several others to make possible the following generalization. In the boreal forests of Ontario, only about 2,000 caribou remain from much higher original numbers (Cumming & Beange, 1993). Moose immigration (beginning about 1900, Peterson, 1955) brought higher wolf densities (Simkin, 1965) that changed conditions for the caribou. Prior to that time, caribou dispersions probably differed from what we find today. Caribou may have occupied more diverse habitats than at present. In addition to the currently used stands of sparsely stocked jack pine and black spruce with substantial ground lichen mats, more heavily stocked stands of these species where ground lichen availability would be marginal, and mixed-wood stands with tree lichens (as currently found on the Slate Islands, Euler *et al.*, 1976), or Canada yew (*Taxus canadensis*, as discussed by Cumming, 1992) could have provided adequate habitat while wolf densities remained low. In some of these habitat types, caribou densities may have built up substantially (similar to recent densities on the Slate Islands, Butler & Bergerud, 1987) leading to early reports of large numbers (DeVos & Peterson, 1951). Caribou probably never used to any extent hardwood stands or moderately- to fully-stocked black spruce stands (e.g., large areas east of Onamon Lake with few moose and few caribou (Cumming & Beange, 1987)).

Decreases in caribou populations before 1900 probably resulted from hunting by European immigrants (DeVos & Peterson, 1951; Cringan, 1957; Bergerud, 1974). From 1900-50, reductions in caribou numbers (DeVos & Peterson, 1951; Cringan, 1957) probably resulted primarily from apparent competition brought about by moose immigration that led to increased wolf densities (Simkin, 1965). Caribou with their lower reproductive rate would have been eliminated from shared marginal coniferous- and mixed-wood stands (as per Holt, 1984), leaving remnant bands only in places where winter predation by wolves could be minimized. Losses after 1950 resulted from disturbance of these wintering areas, often by forest harvesting (Cumming & Beange, 1993).

Continued caribou survival depends on availability of refuges: real refuges on islands or shorelines during open water season, including calving time (Simkin, 1965; Bergerud, 1974; Bergerud, 1985; Cumming & Beange, 1987; Bergerud *et al.*, 1990), and virtual refuges provided by habitat partitioning during winter. Observed caribou recruitment of about 15%; (Cumming & Beange, 1987; Bergerud *et al.*, 1990) has apparently been enough to stabilize caribou in the boreal forest of Ontario in line with Bergerud's (1992) generalization (c.f. heavy adult mortality in Alberta, Edmonds, 1988). Thus, these refuges must be effective. The wintering areas that constitute virtual refuges are forest stands with ground lichens for caribou food, but few shrubs (Antoniak, 1993) to support moose; as a result of optimal foraging choices wolf densities in these areas are generally low (this study, B. Hyer, pers. comm.). Due to this dependence on specific forest stands, caribou wintering areas are relatively fixed. Caribou densities continue well below food carrying capacities (Ahti & Hepburn, 1967) because any major increases would make predation on caribou profitable for the wolves. Despite the apparent excess of foods, caribou probably occupy all winter sites where they can survive.

Caribou bands in Ontario continue to disappear (Cumming & Beange, 1993). Native people currently have little impact on caribou in the boreal forest, perhaps because, like the wolves, they prefer to hunt moose, the more profitable prey (Hamilton, 1984). Loss of caribou geographic range occurs where winter virtual refuges are burned, cut, or invaded by railways and roads, forcing the caribou to move into surrounding areas occupied by moose and wolves at higher densities (Cumming & Beange, 1993). Thus, in the face of apparent competition, survival of woodland caribou in Ontario is dependent on retaining the integrity of refuges for calving, virtual refuges for winter, and travel routes between.

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Evolving perspectives on caribou population dynamics, have we got it right yet?

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Abstract: The roles of food, weather and predation are compared between sedentary and migratory caribou herds. Sedentary herds disperse (space out) at calving time while the cows of migratory herds move in masse (space away) to calving grounds to reduce predation risk. The sedentary ecotype calves on ranges near open water if tree cover is present or in rugged topography in the absence of tree cover. The migratory ecotype aggregates on calving grounds located on alpine mountain plateaus or on the tundra north of the Arctic tree line. The two herds with the greatest densities in North America, the sedentary Slate Islands Herd and the migratory George River Herd both had changes in abundance that followed summer food problems. The hypothesis that winter lichen supplies determine abundance and set the carrying capacity is rejected. Lichens are not a necessary food for caribou. A review of the mortality of young calves documented in the past 30 years provides no support for the hypothesis that hypothermia is a common mortality problem. Young calves documented can be born inviable at birth if their dams are severely malnourished. The migratory caribou in North America reached peak numbers in the 1980's after wolf populations were heavily harvested in the 1970's. The sedentary ecotype is frequently regulated by wolf predation that affects both recruitment (R) and the mortality of adults (M). The balance between R/M schedules commonly occurs when R (calves) represents, about 15% of the herd and when numbers (prorated to the area of the dispersed annual range) approximate 0.06 caribou/km^2. Population limitation of migratory herds by predation has occurred in the NWT and in several herds in Alaska but only when wolf densities were > 6.5/1000 km^2. Wolf predation halted the growth of the George River Herd in 1980 but then wolves contracted rabies and the herd again increased and degraded spring/summer ranges. The reduced summer phytomass resulted in lower birth rates and increased the vulnerability of calves and possibly adults to wolf predation. Stabilizing mechanisms for migratory herds include movements between herds above tree line and range contractions/expansions with resultant changes in demography. It is hypothesized that the most important ecological variable in all seasonal distributions of caribou is predation risk rather than to maximize forage supplies.

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Introduction

In this paper I will review the literature on the classical limiting factors for caribou of food supplies (both winter and summer), weather, and predation. To give the paper more life I will include some unpublished results from the three long terms studies I have been involved with: (1) the Slate Islands Herd on Lake Superior where there are no predators (the experimental herd), 1974 to present, (2) the Pukaskwa National Park Herd also adjacent to Lake Superior where wolves are present (the control herd), 1974-1988, and the George River Herd in Ungava where wolves are also present, 1974-1993.

Migratory/Sedentary ecotypes

In 1988 I proposed that we drop the woodland/ barren ground nomenclature and recognize two ecotypes, sedentary and migratory (Bergerud, 1988a). Sedentary animals are those who stay south of the Arctic tree line and disperse or space out from each other at calving. The migratory mode pertains to those animals where females move to calving grounds north of the tree line (Arctic or alpine) and space away from higher densities of wolves in forested habitats (Bergerud *et al.,* 1984; Bergerud, 1985; Bergerud *et al.,* 1990; Bergerud, 1990). These cows aggregate at calving locations at maximum distances from tree line but where calves can remain cryptic on brown substrates (≤ 75% snow cover at calving) (Bergerud & Page, 1987; Bergerud, 1990). The key factor in distinguishing the two ecotypes is not the length of their migration, nearly all non-insular caribou move locations between winter and calving habitats, but whether the animals are dispersed (spaced out) or aggregated (spaced away) when the young are born.

The migration of cows to calving grounds in April-May cannot be explained by the hypothesis that they are seeking nutritious forage at calving or post-calving. These spring migrations back into winter result in a negative energy balance and weight loss for migratory cows compared to cows that might choose the option of remaining with the bulls farther south following the green phenology north (Russell *et al.,* 1993). The diet quality of cows at parturition is less than that of bulls remaining further south or at lower elevations (Table 1). The weight of calves at birth reflects the condition and weight of their dam (Bergerud, 1975; Cameron *et al.,* 1993) and calf weights are in turn a measure of viability at birth. (Bergerud, 1975; Skogland, 1984; review Cameron *et al.,* 1993). Whitten *et al.* (1992) reported that in the Porcupine Herd 59-74% of the calves that died in three springs within a month of birth (May 27-June 24) did so within 48 hours of birth. These calves that died within 48 hours weighed less than calves that survived this critical period. Thus it is disadvantageous for cows to return to calving grounds prior to green-up on the basis of the intrinsic viability of their neonates. Such a disadvantage can only be compensated by reduced mortality from predation because of a reduced presence of predators on calving grounds (abundance of wolves see Heard & Calef, 1986 and Fig. 1). If the main limiting factor for cows and calves in springtime was nutrition rather than predation risk they could avoid the cost of these long migrations on a winter diet by calving further south and benefiting from an early green phenology. Both the Leaf River and the George

Table 1. Percent nitrogen of caribou at calving compared between males and females on the Slate Islands, Ontario, sharing the same range in spring, and between males and females in migratory herds, segregated at calving by the migration of females to calving grounds. (values in parantheses are sample sizes).

Herd & Collection	Location (Lat°/Long°) and Elevation (m)		km[a] M to F	Percent Fecal Nitrogen[b]		Prob. of No. Diff.
Dates	Females	Males		Females	Males	
Control (Nonmigratory):						
Slate Islands, ONT.						
May 13 - June 7 1985	49/87	49/87	0	3.30 ± 0.165	3.37 ± 0.133	0.7356
	183-212 m	182-212 m		(18)	(26)	
May 20 - June 20 1986	49/87	49/87	0	3.61 ± 0.291	3.74 ± 0.233	0.3574
	183-212 m	183-212 m		(6)	(8)	
June 3 - June 17 1987	49/87	49/87	0	3.23 ± 0.122	3.47 ± 0.133	0.3185
	183-212 m	183-212 m		(21)	(5)	
Experimental (Migratory):						
Delta, AK.	64/147	64/148	50	1.78 ± 0.056	2.32 ± 0.109	0.0001
May 17 - May 26 1984	1200 m	600 m		(20)	(18)	
Fortymile, AK.	65/144	64/143	75	1.99 ± 0.036	2.18 ± 0.079	0.0174
May 27 - June 2 1984	1050 m	725 m		(22)	(10)	
Western Arctic, AK.	69/160	68/159	150	1.98 ± 0.037	2.18 ± 0.027	0.0001
June 6 - June 12 1984	250 m	300 m		(25)	(29)	
Penn Island, ONT.	57/89	57/90	110	1.71 ± 0.034	2.35 ± 0.030	0.0001
May 25 - May 28 1987	< 10 m	< 10 m		(34)	(29)	
George River, QUE.	57/65	56/67	130	1.58 ± 0.032	1.97 ± 0.042	0.0001
June 13 - June 19 1988	1200 m	400 m		(17)	(11)	

[a] Kilometres between locations of Males and Females.

[b] Protein (nitrogen) content is generally acknowledged to determine the nutritive value of forage for ruminants. Caribou select species high in protein in the spring and fecal crude protein has been used to quantify range quality for a variety of ungulates as well as lagomorphs. However, secondary compounds can reduce the digestibility of protein thereby biasing fecal nitrogen determinations. This problem is minimized at the start of the growing season (this study period), because phenols and tannins are at low concentrations.

River herds calved farther south when they were low in numbers and were less conspicuous to predators (personal files, Le Henaff, 1975).

The evidence is now overwhelming that wolf numbers are less on tundra landscapes where there is less alternative prey than in forested habitats (for reviews of wolf numbers see Ballard *et al.*, 1987; Hayes *et al.*, 1989; Fuller, 1989). Wolves that depend heavily on migratory caribou frequently den near the tree line (Kuyt, 1972; Jacobson, 1979; James; 1983; Heard & Williams, 1992; Fig. 1). At such an interface they can maximize their contact with migratory caribou and also find more alternative prey than on the tundra. Caribou cows with young calves should want to maximize their distance from wolves; several of the calving grounds of migratory herds are on the Arctic Coast (Porcupine, Bluenose, Bathurst herds) at the maximum distance that cows could space away from denning wolves and forested habitats.

I propose that the northern boundary of the calving distribution of the sedentary ecotype using forested habitats east of the Rocky Mountains is the presence of muskegs with open water at calving. The open water is needed to reduce predation risk. In Ungava the northern boundary of 505 calving locations of dispersed cows was distributed between the June 1 and June 15 isotherms for the spring breakup of large lakes (Fig. 2). The small muskegs ponds in Ungava where caribou calve are free of ice about two weeks before the large lakes; hence the

Table 2. Correlation matrix of possible parameters that might relate to winter starvation on the Slate Islands (First figure is correlation coefficient, then the probalitity and number of years as n).

	(1) Dead caribou	(2) Fall weights	(3) Spring weights	(4) March snow	(5) Fall density	(6) Start growing[a]	(7) Days growing[b]	(8) Lichen g/m^2	(9) Blowdown trees/Km
(1) Spring dead		-0.0727	-0.580	-0.064	0.609	0.590	-0.580	0.023	-0.076
caribou/Km^2	--	0.002	0.172	0.844	0.009	0.056	0.062	0.938	0.797
(Y_2)		15	7	12	17	11	11	14	14
(2) Fall weight			0.464	-0.379	-0.480	-0.764	0.713	-0.038	-0.129
females		--	0.354	0.281	0.082	0.006	0.014	0.911	0.723
(Y_1)			6	10	14	11	11	11	10
(3) Spring weight				-0.680	-0.821	-0.337	-0.255	0.806	0.689
females			--	0.207	0.024	0.781	0.836	0.100	-.198
(Y_2)				5	7	3	3	5	5
(4) March snow					-0.086	-0.258	-0.035	0.192	0.105
depth				--	0.791	0.576	0.941	0.595	0.787
(Y_2)					12	7	7	10	9
(5) Fall density						0.400	-0.191	-0.023	-0.0007
/Km^2					--	0.252	0.599	0.941	0.998
(Y_1)						10	10	13	13
(6) Start growing							-0.858	-0.190	0.356
season						--	0.0007	0.653	0.433
(Y_1)							11	8	7
(7) Total days								-0.143	-0.685
growing season							--	0.736	0.892
(Y_1)								8	7
(8) Spring lichen									0.767
litter g/m^2								--	0.002
(Y_2)									13
(9) Spring blowdown									
trees/Km									
(Y_2)									

[a] The start of the growing seasons was based on the date the mean temperature on the Slate Island ≥ 6.11 °C. Growing seasons have not been determined at this time for years after 1985.

[b] The lenght of the growing season was the total days after temperatures averaged ≥ 6.11 °C until leaf fall of the major deciduous trees.

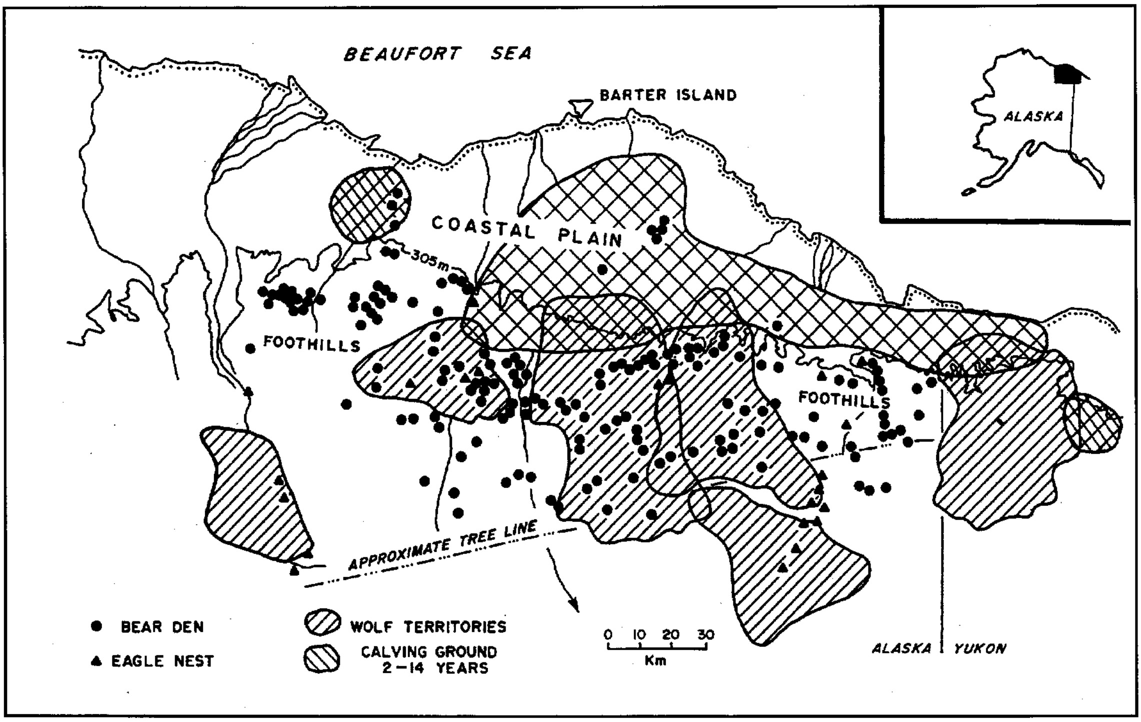

Fig. 1. The composite distribution of the calving grounds of the Porcupine Herd 1972-85. Also shown are indexes to the distribution of the 3 primary predators, wolves, golden eagles (*Aquila chrysaetas*) and grizzly bears (*Ursus arctos*)1982-85. The territories of the wolves in 1985 was mostly near tree line and in the foothills (92%) and the territories overlapped only 17% of the area of concentrated calving. The actual den sites or areas of concentrated summer activity were > 25 km from the southern edge of the calving distribution. The density of the wolves in 1984 and 1985 was very low, 1.4/1000km^2. Adapted from Garner & Reynolds (1986.)

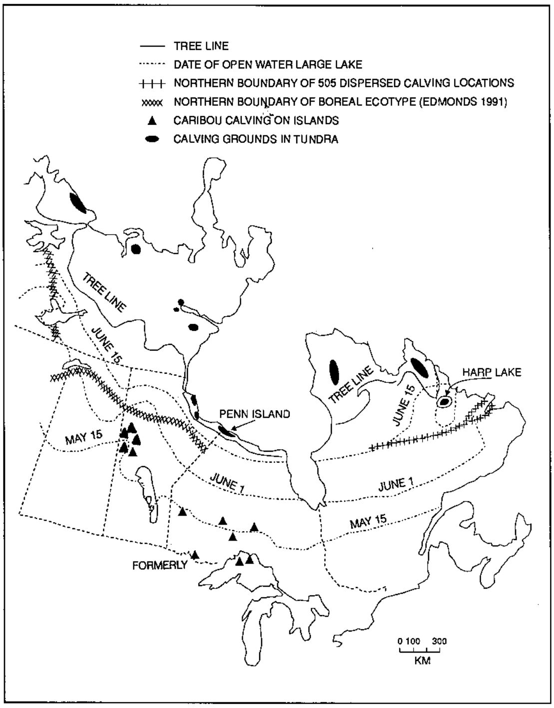

Fig. 2. The northern limit of the sedentary ecotype coincides with the presence of open water in small water bodies at calving. Winter aggregations may be found north of this line. Note there are three distinct tundra areas in Ungava and there are three calving grounds. The open water hypothesis was tested by flying lines north and south from Goose Bay across the Red Wine Herd (sedentary - open water present) and across the Harp Lake calving grounds (migratory - lakes frozen). The Penn Island is a herd that winters in Manitoba and migrates to a calving ground on the coastal tundra in Ontario, north of open waters. Migratory herds when they are high in numbers come south to the northern limit of the sedentary calving distribution.

northern limit of open water in small ponds coincides with the northern limit of calving. The northern boundary of the boreal ecotype (sedentary) in Manitoba and Saskatchewan based on Edmonds (1991) also coincides with the presence of open water in small ponds at calving time (Fig. 2). Since the migratory ecotype only calves north of tree line, there is a broad belt of 400-500 km in central and eastern Canada without calving animals. When the migratory herds are low in numbers they only come south in the winter to within 150-200 km of this northem limit of dispersed calving (see maps in Parker, 1972; and Messier *et al.*, 1988). The common characteristics of the area between tree line and the dispersed ecotype that I believe makes this region unsuitable for calving are the lack of escape water, the lack of mountains and the lack of extensive tundra.

In Newfoundland animals aggregate on calving grounds despite the fact that open water is present. Dispersed calving (spacing out) is a hiding tactic which reduces encounter rates with predators that cannot be left behind by long migrations. However if the animals are easily found because of level open habitats and reduced migration space then they should use tactics of grouping to reduce risk after being detected (Bergerud & Page, 1987). The selection of small water habitats is predicted only within the context of being lost in space; first reduce encounter rates but if this doesn't work have water available as escape habitat.

West of the Rocky Mountains habitats with open water at calving are rare and the animals either disperse to rugged terrain (sedentary ecotype) or aggregate at calving grounds on level plateaus above a alpine tree line or migrate to calving grounds north of the Arctic tree line. If flat treeless plateaus are interspaced with rugged topography both ecotypes should occur and this has been documented for the Denali and Nelchina herds in Alaska (Pitcher, 1983; Adams *et al.*, in press). The Yanert Herd in Alaska is dispersed adjacent to the aggregated Delta Herd (pers. obs.). Predation risk as determined by the habitat options is the precursor to the choice of strategies (ecotypes) .

Limiting factors

Food Supplies

Leopold & Darling (1953), Edwards (1954) and later Scotter (1964, 1967) argued that an increase in forest fires could have caused caribou declines through reduced food supplies and Scotter further felt the reduced lichen pastures would prevent caribou in the Northwest Territories from increasing in the late 1960's. These authors never presented any statistics showing that reduced lichen supplies had adversely affected either birth or survival rates. In fact forest fires had not increased in Alaska and the N.W.T. 1940-70 (Bergerud, 1983a) nor were rates-of-burning correlated with fluctuations in caribou numbers (Bergerud, 1983a) and the herds increased in the 1970's reaching high numbers in the 1980's (Bergerud, 1988a). Skoog (1968) and Bergerud (1974b) argued that winter lichens were not necessary nor did they drive population dynamics.

If the density-dependent or absolute abundance of lichens can regulate numbers then it should be apparent in the starvation of animals in the two herds in North America with the highest densities. The highest density of the sedentary ecotype in North America is on the Slate Islands, Ontario (36 km^2); densities there have exceeded 5/km^2 since 1974 and probably much earlier (see Cringan, 1956). This herd lives under a closed canopy and the primary winter foods are lichen supplies on rocks, on the bark of trees such as paper birch (*Betula papyrifera*) and arboreal lichens that blow down in winter from above the 2 meter browse line. Caribou in this herd commonly die from falling off cliffs when reaching for lichen supplies and also from hanging themselves in birch trees when

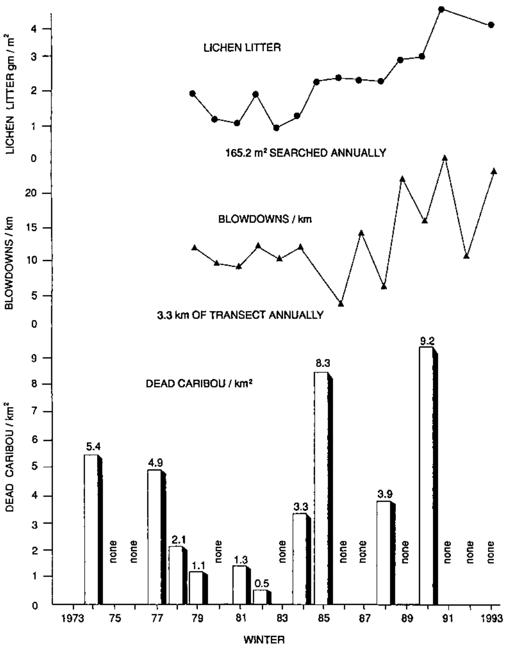

Fig. 3. The caribou that died/km^2 found on the Slate Islands by strip censuses in May-June (below) was not correlated with the number of trees that blew down with lichen loads counted the following spring (middle) nor with the lichen litter found in exclosures in the spring. More lichens are blowing down annually as the forests get older.

reaching and jumping for lichens. Lichen supplies for this herd are extremely meagre (Fig. 3, Bergerud, 1983a). The winter die-offs of this herd, as many as 9 dead caribou/km^2, were not correlated with the variations in winter lichen supplies, as indexed by measuring lichen litter fall (lichens that fell into exclosures) nor the abundance of trees with arboreal lichens uprooted or broken-off in winter storms (Fig. 3, Table 2). Nor were the die-offs correlated with winter snow depths (Table 2. Snow depths in 12 winters in March averaged only 61 ± 4.45cm and were usually similar between winters (CV was 25%). The severity of the winter starvation losses were correlated with the number of animals that entered the winter period (Table 2), but this correlation could reflect forage problems in the summer predisposing animals to winter losses quite independent of winter density interactions or lichens supplies in the winter.

The summer forage on the Slate Islands has also been greatly reduced; we have been unable to find a number of herbaceous species reported by Cringan in 1949 (Cringan, 1956). There has been no successful regeneration in the past 20 years of the four dominant deciduous tree species {paper birch, mountain maple (*Acer spicatum)* mountain ash (*Sorbus americana*), and aspen (*Populus tremuloides*)} except on cliff exclosures.. We have measured the green phytomass (leaves of shrubs and herb of utilized species) several times since 1974. The most recent tabulations were: May 17-23 1994 --31.1 g dry weight in exclosures (total phytomass in 20 m^2) and 3.8 g (12%) outside (20 m^2), May 26-June 1-- 13.6 g in exclosures (20 m^2) and 2.2 g (16%) outside (20 m^2), and June 10-14--22.9 g in exclosures (20 m^2) and 3.5 g/m^2 (15%) outside (20 m^2). The shrub and herb stratas have been severely depleted on the islands and this was most noticeable in summers of high numbers (> 10 animals/km^2)

The extent of the winter die-offs on the Slate Islands was correlated with the fall density of animals, the fall weight of adult females, and the length of the growing season preceding the winter die-off (Table 2). These correlations indicate that the density regulating factor for this population living without predators was the abundance of summer foods.

The highest density of the migratory ecotype in North America was the George River Herd 1984-88 (Crete *et al.*, 1991) (Table 3) where winter densities prorated to the annual winter ranges ≥ 2/km. I measured the lichen stands on the winter range in the summer of 1988 (Bergerud, 1988b) by recording the percent lichen cover disturbed (thalli lying horizontally or shattered) and undisturbed, and recording lichen heights between disturbed and undisturbed and also on rock exclosures. Only 11 ± 1.53 % (*n*=39 stations) of the lichen cover had been disturbed or shattered on winter ranges below tree line and 32 ± 3.29% (*n*=19) on ranges used in fall migration and early winter. The percent lichen phytomass removed from the cryptogam was 9 ± 2.31% (*n*=24) for winter ranges and 26 ± % 4.43 (*n*=18) for migration ranges. Thus major lichen supplies remained.

The animals in this herd were not malnourished in the spring. The percent bone marrow fat in the leg bones for this herd following migration from winter ranges in April (1976 to 1992) has averaged

Table 3. A comparison of the densities above and below treeline[a] for the major migratory herds in North America.

	Recent Maximum Population estimate	Kilometres (1000) below treeline	Kilometres (1000) above treeline	Density caribou/km^2 [b] below treeline	Density caribou/km^2 [b] above treeline
George River	650,000	429	47[c]	1.5	13.8
Leaf River	250,000	179[d]	246	1.4	1.0
Kaminuriak	236,000	314	103	0.8	2.3
Beverly	335,000	362	152	0.9	2.2
Bathurst	385,000	232	208	1.7	1.9
Blue Nose	120,000	90	130	1.3	0.9
Porcupine	178,000	259	44	0.7	4.4
Western Arctic	500,000	117	206	4.3	2.4

[a] Treeline in Canada based on Rowe 1959 and in Alaska on map National Geographic June 1956 Vol ClX, No. 6.

[b] The densities are based on the use of the entire range at maximum numbers . Actual densities would be much higher.

[c] Includes only the tundra used in the summer in Eastern Labrador and excludes much of the Torngat Mountains that were not visited. George River animals also used the western tundra north of the Leaf River (129,000 km^2) but only in the winter (mostly March).

[d] The extend of the range below treeline should increase as the herd continues to increase.

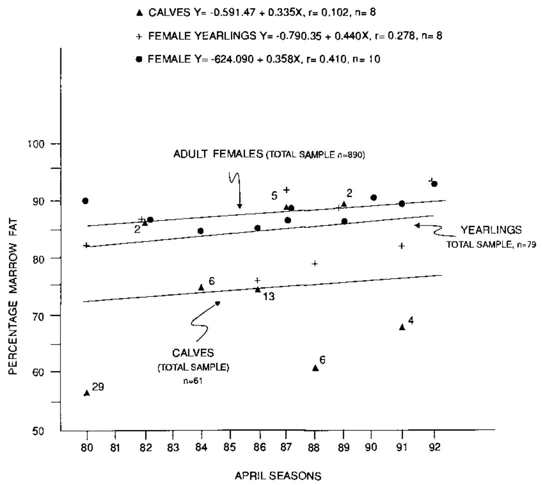

Fig. 4. The percentage of bone marrow fat in leg bones of caribou in the George River Herd from 1980 to 1992 showed no trend as the herd increased. Collections were in April (generally west of Nain) after the animals had migrated back to the tundra. The 1980 figures are from Parker (1981).

annually 87% for adult females, 84% for female yearlings and 74% for female and male calves (Fig. 4). These percentages showed no trend as the herd increased from 176,000 animals to 600,000 (Fig. 4). Animals in this herd have not starved in the winter despite the fact that this herd faces the greatest snow depths of any migratory herd in Canada (Thomas, 1953). And certainly the burning rate on the herd's winter range has not been atypical for the boreal forest; Payette *et al.* (1989) reported 19.7 % of the area below tree line burned, 1944-84, and Couturier & St. Martin (1990), 16.5%, 1972-89.

On the other hand the summer foods for the George River herd above tree line in 1988 had been decimated. The percentage of birch (*Betula glandulosa*) dead was 34 ±3.67 (n=23), and the percentage of the ground covered in turf created by caribou was 20 ± 2.23 (n=23). A comparison of plant abundance along the George River in 1975 vs 1993 showed that tundra shrubs had declined by 70.5 ± 5.10% (n=8 species) at one station and had declined by 57.4 ± 9.60% (n=10 species) at another location. In 1975 24 species of forbs were found and in 1993 only 11. The density of the animals in this herd on the calving ground, along the George River, and in the insect relief habitat on the coast has been in the order of > 12 animals per km^2 1984-88. Our results indicated that 37,000km^2 had been degraded and landsat imagery showed a thrashed June/July range of 46,000 km^2 (Anonymous, 1992).

This degradation of summer range should not be extrapolated to other herds since the George River has the smallest summer area north of tree line of any of the large migratory herds in North America except the Porcupine Herd (Table 3). However the Nelchina Herd probably had similar high summer densities (> 10/km^2) at peak numbers in 1962 and the mandible lengths in this herd, similarly to the George River (Couturier *et al.*, 1989), were reduced in length from when there were fewer animals (Valkenburg *et al.*, 1991)

Overwinter Weight Loss and Starvation

Consider that there is a threshold weight that results in starvation. The mean spring weight of females on the Slate Islands in 5 years when animals died the previous winter was 78.1 ± 0.63 kg and in three springs following good winter survival was 87.2 ± 0.81 kg. These animals needed to maintain weights greater than 75-80 kg to successfully overwinter. In the fall of 1989 the females averaged only 79.5 ± 0.78 kg already at the threshold starvation weight, and the meagre lichen supplies latter would not matter. The higher the weights are in the fall the less likely the animals will reach the starvation level. Hence winter lichen supplies may affect the slope of the overwinter weight change but their availability could still be density independent.

The July-August weight of females on the George River in high density years commonly reached lows of 70 kg and some females died in the summer. But animals in this herd left the degraded June-July range in August and crossed the tree line where they were able to gain weight prior to deep snows. This weight gain plus adequate winter lichen supplies resulted in weights higher in April than October (Huot & Goudreault, 1985) and above the starvation threshold.

Adult caribou on Coats Island, N.W.T. starved in the winters of 1974-75 and 1979-80 (Gates *et al.*, 1986). Gates *et al.*, felt this starvation was density independent but Ouellet *et al.*, (in press) implied it was density dependent and Heard & Ouellet (1992) stated for the Coats population that the effect of weather in causing starvation was not independent of density.

I think the animals on Coats had some forage problems similar to the Slate Islands. Originally the Coats animals in the 1970's had large body sizes and antlers (Parker, 1975); this sequence also occurred on the Slate Islands (Butler & Bergerud, 1978). Both islands had no predators and also few insects. Conditions for summer growth and reproduction must have been excellent. Further both populations had substandard lichen stands prior to high densities (Cringan, 1956; Parker, 1975). Ultimately high densities in both situations reduced these stands even further. Summer foods were reduced on the

Slate Islands and I hypothesize also on Coats Island; caribou on Coats Island weighed less than animals on nearby Southhampton Island in the fall of 1983 (Gates, pers. comm.). Animals in both populations died in the winter when summer numbers where high and the already meagre lichen supplies were generally unavailable because of snow cover on Coats Island and lack of winter storms on the Slate Islands.

But my argument is that starvation in both cases is density independent of winter forage abundance and nonregulatory. Lichens grow so slowly that once they are reduced by high numbers they cannot show annual responses to rapidly changing animal numbers. However summer vascular foods can respond rapidly and their annual abundances are not masked as is the case for lichens by snow cover. Note that all the authors reported that the Coats population made major summer recoveries following density reductions after the die-offs. On the Slate Island the highest fall weights occurred after the two greatest die-offs; females in the fall of 1985 weighed 106.4 ± 5.82 kg and in 1990 101.1 ± 0.87 kg. The mean weight of females in 15 autumns was 93.8 ± 1.86 kg and was significantly correlated with spring numbers (r=-0.571, P = 0.026).

Thomas (1980) said "most biologists agree that available forage on winter ranges is the key factor governing the potential upper limit of population size (Klein, 1970)". We have had it wrong for the past 30 years. The annual abundances of winter lichens are density independent and do not determine carrying capacity. We must finally reject the critical winter range hypothesis.

But summer forage resources can have serious density-dependent consequences on demography contrary to my earlier view (Bergerud, 1980), if densities in June-July exceed 10 animals/km^2. In the George River herd pregnancy/parous percentages for 15 years were negatively correlated with July densities (r=-0.861, P<0.01) (pers files) also Messier *et al.*, 1988; Couturier *et al.*, 1990). Annual mortality rates of adult females have increased from 10-11% in 1984 to 17-19% in 1992-93 (Messier *et al.*, 1988; Hearn *et al.*, 1990; Crête *et al.*, in press). These consequences are compounded because the migratory ecotype is prepared, similar to the sedentary ecotype, to sacrifice high quality foraging, to remain in habitats above tree line with low predation risk. Forage selection will occur in the summer but only within the options provided by the low risk habitats (see Ferguson *et al.*, 1988).

Table 4. Percentage of calves in the Northwest Territories herds in late winter between years when there was light precipitation in the spring vs heavy precipitation.

Low Precipitation < 12 mm			High Precipitation > 12 mm		
Year	Precipitation (mm)	Percent[a] Calves	Year	Precipitation (mm)	Percent Calves
1949	6.9	16.4	1950	12.5	7.6[b]
1953	2.0	15.4	1951	31.2	11.0[b]
1954	8.1	12.2	1952	17.0	26.6
1956	1.5	8.0	1955	44.5	6.9
1957	7.1	11.3	1958	14.7	20.0[b]
1959	10.8	25.0	1967	22.9	10.0[b]
1960	2.3	21.5	1971	15.0	19.0
1966	0.3	10.5	1977	20.3	23.0[b]
1968	2.5	11.4	1978	17.5	13.5[b]
1972	9.9	10.3	1979	37.9	28.0
1980	6.9	18.5	1981	20.3	25.5[b]
1982	2.8	21.0			
1983	10.7	21.0			
Mean	5.5±1.04	15.6±1.50		23.7±3.13	17.4±2.38

[a] Average percent calves for Kaminuriak and Beverly herds; no corrections made for unrepresentative proportions of male and female adults.

[b] Cold years when mean minimum temp. < -2.0 °C (mean cold wet years = 15.7 ± 2.59).

Weather/climate hypotheses

Hypothermia

Another population limitation hypothesis that dates back to the 1960's and is apparently still supported (Klein, 1991) is that inclement weather can cause hypothermia of newborn calves resulting in major mortalities (de Vos, 1960; Pruitt, 1961; Kelsall, 1968). The original evidence was the finding of the intact remains of young calves often in clumps. In one case the remains were not located until the following year. Miller *et al.* (1988) studied the early mortality of 287 calves in 3 years on the Beverly Herd and found calves were not dying from hypothermia but instead the chief cause was wolf predation. They stated that not a single calfs death during the 3 years of this study could be linked directly or indirectly to exposure to adverse weather. The wolves often killed several calves on one occasion and frequently consumed none or little of the carcass. These workers felt that surplus killing was the explanation for the majority of the deaths formerly attributed to hypothermia (Miller *et al.*, 1985).

I have been with caribou during 25 calving seasons which includes herds in Newfoundland in the freeze/thaw zone and herds in the Arctic (Western Arctic, Kaminuriak, Bathurst and George River) where snowstorms and high winds are common. I have not found calves that died from exposure. Skogland (1989) watched caribou calving in 17 springs in Norway and Svalbard and reported no exposure deaths with the possible exception of one calf in Svalbard. The calves in Svalbard weigh only 3-4 kg at birth (Tyler, 1987). Radio collars have been placed on 615 newborn calves in 4 herds with only one reported weather related death (Page, 1985; Mahoney *et al.*, 1990; Adams *et al.*, (in press) and Whitten *et al.*, 1992). A comparison of the percentage calves in the N.W.T. in the winter following cold/wet springs vs moderate springs for 25 cohorts showed no correlations with weather (Table 4): the correlation with mean min. Temp June 1-20 $r = 0.299$, $n = 25$, and total precipitation $r = 0.084$, $n = 24$. In years when there was heavy precipitation (> 10.7 mm) and it was cold < -2.0 °C) the calf percentages were 15.7 ± 2.59 ($n = 7$) not significantly different from the mean of all years 16.4 ± 1.34 ($n = 24$) (Table 4) .

Possibly wolves may be more successful killing young calves during snowstorms with reduced visibility (Kelsall, 1968). Still wolves have no difficulty, killing large numbers of calves on calving grounds at any time. Lo Camps (biologist) observed 3 wolves as they killed 11 2-week old calves in 84 minutes on the George River, July 2,1991. As with the case of density-dependent winter starvation, we must discard the hypothermia hypothesis; a hypothesis that once was exciting but has not stood the test of time. Miller & Gunn (1986) stated that caribou biologists have no sound basis for assuming that adverse weather frequently causes major loss of newborn barren-ground caribou.

Weather Cycles

Klein (1991) proposed that the synchrony of population fluctuations in the past two decades is most parsimoniously explained on the basis of continental wide weather patterns. He provided no mechanism on how weather could drive demography.

Table 5. The mean annual harvests of wolves by 5 year winter intervals.

Time	Mean Annual Harvest [a, b]				
Period	N.W.T.	Manitoba	Saskatchewan	Alaska	Yukon
1940-45	579	too high	619	455	285
1945-50	671	359	241	389	42
1950-55	479	284	53	898	40
1955-60	267[c]	131	27	595	21
1960-65	186	143	50	632	56
1965-70	400	155	107	1486	55
1970-75	807	314	234	1020	136
1975-80	805	397	257	934	123
1980-84[d]	537	415	227	589	132

[a] Source: Novak *et al.*, 1987.

[b] Ontario and Quebec not included because of recent northern and eastern extension of coyotes (*Canis latrans*) and confusion with wolves in harvest statistics.

[c] Many more taken with control (see Heard, 1983).

[d] 1984-85 not available.

All the large migratory herds in the world were increasing in the 1980's and peak numbers were probably reached in that decade (Bergerud, 1988a). At the same time the sedentary populations were declining world-wide. But synchrony in growth phases in other decades has not been the case for the migratory herds in the past (Skoog, 1968; Thomas, 1980) nor does it now prevail, since several major herds are now out-of-step in Alaska, N.W.T., and Ungava.

An alternate explanation for the increase in the migratory herds in the 1980's is Man's influence on predator-prey interactions. First in the 1950's we had synchronous wolf reduction programs in Alaska and Canada; then control ceased coincidentally. Then the skidoo was introduced into the North in the late 1960's profoundly increasing the harvest of wolves above tree line. Now we have a worldwide boycott of wild furs. Peak caribou numbers in the 1980's followed the increased harvest of northern wolves (Table 5).

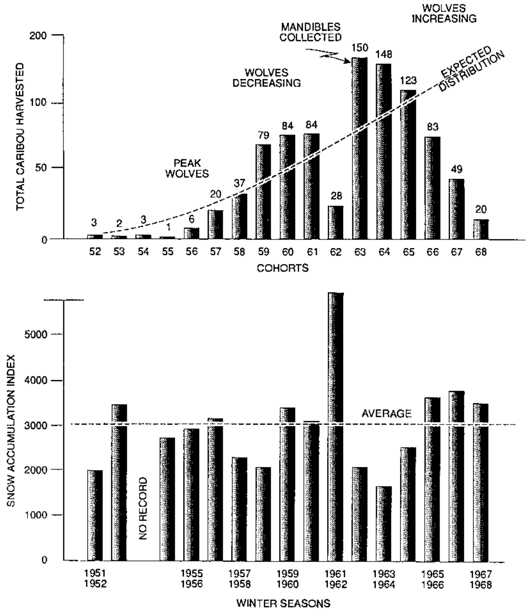

Fig. 5. The size of the 1952 to 1968 cohorts of the Kaminuriak Herd taken from Miller, 1974:Fig. 21. The 1967 and 1968 cohorts are under represented by the collection schedule. The 1962 cohort is far less than expected and follows the worst winter in 16 years (below) when dead animals were observed (Kelsall, 1968). Also shown above is the expected age distribution based on animals collected by Thomas & Barry (1980) from the adjacent Beverly Herd (age array smoothed by Taylor, 1991). Wolf numbers decreased for the Beverly Herd 1955 to 1961 from control (Kelsall, 1968) and then increased.

Weather and Fetal Malnutrition

Calves may be inviable at birth if their dams are severely malnourished during gestation. Such mortalities could be confounded with deaths from hypothermia or surplus killing. Calves of low viability were probably born in the N.W.T. in 1962. The winter snowfall in 1961-62 was by far the most severe in 16 years (Fig. 5, Dauphine, 1976). Kelsall (1968) reported that adults starved. The 1962 cohort had the lowest survival of 12 cohorts analyzed by Miller (1974) (Fig. 5) and males were more common than females for that cohort. Yet spring temperatures and precipitation were favorable in June 1962 and wolves were probably at an all time low following 11 years of control (See Heard, 1983: p.44). The loss of this cohort just when calf survival was expected to be highest may have confounded an evaluation of the importance of the wolf reduction programs on herd growth. In Alaska the Nelchina Herd declined after 1962 when three cohorts (1964, 1965, and 1966) had low survival (Bergerud & Ballard, 1988). These three cohorts were born at lower elevations than in other years and nearer to predators, but these calves may also have had low birth weights because of their dam's winter nutrition and been more vulnerable to predation.

A relationship between female malnutrition and calf viability is also suggested from our Slate Island work. In the spring of 1985 after a very extensive die-off (Fig. 3) we found the legs of extremely small calves that had no wear on their hooves at fox (*Vulpes vulpes*) dens; these calves may never have stood and nursed. Calf recruitment in the fall of 1985 was 10.7% calves (n = 291) compared to a mean of 14.4 ± 1.28 % in 10 other autumns.

A fourth example of calves of low viability is from the George River Herd in 1992. Calves born in 1992 were very small, a mean birth weight of 4.7kg (n = 80) (S. Couturier, pers. comm.) 2 kg less than that recorded in 5 other years. Couturier noted many dead calves. We estimated calf mortality in 1992 at about 2 weeks of age at 20%, based on cows with regressing udders not followed by calves (n = 308 cows) (udder counts corrected for cows with small udders still nursing yearlings); the mean mortality of calves of this age in 8 other years was 6.6 ±1.24% (mean sample size of females 2,406 ± 578). The growing season in 1992 was the latest on record in 37 years; the ice did not go out of Knob Lake, Schefferville until June 29, the mean date of breakup from 1955 to 1993 was June 13 (the previous extremes were May 28, 1959 and June 25, 1972 (McGill Research Station records). Cows in 1992 did not switch to new birch growth until July 8 about 2 weeks later than in the four previous years.

In this spring we actually had a cow with a calf swim a river in front of the crew and then fall down and die.

Weather is not Regulatory

At this conference it has been shown that winters with deep snow have played a role in the recent declines of caribou of the Alaska Range 1991-94. Reduced nutrition from a relative food shortage has lowered conception rates and increased winter and summer mortality rates of adults and calves (Boertje *et al.,* 1993; Valkenburg, 1994; Adams *et al.,* in press). Both caribou at high densities as in the Delta Herd (0.9/km^2) and at low densities as in the Denali Herd (0.4/km^2) have been affected.

Winter snow depths are not an ultimate explanation in the *sensu* of Lack (1954). Ultimate factors are those that drive survival in an evolutionary sense whereas proximate factors are behaviour and physiological influences that modify ultimate factors. For example the ultimate regulatory factor for wolves is their prey biomass (Keith, 1983; Fuller, 1989). But the proximate adaptation that influences how the ultimate factor operates is territorial behaviour (see Packard & Mech, 1983).

Weather is density independent hence not regulatory. Weather can only cause death as an interaction since animals don't die directly from exposure, if in good nutrition (and or in the absence of predation). Both starvation and predation may be density dependent and regulatory; weather alone cannot. Hence weather is not a sufficient mortality factor, either nutrition or predation are necessary interactions to bring death and influence population dynamics. Caribou and wolves are in a predator x prey adaptive race with the extrinsic environment the arena. At times weather favors the prey and at other times the predator in this dynamic competition.

We should distinguish between climate and weather. There have been long term climatic trends such as the Little Ice Age that have modified the distribution and abundance of caribou. I am sure we are all concerned about the potential for disaster if there is a global warming trend. Deer (*Odocoileus virginianus*) and moose (*Alces alces*) would expand north bringing increased disease and predation to sedentary herds and increased freezing/thawing patterns would cause high mortality to Arctic Island herds. However such major changes are the pages of time.

Natural predation

I proposed in 1967 that wolf predation might regulate the numbers of the George River Herd (Bergerud, 1967) and later expanded this hypothesis to other herds but was more cautious by using the words limiting factor rather than regulation (Bergerud, 1974b). To make the hypothesis more specific and testable Bergerud & Elliot (1986) predicted that wolves would halt herd increases if wolf numbers exceeded 6.5/1000 km^2. The recruitment needed to stabilize numbers (R_S) in the 1986 paper was 12 % calves (sedentary and migratory ecotypes). A later analysis indicated that R_S for only sedentary herds was closer to 15% (25 calves/100 females) the finite-rate-of-increase regressed on percentage of calves was $Y = 0.757 + 0.016X$, $r = 0.737$, $n=32$ (Bergerud, 1992).

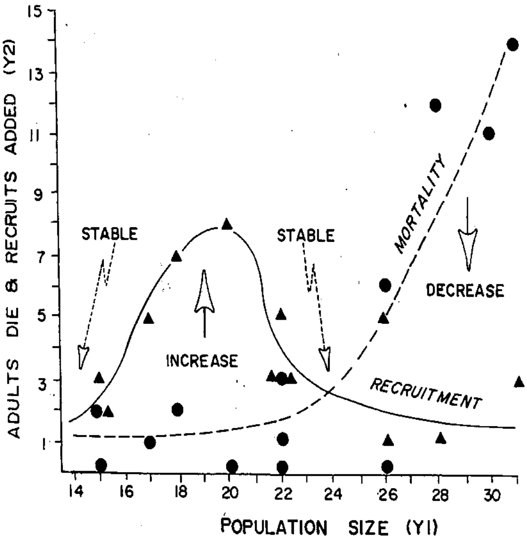

Fig. 6. The upper and lower stabilizing numbers (R = M) for the Pukaskwa National Park (1974-87) a herd of < 35 animals that lives along the coast of Lake Superior, Ontario. The major cause of adult mortality was wolf predation. The cause of calf mortality is not known but calf survival has been high on Otter Island in the presence of lynx, and bears are rare along the coast.

The predicted density of 6.5 wolves/1000 km^2 postulated to halt growth has been useful. Herds when faced with < 6.5 wolves/1000 km^2 have generally increased in recent years (Western Arctic, Central Arctic, Porcupine, Blue Nose, Leaf River and George River herds). Herds when they were exposed to ≥ 6.5/1000 km^2 wolves have remained stable or declined (Finlayson, Denali, Quesnel, Pukaskwa, Tweedsmuir). For example wolves in the Denali Herd reached 7.0-8.0/1000 km^2 in 1989 and 1990 and the herd declined from 1990 to 1991 (Adams *et al.,* in press). A major exception to the 6.5/1000 km^2 yardstick was the Delta Herd where wolves reached ≥ 10/km^2 but caribou still increased and the wolves may have continued to hunt mostly moose.

Sedentary Herds

The sedentary herd that I have examined (1974-87) relative to predation regulation is in Pukaskwa Park, Ontario (Bergerud, 1985; Bergerud, 1989). This herd of less than 35 animals resides in a 2 km strip along the coast (or at density of about $0.06/km^2$) near water escape habitat whereas moose and wolves are more common inland (Bergerud *et al.*, 1983). The percentage of calves in the herd in late winter (Y_2) declined as total numbers increased in Y_1, $r = -0.681$, ($n = 11$) or $r = -0.828$ ($n = 12$) . The annual percent mortality of adults was also density dependent on total numbers ($r = 0.757$ $P < 0.05$ ($n = 13$) . In the winter of 1993-94, 3 of the 4 tagged cows in the herd were killed by wolves. Recruitment in this herd equalled adult mortality at a lower stabilizing number of 14 animals and at a upper stabilizing herd size of 24 (Fig. 6). When we modeled this system by reducing the wolves the caribou went extinct because with less wolves the moose increased beyond $0.2-0.3/km^2$ which ultimately permitted many more wolves in the system (wolf biomass modelled after Fuller, 1989).

This predator x prey system was complexed by snow and ice, density independent processes, that changed the distribution of moose. The wolves in the Park hunted mostly moose inland (Bergerud *et al.,* 1983) but even when on the coast they still spent more time searching for moose rather than caribou; the correlations in the distributions of moose, caribou, and wolves on the coast in 15 years in 26 $4km^2$ blocks adjacent to the shore were: moose and caribou $r = -0.0702$ ($P = 0.734$), caribou and wolves $r = -0.1042$, ($P = 0.613$), and moose and wolves $r = 0.4257$, ($P = 0.032$). But when the moose moved towards the coast with deep snows the wolves did likewise (the regressions of mean annual km from shoreline of aggregations or tracks seen vs snow depths were for moose, $Y = 85.28/(12.49 + X)$, $r = 0.666$, $n = 13$; and for wolves $Y = 1.783 - 0.021X$, $r = 0.578$, $n = 13$. This shift of moose and wolves compromised the displacement of the caribou. Additionally there was generally more landfast ice in winters with deep snows; this landfast ice in Lake Superior reduced the opportunity for caribou to escape to water and further facilitated the searching of wolves along the coast.

The majority of the other sedentary herds in North America have similar low densities as those in Pukaskwa (Bergerud, 1992). Generally when herds in North America had densities greater than $0.06/km^2$ they were decreasing and when less increasing (27 herds graphed in Bergerud, 1992, page 1011). A regression of the annual recruitments from 9 herds on herd densities that ranged from 0.03 to $0.15/km^2$ was $r = -0.646$ ($n = 29$) and a recruitment of 15% (R_S) intersected densities at $0.06/km^2$ ($Y = 30/[1 + (1.350X*10^{(0.8565)}$ (Bergerud, 1992) . I termed the density of $0.06/km^2$ the stablizing density (D_S)

There now seems to be a consensus by many biologists that predation is the greatest and most consistent cause of natural deaths in these sedentary herds. The concern now is how to preserve sufficient space for these caribou in the face of habitat alienation (primarily logging) so the predators will not be more successful in finding the animals (Bergerud, 1990). The older hypothesis that logging reduced lichens as a necessary food directly precipitating declines is no longer a viable alternative. In fact the thinking has changed so strikingly that when you mention increased forest fires to biologists now, instead of relating fires to reduced lichen supplies, as in the past, these workers may assume you are speaking of how burning drives changes in forest succession and could result in more moose in the system thus more wolves and more predation of caribou (D. Seip, pers.comm.) .

Migratory Herds

However in the case of migratory caribou the role of wolf predation in regulating numbers has been questioned (Kelsall, 1968; Messier *et al.*, 1988; and Klein, 1991). The fluctuations in these herds are of such long duration that density dependant interactions are hard to visualize. And also wolf predation has not halted the growth of several large herds in Alaska in recent times (Davis & Valkenburg, 1991) and in Ungava the George River Herd, overgrazed its summer range.

Back in the 1950's wolves exceeded $7/1000\ km^2$ in N.W.T. (Kelsall, 1968) and did take sufficient calves at least in the Beverly and Bathurst herds to halt population growth. Late winter calf percentages were less than 12% needed for stability for the 1950, 1951, 1955, 1956, and 1957 cohorts (Kelsall, 1968). The correlation of calf percentages with wolf harvest statistics was $r = -0.633$ ($n = 10$) $P < 0.05$ (Fig.7). The wolf population declined from control after 1955-56 (Fig. 7, Kelsall, 1968). Thomas, (1980) stated, "Kelsall's, (1968) data and subsequent data suggest that the population of the central mainland declined until about 1957 when a pronounced upsurge began."

Parker (1972) concluded for the Kaminuriak Herd that wolf predation was the chief natural limiting factor 1966-68 and the 1966, 1967, and 1968 cohorts were all less than 12% needed to maintain numbers and indeed the herd continued to decline until 1980 (Heard & Calef, 1986). A cohort analysis of this herd from collections 1966-68 compared to the age structure of the Beverly Herd 1980-87,

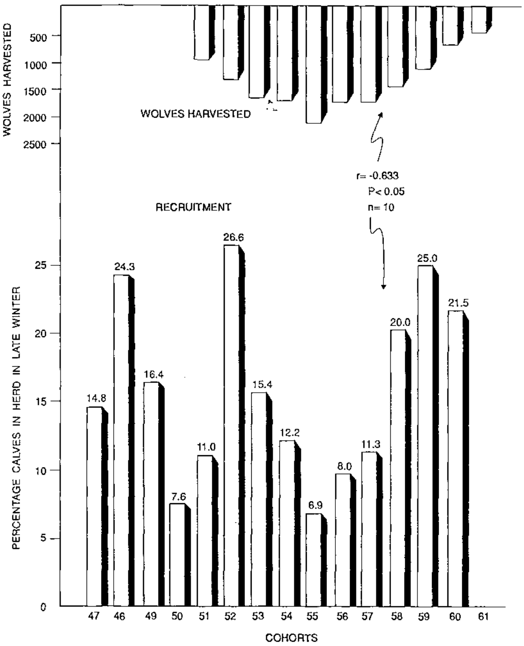

Fig. 7. The late winter recruitment of the caribou in the western herds in the N.W.T. (Kelsall, 1968:Table 18) compared to the estimated harvest of wolves from control (Kelsall, 1968:Fig. 14).

when there was no wolf control (Thomas & Barry, 1990; Taylor, 1991), showed that the 1959, 1960, 1961, 1963, 1964 and 1965 cohorts had more calves than expected and the 1955, 1956, 1957 and 1966 cohorts less than expected (1962 cohort reduced from inviable calves) (Fig. 5). These results are consistent with the changes in the abundance of wolves from the reduction program. If in the future the harvest of wolves in the N.W.T. declines we should again see the limiting effects of predation on these herds.

In Alaska it has not been shown for the herds on the North Slope that wolf predation is regulatory. Wolves there have not exceeded 6.5/1000km^2. These wolves are now heavily hunted from skidoos and there is some history of rabies (Rausch, 1958; James, 1983; Garner & Reynolds, 1986). But for the herds farther south, the Denali, 40-mile, and Nelchina, previous studies have shown that when wolf numbers exceeded 6.5/1000 km^2 recruitment was less than needed to maintain numbers and in the case of the Delta, 40-mile and Nelchina Herds the experimental removal of wolves was followed by sufficient recruitment that allowed the herds to increase.

In Newfoundland the migratory herds have not been regulated by density-dependent predation. The wolves on the Island went extinct in the early 1900's. In their place lynx (*Lynx canadensis*) became the main predator. Lynx reached extremely high numbers following the introduction of snowshoe hares (*Lepus americanus*) into the Province in the late 1800's. Millais (1907:249) said about lynx "Doubtless they were very scarce until recent years, but now are the most abundant of all carnivora... Everywhere one sees their tracks. A good trapper will kill 50-100 in a season." At the same time he said bears had been reduced in numbers. When the hares crashed in their cycles the lynx switched to caribou (Bergerud, 1971) and caused long cycles in calf survival (Bergerud, 1983b). Three cycles documented were 8-9 years duration (Bergerud, 1983b). Lynx predation and overhunting may have caused the decline of the caribou herds in the early 1900's (Bergerud, 1971) but since the 1950's caribou have increased despite this predation, probably because hare numbers drive lynx abundance rather than caribou. By the 1970's lynx had been reduced from trapping (Bergerud, 1983b; Mahoney *et al.*, 1990) and bears (*Ursus americanus*) and lynx were taking similar numbers of calves (Mahoney *et al.*, 1990). Bears had been rare on the calving grounds in the 1950-60's (Bergerud, 1971); I saw two bears in 11 calving seasons and little bear sign. Now bears are a major predator of caribou, perhaps in response to major increases in caribou and moose. But still the herds have had positive growth. The numerical and functional predator responses of bears to caribou prey has not been documented, but bear predation elsewhere has been described as density independent (Boertje *et al.*, 1988). Perhaps the new predator in Newfoundland, the coyote (*Canis latrans*) will regulate numbers, but both lynx and bears while being major limiting factors have not shown density dependence in their predation.

The George River Herd in Ungava increased from 1958 to 1984 at a finite-rate-of-increase of 1.11 (Messier *et al.*, 1988) . Wolf predation did not regulate numbers as the herd grew to > 2/km^2 contrary to what I had hypothesized (Bergerud, 1967). However wolf predation was the most important limiting factor in the growth of the herd 1974-84. The size of the annual cohorts declined each year 1976 to 1980, and adult mortality and calf recruitment were about balanced in 1980 (Fig. 8). Wolf predation in 1980 I argue temporarily halted the growth of the herd while forage was still abundant. The wolves developed rabies in 1980-82 and wolf numbers dropped drastically. No wolves were seen in 6 caribou classification surveys (each flight > 7 days) 1982-84. The mean number seen per survey 1976-80 was 4.8 ± 0.83 and 1984-87 3.3 ± 1.48. The mean pack size 1976-79 prior to the outbreak was 4.4 ± 1.18 (18), during the outbreak 1.7 ± 0.17

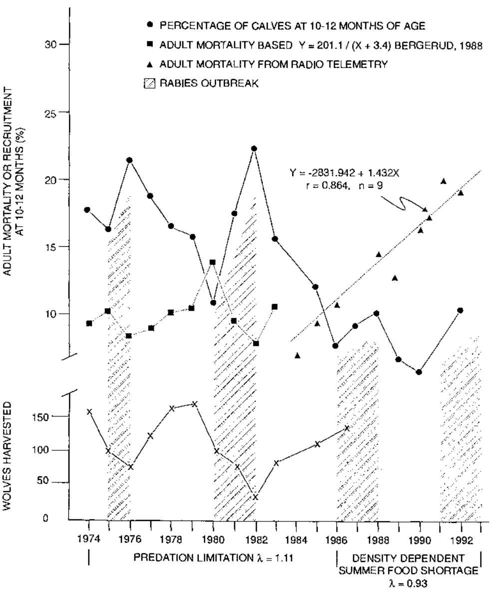

Fig. 8. The recruitment of calves at 10-12 months of age for the George River Herd (1974 to 1992 cohorts) compared to the mortality of adults. Adult mortality 1974 to 1983 is based on Y=201/(X + 3.4), Bergerud, 1988) and is not independent of adult mortality. Adult female mortality 1984-1992 based on Hearn *et al.*, 1990 and Nfld files. Adult male mortality based on $M_m = 1 - [(1-M_f + \beta r)(M_2/F_2 - \alpha r)](F_1/M_1)$ where: M_m= male mortality, M_f = female mortality, r= ratio calves/females, α = fraction of male calves, β= fraction of female calves, F_1 = number of females 1st year, F_2= number of females 2nd year, M_1 = number of males 1st year, M_2 =number of males 2nd year. Formula can be reduced because of constant adult sex ratio to $M_m = M_f + (\alpha F/M - \beta)r$. Wolf harvest figures (below) from Kuujjuaq and Nain. Rabies outbreak based on confirmed (positive) cases in northern canids by government health officials.

(27) and after in 1984-86 4.2 ± 0.67 (10). The harvest of wolves from Nain and Kuujjuaq declined to a low of 30 animals in 1982-83 (Fig. 8). With such a major reduction in wolves the herd escaped the predation limitation and with the addition of the very large 1981 and 1982 cohorts (see age structure in Messier *et al.,* 1988) went on to degrade its June/July habitat and start to decline from unfavorable R/M schedules (Fig.8).

One further comment on the interaction of forage and predation in this herd. The winter mortality of calves from October-November to April-June was positively correlated with July densities (r = 0.574, n= 18 years, P = 0.0127) yet the calves that died overwinter did not starve (Fig. 4). The calves (1984-89) were smaller in body size (Couturier *et al.,* 1989) and should have been more vulnerable to predation. But if the wolves had not been in the system this increased mortality would not have resulted. In cause/effect argument the reduced nutrition is not sufficient for the increased mortality, predation was necessary.

Stabilizing space and mobility

Andrewartha & Birch (1954) told us at the beginning that abundance and distribution were two sides of the same coin, and I have argued in the past that caribou use their mobility and space to successfully cope with wolves. For sedentary caribou the stabilizing mechanisms are easier to visualize; cows seek safe sites alone for calving, show philopatry and dispersion from predators and altemative prey. Spacing strategies of migratory caribou are harder to quantify with the confounding effects of group interactions. For these herds we need to view the herd as the individual that successfully interacts with predators. The calving locations of individually tagged cows in the George River Herd were farther apart between consecutive years than were the centers of the entire calving distributions in the same adjacent years (see also Fancy & Whitten, 1991) Some of the shifts between years depended on snow cover, but it is not clear whether these movements related to maintaining young calves on brown cryptic landscapes or related to locating forage. The herd did continue to show a philopatry to a relatively safe range. I believe that if the abundance of predators changes we should expect changes in calving distributions. The Leaf River herd once calved at 58° N but by 1991 the center was 320 km farther north (60°30′) . (S.Couturier, pers. comm.) .

Movement Between Herd Areas

There can be major movements between caribou herds (Kelsall, 1968; Skoog, 1968). The Kaminuriak Herd was censused at 149,000 animals in 1955 but the herd had declined to 40,000 animals three years later (1957-58) (See review in Parker, 1972). Coincident with this decline Kelsall (1968) noted thousands of caribou migrating west from Dubawnt Lake in July 1956; the animals moved across the range of the Beverly Herd and the Bathurst Herd; some animals continued to the range of the Bluenose Herd. Twenty-five years later the Kaminuriak Herd showed another unexpected change in numbers; it increased from 39,000 in 1980 to 180,000 in 1982; additional counts in 1983 gave > 120,000 animals, 1985 > 200,000 and 1985 > 148,000 caribou (see Heard & Calef, 1986) These two unexpected major changes in the Kaminuriak Herd cannot be wished away by faulting census techniques. Nor could they have come about by internal R/M changes (see Heard & Calef, 1986). If we understand why females calve where they do, we can predict when these traditions should be abandoned and major range shifts within the tundra will result. If in fact these shifts are influenced by the abundance of wolves they could have important stabilizing results.

Range Expansion/Contraction

When caribou numbers are low migratory herds become more sedentary and often remain throughout the year above tree line in their most constant range (the center of habitation, Skoog, 1968; also see Kelsall, 1968). Reproductive performance is enhanced because of a high green phytomass and reduced energy expenditure in travelling. Furthermore animals are spaced away from many wolves near tree line. The great advantage caribou have over wolves is their precocial progeny allowing them to be mobile soon after parturition whereas wolves have helpless young and are tied to dens sites for the spring-early summer. If wolves denned on calving grounds they would be satiated for two weeks and then left stranded when the caribou left, especially if the calving ground had few alternative prey. In winter an advantage to caribou in staying north is the reduced snow depths. With less snow, less energy is spent cratering and the caribou are less impeded in their displacements from wolves. With caribou on the tundra in the winter we could expect the wolves to have a decreasing demography. Difficulties for the wolves could include: (1) the problems in finding caribou (less predictable patterns), (2) choosing between caribou and alternative prey that are near the tree line, (3) and the increased mobility of caribou that would minimize contact time. The predator functional response should be reduced on the tundra compared to that south of the tree line. In the tundra ambush is more difficult, lead-times are enhanced and caribou can group together more quickly and evaluate the predators threat relative to the appropriate evasive action.

The Western Arctic herd in the 1970's an example of a large migratory herd in which a proportion of the herd shifted to a more northern distribution above tree line on the North Slope when its numbers were low. In such a location the herd relied more on shrubs for forage rather than lichens (Davis *et al.*, 1982). Kelsall (1968) provides other examples where large numbers of caribou remained on the tundra in the winter on ranges where shrubs were more common than lichens. Lichens are not necessary even for a relatively large migratory herd.

However the major shortcoming that most ranges above tree line have is a reduced phytomass after leaf fall. Moderate numbers of caribou can successfully cope with this but when numbers grow the reduced phytomass will not hold the herd. When caribou herd numbers expand, the animals spend more time south of tree line and less nutritious lichens dominate the diet. This range expansion south of tree line and nearer to wolves occurs between the end of the insect season and the period of deep snow and is a density dependent food interaction, not social facilitation (pers. files).

The densities of caribou south of tree line for the 8 major migratory herds in the 1980's ranged from 0.7 to 4.3 animals/km^2, mean 1.6 ± 0.41 (densities based on total maximum numbers divided by the maximum range) (Table 3). Within this density range R/M schedules should turn sour, primarily from increased wolf predation. The physical condition of the animals will be reduced resulting from the longer migrations, cratering in deeper snows, possibly summer forage problems, and the less satisfactory winter diet of lichens. Animals should not starve from a density dependent absolute food shortage, but their reduced physical status may increase their vulnerablity to predation. Wolves on these winter ranges can affect both numerical and functional responses when caribou mobility is reduced by cratering for lichens through deep snow. In forested habitats lead times are reduced and ambush is more feasible. The large caribou aggregations provide a highway of trails for wolves (Kelsall, 1968) and the demographic equation moves $R < M$ and retraction begins.

Thus I believe that two major stabilizing mechanisms in migratory caribou fluctuations are (1) major movements between herds especially relative to above tree line distributions and predation pressures and (2) range contractions to above tree line optimum habitats when numbers are low and range expansions when numbers are high into more marginal lichen habitats below tree line. Involved in these stabilizing mechanisms are elements of density dependent regulation by wolves but also a density dependent caribou x food interaction. The important insight is Skoog's (1968) center of habitation hypothesis. These stabilizing mechanisms are final solutions that help buffer major fluctuations. Many other limiting factors can occur at lower numbers so that these processes do not result.

The periodicity and amplitude between these range contractions / expansions hence fluctuations for migratory herds would be in the order of decades. There would be lags because of the caribou x food interaction, the continuum of increasing contact with wolves and lags in wolf demography. For the sedentary caribou there are no lags due to food and total ranges remain stationary as populations rise and decline as the spacing between preparturient females increases and decreases. The time interval between peak numbers in the Pukaskwa herd was 3.5 ± 0.28 years ($n = 4$) amplitude 1.8. Interestingly the periodicity on the Slate Islands with its caribou x food rather than caribou x wolf interaction was 3.3 ± 0.48 years ($n = 4$) and the amplitude also about 2 times. In contrast the George River Herd decreased from a high in the 1880's to another one 100 years later with an amplitude of 100 times (Bergerud, 1988b).

Recent census results of the Beverly and the George River herds (N.W.T. news release, Russell, in press) do not agree with predictions from R/M schedules. The Beverly herd should have remained stable (R taken from Williams *et al.*, 1989; and M from Thomas & Barry, 1990; Taylor, 1991) rather than declined and the George River Herd should have had a major decline rather than remained stable. We need to consider that there could have been major lateral movements. In June 1988 4 of 22 (18%) of the radio cows from the Leaf River Herd were found on the George River calving ground and in 1993 2 of 5 (40%) Leaf River cows were with the George River cows (Couturier, *et al.*, in press). My understanding is that wolves are now more common on the range above tree line of the Leaf River Herd than the George River range (S. Luttich, pers comm.); again the Beverly Herd has a history of more wolves on the calving grounds than either of the two adjacent herds (Fleck & Gunn, 1982; Heard & Calef, 1986) and this could have been a factor in the unexpected changes in the size of the Kaminuriak discussed earlier. We should consider reinstituting winter censuses, when the herds may have less interchange. At this time the George River winters in the east whereas the Leaf River winters farther west in Quebec. We need to give these caribou more credit than we usually do; fitness theory would predict that animals should displace from situations when the risk to neonates has increased. There is nothing unique about the habitat quality of calving locations (Fleck & Gunn, 1982; Fancy & Whitten, 1991) except the low risk character.

Habitat selection

The conventional wisdom that we've all been indoctrinated with is that the resources of the habitat best describe and delimit where an animal will be found – intraspecific food and cover rather than interspecific risk and relief considerations. With caribou, biologists first questioned this view when they found animals standing on barren mountains even on snowfields to find relief from insects. Then we found calving females on mountains, islands, and calving grounds with low phytomass. Then we realized that males and females had different fitness requirements and they could be expected to chose different habitats. The next step in this evolution is to question the view that caribou select habitats in the fall and winter primarily on the basis of food resources. By fall calves are no longer excessively at risk from predators but then too the season of protein and growth is ending. Thus survival vs nutritive needs are both more muted and distinguishing the first-order priorities requires finer measurements.

At the 3rd caribou workshop in 1988 H. Butler evaluated 3 hypotheses for habitat selection in the breeding season for 22 sedentary herds: (1) caribou chose rutting areas with the best prospects for forage, (2) caribou chose breeding areas that minimized the risk of predation, and (3) they chose areas that facilitated sexual aggregation and display for breeding. For each herd forage was segregated as to whether it was best where they rutted or better elsewhere and predation risk was classified as low (bears only), medium (bears and 5-10 wolves/1000 km^2) or high, wolves > 10 /1000 km^2). The third hypothesis was evaluated on the visibility of the habitat (open/closed canopies).

Butler reported the following: with no predators 2 herds selected sites of optimal forage, with low predators 4 herds optimally foraged and 6 herds selected safety first, with medium predators all 4 herds rutted in suboptimal forage sites, and with high predators all 6 herds selected more safe sites over forage considerations. Relative to H_3 she stated most herds had traditional open sites to breed. However such openness was not needed and tradition could be perpetuated at closed canopy sites and further males would disperse to find females if the cows were not at the traditional sites.

From my experience the clearest example of animals selecting low risk sites over forage for breeding was on Otter Island (1.3 km^2) in Pukaskwa National Park. Every year males and females met on this island (Bergerud, 1989). The island was mostly closed canopy with few lichens and was heavily grazed; food was certainly better elsewhere but the island was safe as long as landfast ice did not form (Fig. 9).

Another herd that rutted in a degraded food habitat but where predation risk was low was on Pic Island (11.1 km^2), Ontario, an island only 1 km from the undisturbed mainland that had unutilized food supplies. But even on the island a female with a calf further restricted herself to the shoreline of the island; but the males on the island foraged in a central valley where they optimized the available island forage but where their location meant wolves would find them first when they occasionally visited (Fig. 9) (Ferguson *et al.*, 1988).

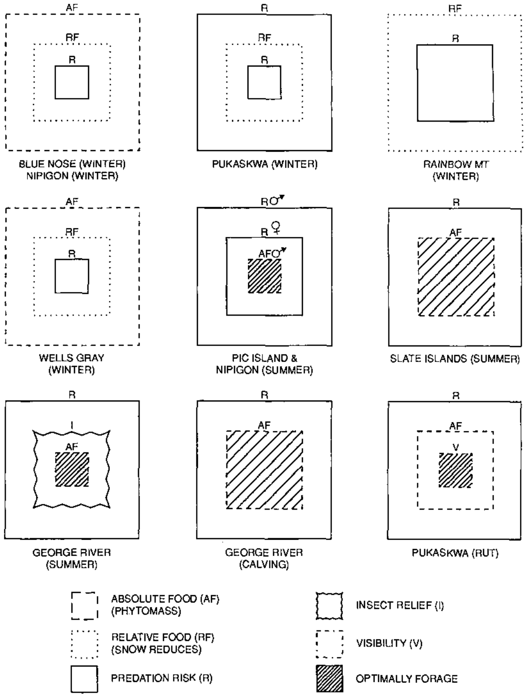

Fig. 9. The habitat niche is visualized as decreasing space areas as selection requirements increase. Ecological factors considered are food resources, snow depths, insect relief and predation risk. For example the winter distribution of the Bluenose Herd (Carruthers *et al.,* 1986) is first determined by the absolute abundance of winter foods (animals will not winter where there is no food), within this area animals select areas of reduced snow cover (relative abundance of food) and within this area they select areas with reduced risk. The other niche presentations in the figure are based on my personal observations.

Both males and females used the islands in Lake Nipigon, Ontario but only during the open water season. Here too animals further restricted themselves to shorelines with reduced food supplies. The animals remained during the rut breeding under closed canopies (Fig. 9) (Bergerud *et al.,* 1990).

Turning to the winter the sedentary ecotype may be dispersed or aggregated in the winter and we need more information in most situations to decide between risk and forage options. The real problem is that biologists seldom radio track both predator and prey simultaneously to understand how wolves search and caribou space relative to risk.

The animals in Pukaskwa National Park are dispersed along the shore of Lake Superior in winter, water escape was available if landfast ice did not develop. The shore is an area of low snow fall and lichens are available on exposed bedrock shoulders. But the caribou show preference for islands and peninsulas. Caribou are probably so rare along the shore that they don't attract much searching time from wolves, but still the caribou are in the safest locations available (Fig. 9).

In the Rainbow Mountains of British Columbia I observed that a herd in 1974 that was separated from wolves hunting moose at lower elevations by deep snows but when I visited the herd the wolves used my snowshoe tracks to make contact with the herd. Seip (1992) has reported how the mountain caribou he studied were seldom hunted by wolves who distributed themselves relative to the moose abundance. In Wells Gray Park I have noted caribou in small islands of old growth surrounded by soft snows too deep for wolves (> 40 cm). Is this solely a snow lift to reach more arboreal lichens and or are they there to avoid wolves?. Given that predators are absent we can assume caribou in winter optimally forage; with wolves present we can not make this assumption in the absence of data.

The distribution of migratory caribou in the winter is more a product of snow cover than phytomass (relative not absolute abundance). This sequence applies to populations with and without predators (Bergerud, 1974c; Skogland, 1978; and Russell *et al.,* 1993). There is a niche of reduced snow cover within the wider food niche (Fig. 9). But is there a further reduction in the snow cover niche to occupy ranges with less risk? Carruthers *et al.* (1986) argued that caribou in the Bluenose Herd selected areas with smaller lakes that increased the searching time for wolves and possibly improved escape opportunities for caribou. We also know that males with their longer legs are commonly in deeper snows than females (Kelsall, 1968) and more dispersed than females. If wolves are selecting calves (Miller, 1975) then males being apart and dispersed should attract less predator attention. It is unlikely that forage is better where males locate and males certainly are not displacing to draw predation pressure from females or reduce food competition with females. Wolves show a numerical response to large winter aggregations (Miller, 1975; Fleck & Gunn, 1982). But the habitat components that affect the functional response have not been documented.

Where to live relative to food and risk should be viewed in a fitness sense. In the past 20 years caribou from the Slate Islands have been introduced twice to the mainland. Both colonizations failed from predation whereas two introductions to islands without wolves succeeded. In a fifth instance a radio tagged male was released on the mainland after the rutting season in 1983. This male (No 169) left the land of milk and honey on the mainland (all that untouched food) and swam 11.3 km back to the degraded barnyard of the Slates where he died from malnutrition in the winter of 1984-85. He faced certain and swift death on the mainland from wolves. By returning he probably increased his fitness by breeding females in the fall of 1984 (he had good antler development). Survival will always take precedent over where to find the next meal. Give these caribou some credit for understanding their priorities and environment better than we do. They've made it this far.

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Section 2.

Caribou-forestry Interactions

The Sixth North American Caribou Workshop,
Prince George, British Columbia, Canada,
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Managing Woodland Caribou in West-Central British Columbia

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Abstract: Initial long term planning for logging on the Tweedsmuir-Entiako caribou winter range began in the early 1980's. Because little information was available on which to base winter range management, the British Columbia Fish and Wildlife Branch began studies on radio-collared caribou in 1983, and an intensive study on caribou winter habitat requirements was conducted from 1985 to 1988. Terrestrial lichens were identified as the primary winter food source for the caribou, and in 1987, caribou winter range ecosystem maps, which emphasized abundance of terrestrial lichens, were produced. The ecosystem maps and information from the caribou study, including potential direct and indirect effects of timber harvesting on the caribou population, were used to develop a management strategy for the winter range. The management strategy comprised two levels of management: a landscape level (Caribou Management Zones); and a site-specific level (caribou habitat/timber values). Timber information associated with BC Ministry of Forests forest cover maps was integrated using a Geographic Information System. Six winter range management options were proposed ranging from harvesting low value caribou habitats only throughout the winter range to total protection of the entire winter range. Impacts of those options on both the caribou population and on the timber supply were evaluated. The options were reviewed through a public planning process, the Entiako Local Resource Use Plan, and recommendations from that process were forwarded to the British Columbia Protected Areas Strategy.

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Introduction

West-central British Columbia has been identified as a high priority management area for woodland caribou (*Rangifer tarandus*) in British Columbia (Stevenson & Hatler, 1985). Two populations of caribou live in west-central British Columbia. The Itcha-Ilgachuz-Rainbow herd, which consists of about 1500 caribou, summers in the Itcha, Ilgachuz and Rainbow Mountains, and winters primarily in low elevation forested habitat to the west of the Itcha Mountains, and to a lesser extent, in the northern Ilgachuz and Rainbow Mountains (Fig.. 1). The Tweedsmuir-Entiako herd, which consists of about 400 caribou, summers in northern Tweedsmuir Park and winters in low elevation forested habitat in the Entiako Lake area to the east of the park. The ranges of the two populations occupy over 1 500 000 ha of provincial forest and provincial park land and are managed through cooperation between BC Environment, BC Parks, and BC Forest Service, with involvement from public and interest groups.

Because caribou in both areas winter primarily in lower elevation forested areas outside of Tweedsmuir Park, potential conflicts with logging were anticipated. Increasing concern over current population status, habitat disturbance by logging and increased accessibility prompted the initiation of studies on radio-collared caribou by the British Columbia Wildlife Branch. Caribou in both the Tweedsmuir-Entiako area and the Itcha-Ilgachuz-

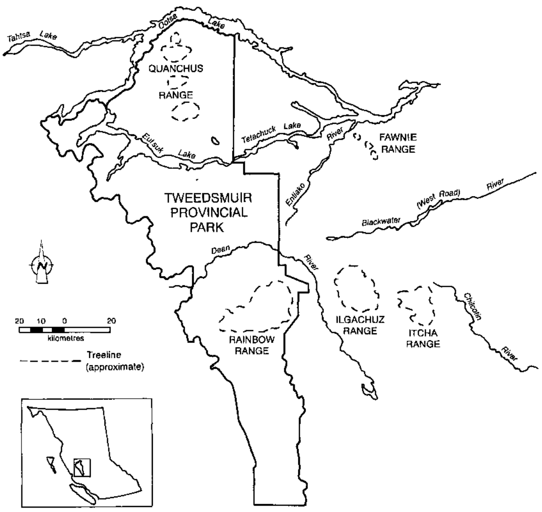

Fig. 1. Location of the study area in west-central British Columbia.

Rainbow area were radio-collared between 1983 and 1985 and basic information on habitat use, seasonal movements and population dynamics was collected (Marshall, 1983, 1984, 1985, 1986; Smith & Hebert, 1986). Because issues and study objectives were similar for both winter ranges, the two projects were combined in 1985 and expanded to include more intensive investigations of winter ecology and population parameters of the caribou. The winter field investigations were conducted for 3 years (Cichowski, 1989), and winter habitat maps were developed for both winter ranges (British Columbia Ministry of Forests, 1987a, 1987b). A winter range management strategy was then developed for the Tweedsmuir-Entiako caribou winter range based on the winter habitat map and the results from the winter ecology study (Cichowski & Banner, 1993). A similar process was also used to summarize caribou winter range characteristics and to develop 5 proposed scenarios for management of the Itcha-Ilgachuz-Rainbow caribou winter range. Winter range management planning for both areas is currently being conducted through public land management planning processes.

The availability of both a caribou winter habitat map and a study on caribou winter habitat requirements was a key factor in developing a management strategy for caribou winter range in west-central British Columbia. Because the ecology and issues of both herds were similar and the winter range management strategy was initially developed for the Tweedsmuir-Entiako herd, this paper summarizes the evolution of the current state of management for the Tweedsmuir-Entiako winter range, and includes:

1. the initial caribou winter range study
2. the caribou winter ecology study and winter habitat mapping
3. the winter range management strategy and options; and
4. land use planning processes and winter range management.

Study area

The Tweedsmuir-Entiako caribou winter range is located in west-central British Columbia, 200 km south of Smithers (Fig. 1). Most of the winter range lies between 850 and 1300 m on the Nechako Plateau and is characterized by flat or gently rolling terrain (Holland, 1976). The round-topped Fawnie Mountains in the eastern portion of the study area rise up from the Nechako Plateau to 1920 m. Most of the study area is included within the moist cold subzone of the Sub-Boreal Pine-Spruce (SBPSmc) Biogeoclimatic Zone (Pojar *et al.*, 1988). A dry, cool subzone of the Sub-Boreal Spruce Zone (SBSdk) occurs in the northern portion of the study area and the Engelmann Spruce-Subalpine Fir Zone (ESSF) occurs above 1200 m in the Fawnie Mountains, below the Alpine Tundra Zone (AT). Only the SBPS and SBS zones were mapped because they encompass most of the forested terrestrial lichen caribou winter habitat.

Low elevation forests consist mostly of lodgepole pine (*Pinus contorta*) or mixed lodgepole pine/white spruce (*Picea glauca*) stands. Spruce stands occur primarily on wetter seepage sites and as bands along lake shorelines and wetlands. Black spruce (*Picea mariana*) is generally restricted to forested wetlands, as well as to cooler north and east facing upland sites. Subalpine fir (*Abies lasiocarpa*) occurs only at higher elevations in the eastern and (though rarely) northern-most part of the study area. Deciduous stands of trembling aspen (*Populus tremuloides*) are not extensive except in the northern portion of the study area. Lakes and sedge fens are common and often occur in mosaics of lakes, fens, and fringe forests of spruce.

Most of the pine and pine/spruce stands that dominate the study area have poorly developed shrub and herb layers. Common understory vascular plant species are *Shepherdia canadensis, Spiraea betulifolia, Rosa acicularis, Arctostaphylos uva-ursi, Linnaea borealis, Cornus canadensis,* and *Vaccinium caespitosum.* Drier stands on coarser textured tills and glaciofluvial sands and gravels typically have from 30 to 50% cover of ground lichens (mainly *Cladina* and *Cladonia* spp. and *Stereocaulon* spp.). Arboreal lichens (primarily *Bryoria* spp.) occur throughout the forested habitats, but are especially abundant in forested wetlands and spruce fringes surrounding lakes and fens.

The study area lies within the rainshadow of the Coast Mountains and is characterized by a dry continental climate. Summers are typically cool, short, and dry, and winters are very cold, long and dry. Soils throughout the winter range are predominantly Brunisolic Gray Luvisols and Dystric Brunisols on morainal and glaciofluvial deposits (Lewis *et al.*, 1986; B.C. Ministry of Forests, 1987b).

Fire is an integral part of the vegetation landscape in west-central British Columbia. Fire interval for the SBS and SBPS averages 100 to 175 years and fire size averages 50 to 500 ha (Parminter, 1992).

During winter, moose (*Alces alces*) and wolves (*Canis lupus*) also occupy the caribou winter range, however, no data are available on populations densities of those species.

Initial caribou winter range study (1982-1985)

Concern over the Tweedsmuir-Entiako caribou winter range began in the late 1970's when logging was first proposed for the area. Although specific winter ranges had not yet been identified, incidental observations of caribou suggested that caribou wintering areas occurred outside of Tweedsmuir Park, with the Entiako area identified as a major wintering area (Hatter, 1979). Historically, caribou wintered north of the Ootsa Lake area, but the flooding of the Ootsa Lake complex by the Kenny Dam in the early 1950's, likely contributed to the abandonment of those winter ranges (Hatter, 1979), thus increasing the significance of the winter ranges east of Tweedsmuir Park.

In November 1983, the BC Wildlife Branch, with cooperation from the Tweedsmuir Rod and Gun Club, captured and radio-collared 13 caribou as they moved south across Tetachuck Lake during fall migration (Marshall, 1983). An additional 6 caribou were collared in November 1984 (Marshall, 1984). The BC Wildlife Branch began locating radio-collared caribou on a monthly basis to determine general seasonal movements and habitat use (Marshall, 1984, 1985, 1986).

During summer, caribou were found in northern Tweedsmuir Park in a variety of habitats. In November, caribou migrated out of Tweedsmuir Park and south across Tetachuck Lake to low elevation forests on the Nechako Plateau. During winter, caribou used primarily mature pine forests at low elevations in the Entiako and Laidman lakes area.

Caribou winter ecology study and winter habitat mapping (1985-1988)

In April 1985, the West-central B.C. Caribou Research Project was initiated to investigate the potential effects of logging on caribou (Cichowski, 1989). The focus of the study was to determine habitat use and foraging strategies.

Radio-collared caribou were located on a weekly basis from December to March to monitor winter habitat use and movements and to identify areas for ground investigations of feeding sites. Results indicated that caribou were selecting mature pine forests on low productivity sites, and were feeding primarily on terrestrial lichens. Selection of feeding sites within forested areas depended primarily on lichen presence and abundance; snow characteristics were less important. Arboreal lichens were used to a lesser extent than terrestrial lichens, and were most heavily used where arboreal lichens were abundant (trees in forested wetlands and on the margins of wetlands and lakes).

From this initial information, a winter range habitat map was developed for the study area (1: 50 000 scale) based on terrestrial lichen abundance (BC Ministry of Forests, 1987a). Seven site units were described: Dry Lichen, Lichen Moss, Moss, Seepage Forest, Aspen Forb, and Forested and Nonforested Wetlands. Dry Lichen sites contain the greatest abundance of terrestrial lichens followed by Lichen Moss sites. Moss, Seepage Forest, Aspen Forb and Wetland sites generally contain few or no terrestrial lichens. Because terrestrial lichens are poor competitors against vascular plants (Kershaw, 1977; Hale, 1983; Rowe, 1984), terrestrial lichen abundance was closely associated with site productivity. Dry Lichen and Lichen Moss sites are less productive than Moss, Seepage Forest and Aspen Forest sites (Cichowski & Banner, 1993). Lichens are also very slow growing (Ahti, 1977; Johnson, 1981) and are most abundant late in succession. In the Tweedsmuir-Entiako winter range, *Cladina* spp. only start becoming abundant in stands of 50 years and greater.

Because of the scale of mapping, each map polygon contained several site units resulting in a large number of polygons with unique combinations of site units. To facilitate use of the map, polygons were aggregated into Caribou Habitat Types based on site unit combinations. The resulting Caribou Habitat Types, in descending order of terrestrial lichen abundance, were:

- Dry Lichen / Lichen Moss (DLLM)
- Lichen Moss (LM)
- Dry Lichen / Lichen Moss Ecomosaic (DLLM MOSAIC)
- Moss - Dry Lichen / Lichen Moss (MDLLM)
- Moss / Seepage Forest - Aspen Forb (MSF/AF)
- Wetlands / Moss - Seepage Forest Wetlands (W/FW)

The Dry Lichen / Lichen Moss Ecomosaic consisted of polygons which contained a Dry Lichen or Lichen Moss unit associated with a Wetland, Forested Wetland or Seepage Forest unit. These polygons contained a combination of both abundant terrestrial lichens (Dry Lichen and Lichen Moss units) and abundant arboreal lichens (Wetlands, Forested Wetlands, and Seepage Forest units).

Radio-collared caribou locations were then used to verify the predictive capability of the caribou winter habitat map. Locations were plotted onto the map and frequency of use of each Caribou Habitat Type, and the availability of each Caribou Habitat Type were determined and compared. The analysis indicated that caribou primarily used mature DLLM and LM Caribou Habitat Types and use of those habitats exceeded their availability (Cichowski, 1989). Consequently, the winter range habitat map was determined to be a good predictor of caribou habitat value.

Information was also collected on population status of the Tweedsmuir-Entiako caribou. Low calf recruitment and high adult mortality suggested that the population was declining (Cichowski, unpubl. data). Wolf and bear predation was documented, mostly during summer months, however, the population limiting factor has not yet been determined (Cichowski, unpubl. data). Because of the declining population trend, it was necessary for the winter range management strategy to address the potential impacts of forest harvesting on the caribou population as well as on caribou habitat.

Winter range management strategy and options

Potential Impacts

With the completion of the caribou winter ecology study and the caribou winter range habitat map, enough information was available to identify important habitats for winter range management purposes. Because terrestrial lichens are highly susceptible to mechanical damage, and regeneration could take 50-100 years (Hale, 1983; Rowe, 1984), a conservative approach is necessary to ensure an adequate winter food supply for the caribou. However, because terrestrial lichens are most abundant where competition from vascular plants is low (ie. where site productivity is low), the best caribou habitat (DLLM) occurs on poor growing sites for timber. Potential conflicts with forest harvesting will occur mostly on LM habitat types where caribou winter habitat value is high and growing potential for timber is adequate.

Identifying and managing for important caribou habitat only considers the potential direct effects of logging on caribou (i.e. reduction of the winter food source). However, potential indirect impacts of logging on caribou may also significantly affect the caribou herd. Potential indirect impacts of logging include increased human disturbance, hunting and poaching as a result of improved access, and altered predator-prey relationships.

Altering the mosaic of forested stand areas and ages may favour habitat for other ungulate species such as moose. Currently, the landscape is dominated by large scale disturbance patterns. Extensive stands of even-aged lodgepole pine have been shaped in the past by stand destroying fires. A logging scenario consisting of small clearcuts with lots of edge habitat, may be more favourable to moose than to caribou. An increase in the number of moose may result in an increased number of wolves which in turn could result in increased predation pressure on the caribou population (Bergerud *et al.*, 1984; Racey *et al.*, 1991). Wolf predation has been implicated as the major limiting factor of woodland caribou populations in Alaska, the Yukon, western Alberta and southeastern British Columbia (Gasaway *et al.*, 1983; Farnell & MacDonald, 1987; Edmonds, 1988; Seip, 1992). In southeastern British Columbia, predation pressure on caribou was lower in Wells Gray Park where caribou were spatially separated from moose, than in the Quesnel Highlands, where less spatial separation existed (Seip, 1992).

One anti-predator strategy of caribou is to space out over large areas and to exist at low densities so that it is harder for predators to find them (Bergerud *et al.*, 1984; Bergerud & Page, 1987). If the available mature forested habitat for caribou is reduced, their density within that habitat will increase which could result in increased predator efficiency. Predator efficiency may also be improved if ploughed roads or snowmobile tracks provide easier travel routes for wolves (Edmonds & Bloomfield, 1984).

Therefore, both potential direct and indirect effects of logging on caribou were considered while developing a management strategy for the Tweedsmuir-Entiako caribou winter range.

Management Strategy

To consider both potential direct and indirect impacts in the Tweedsmuir-Entiako Caribou Winter Range Management Strategy, a two level management approach was developed (Cichowski & Banner, 1983). At the landscape level, the winter range was divided into Caribou Management Zones based on caribou habitat value and use. At the site specific level, both caribou habitat and timber values were considered. The advantage of the dual level approach was that site specific management strategies could vary between zones, depending on the zone's significance to the caribou population and winter range.

Thirteen Caribou Management Zones were delineated based on areas of similar caribou habitat value, consistent use by radio-collared caribou, and special considerations such as travel corridors and late winter ranges (Fig. 2, Table 1). Caribou habitat value was visually determined from the winter habitat map, which was colour-themed by Caribou Habitat Type. Each zone was rated as low, medium or high value caribou winter range. Zone 4 was delineated as the core of the winter range and was considered the most important zone in terms of winter range value.

For the site specific level, the PAMAP Geographic Information System (PAMAP Graphics Ltd., 1989) was used to overlay the Caribou Habitat Type map with the Ministry of Forests forest cover map. The resulting map was colour-themed based on a combination of caribou habitat and timber value. The colour-themed map could then be used to determine which stands had the lowest potential

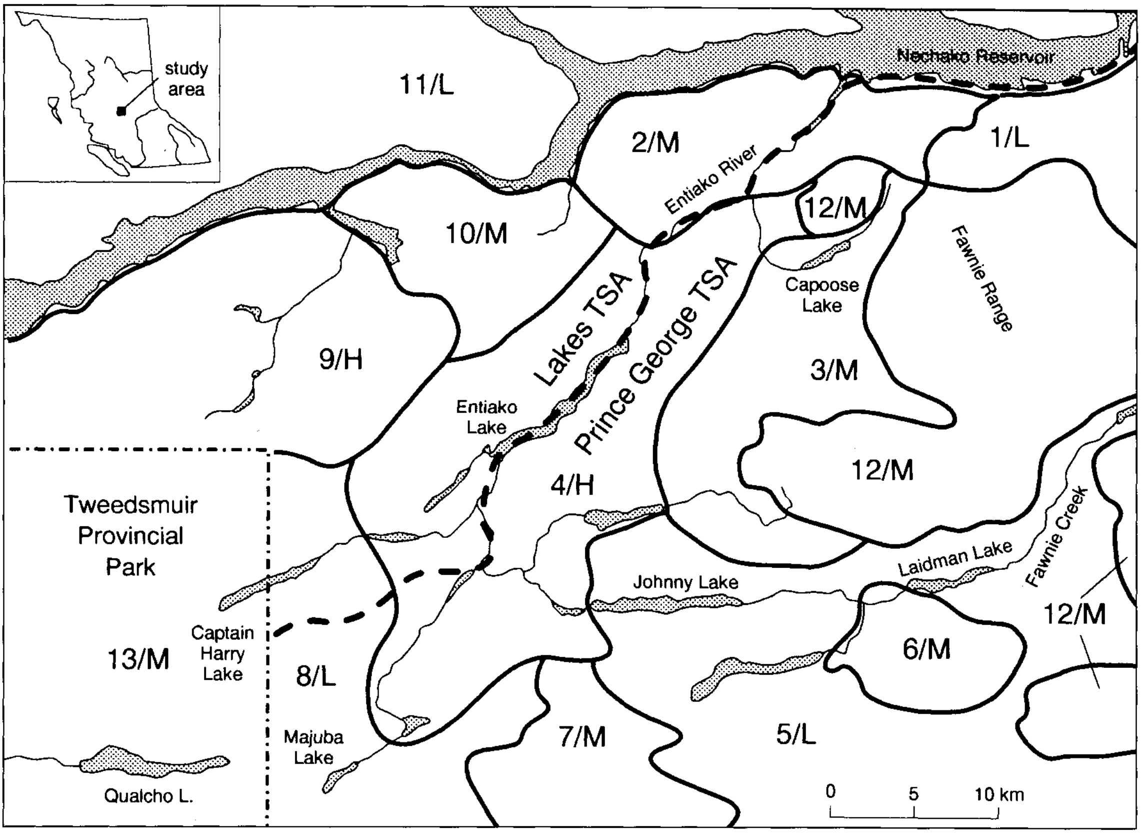

Fig. 2. Location of 13 Caribou Management Zones (solid lines) in the Tweedsmuir-Entiako caribou winter range. Caribou winter habitat value is indicated by H - high, M - medium, and L - low. Timber Supply Area boundary is indicated by a dashed line.

Table 1. Summary of Caribou Management Zones (CMZs) of the Tweedsmuir-Entiako caribou winter range.

CMZ	Area (ha)	Percent of study area	Caribou winter habitat value	Special values
1	8 412	2.5	low	
2	14 329	4.2	moderate	-late winter range
3	12 475	3.7	moderate	-migration corridor
4	43 982	13.0	high	-core winter range, migration corridor
5	45 452	13.5	low	
6	5 467	1.6	moderate	
7	9 969	3.0	moderate	
8	18 697	5.5	low	-adjacent to Tweedsmuir Park
9	28 310	8.4	high	-early winter/late winter range
10	11 300	3.4	moderate	-late winter/early spring range
11	59 786	17.7	low	-spring migration route
12	43 801	13.0	moderate	-not mapped; alpine and high elevation forests; mid-winter range; may be important during deep or extreme crusty snow years
13	35 554	10.5	moderate	-Tweedsmuir Park; early winter range

Total area = 337 534 ha

for conflicts between caribou habitat and timber values (i.e. high caribou habitat value on low value timber stands, high value timber stands on low value caribou habitat).

Options

With the two level management approach, a timber harvesting strategy could be developed for the winter range which considers both direct and indirect impacts on caribou. At the landscape level, a harvesting strategy could be prescribed for each Caribou Management Zone based on its unique characteristics. Site specific management is achieved by restricting timber harvesting to specific Caribou Habitat Types or site units.

Table 2. Management options for the Tweedsmuir-Entiako caribou winter range.

1. No harvesting.
2. No harvesting in CMZ[1] 2, 4, 9, 10.
   - Other moderate value zones: harvest in MSF/AF[2], MDLLM[3], ESSF[4]
   - Low value zones: harvest in MSF/AF, MDLLM, ESSF
3. No harvesting in CMZ 4, 9.
   - Moderate value zones: harvest in MSF/AF, MDLLM, ESSF
   - Low value zones: harvest in MSF/AF, MDLLM, ESSF
4. No harvesting in CMZ 4.
   - Other high value zones (CMZ 9): harvest in MSF/AF, ESSF
   - Moderate value zones: harvest in MSF/AF, MDLLM, ESSF
   - Low value zones: harvest in MSF/AF, MDLLM, ESSF
5. Restricted harvesting.
   - High value zones: harvest in MSF/AF, ESSF
   - Moderate value zones: harvest in MSF/AF, MDLLM ESSF
   - Low value zones: harvest in all habitat types
6. Restricted harvesting.
   - All zones: harvest in MSF/AF, MDLLM, ESSF

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[1] Caribou Management Zone.

[2] Moss/Seepage Forest - Aspen Forest Caribou Habitat Type.

[3] Moss - Dry Lichen/Lichen Moss Caribou Habitat Type.

[4] Engelmann Spruce-Subalpine Fir Biogeoclimatic Zone.

For the Tweedsmuir-Entiako area, to best mimic historic fire disturbance patterns that caribou evolved with, partial retention timber harvesting was recommended. Opening sizes of 200 to 300 ha were suggested with islands of trees within the openings and stringers of trees along wetlands and creeks.

Six management options were proposed which varied from total protection of the winter range in Option 1 to a moderate level of harvesting throughout the winter range (Table 2). Options 1 to 4 varied by the number of Caribou Management Zones from which harvesting was restricted. All had the common element of protection of Zone 4, the core of the winter range. Protection of the core of the winter range was considered a minimum requirement for caribou management. Options 5 and 6 allowed harvesting in all zones and varied in the intensity of harvesting within several Caribou Management Zones. In option 6, the Caribou Management Zone classification system was ignored; the same harvesting strategy was applied to all zones, although high quality caribou habitat was protected in all zones.

The impacts of each option on the caribou population and on the timber supply were evaluated and compared. Although absolute impacts on caribou could not be determined, each successive option allows harvesting in an increasing number of zones and will likely result in progressively increasing impacts on the caribou. The impact of each option on the timber supply was evaluated using the forest inventory database associated with the forest cover map, which was overlaid onto the caribou habitat map. The Tweedsmuir-Entiako caribou winter range encompasses portions of two Timber Supply Areas (TSAs), the Lakes TSA and the Prince George TSA (Fig. 2). Because timber supply calculations differed between the two TSAs, the impacts on the timber supply had to be evaluated separately. To simplify the analysis, it was assumed that clearcut harvesting would occur within the Caribou Habitat Types where harvesting was permitted.

The impacts generally decreased for both Timber Supply Areas from option 1 to option 6 (Table 3). The most significant change in impact occurred between options 1 and 2 for the Prince George Timber Supply Area and between options 2 and 3 for the Lakes Timber Supply Area, since the Lakes Timber Supply Area contained most of the high and moderate value Caribou Management Zones (Fig. 2). The impacts of Option 6 on the timber supply were similar to those of options 3, 4 and 5 in the Prince George TSA and options 4 and 5 in the Lakes TSA. Although the impacts to the timber supply were similar for those options, the implications to the caribou population differ significantly. Because Options 3 and 4 offer some degree

Table 3. Relative effects of management options (as a percentage of Option 1 [no harvesting]) for the Tweedsmuir-Entiako caribou winter range on the harvestable forest land base of the Prince George and Lakes Timber Supply Areas.

	PRINCE GEORGE TSA Reduction to harvestable land base		LAKES TSA Reduction to harvestable land base	
Options	%	ha	%	ha
1	100.0	81 856	100.0	39 412
2	38.5	31 477	97.9	38 587
3	36.7	30 064	69.1	27 246
4	36.7	30 064	60.6	23 890
5	28.4	23 254	60.3	23 763
6	33.2	27 180	54.1	21 311

of protection to the winter range, they will have fewer impacts on the caribou population than Option 6 which ignores the zonation scheme. Option 2 was recommended as the best option for caribou given some level of harvesting in the caribou winter range (Cichowski & Banner, 1993).

Because some harvesting was proposed, additional recommendations included prohibiting access to the winter range on forest access roads, monitoring caribou movements and habitat use in relation to first pass forest harvesting, developing a fire management plan for that portion of the winter range that will be protected, and conducting research on harvesting techniques that would mimic disturbance to terrestrial lichens and that would accelerate regeneration of terrestrial lichens after forest harvesting.

Although six options were assessed in the Tweedsmuir-Entiako winter range management strategy and options report, an infinite number of options were possible. The purpose of the Tweedsmuir-Entiako winter range management strategy was to develop a framework from which a management plan could be developed. Through the management planning process, existing options could be modified or new ones developed.

Land use planning processes and caribou winter range management

In British Columbia, although BC Environment sets objectives for wildlife population and habitat management, the BC Forest Service is responsible for forest land planning with cooperation from other agencies such as BC Environment and BC Parks, as well as involvement by the public. Currently, Land and Resource Management Plans (LRMPs) are being developed to guide harvesting strategies in each Forest District. In areas within a Forest District where specific issues need to be addressed, a Local Resource Use Plan (LRUP) is developed. A provincial land use strategy is also being developed for the province, spearheaded by the Commission on Resources and the Environment (CORE). A major part of that land use strategy is the Protected Areas Strategy which is currently considering areas of interest for future protection.

The Entiako LRUP was initiated in August 1992 to address caribou winter range requirements and other issues in the Entiako area (Entiako Local Resource Use Plan Working Group, 1993). Participants ranged from interested individuals to forest industry representatives. Some timber harvesting had already occurred in the southeastern part of the winter range and new logging had been approved but redirected to lower value CMZs. As part of the LRUP planning process, results from the caribou study and the winter range management strategy and options were presented to the group. That information was considered and several new management options were developed. Most of those options proposed protection of some portion of the caribou winter range and were subsequently forwarded to the Protected Areas Strategy for consideration for protected area status.

The Protected Areas Strategy is currently evaluating the Entiako area as a candidate for an area of interest for protection. Pending that outcome, the Entiako LRUP planning group will reconvene to develop a plan for that part of the winter range not proposed for protection or recommend that the issue be addressed by the new Land and Resource Management Planning groups in both Forest Districts. The planning group will address issues such as access management and forest harvesting techniques. For that part of the winter range that will be protected, a fire management plan will be developed to accommodate protection and regeneration of caribou winter habitat.

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Issues of Caribou Management in Northeastern British Columbia

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Abstract: Woodland caribou inhabit most of Northeastern British Columbia. They live across a variety of climatic and geographic gradients and in areas with as many as seven other ungulate species and seven predatory species. This apparent variability in habitat use may suggest that caribou in the Northeast are wide ranging and ecologically plastic. Conversely, caribou in Northeastern B.C. may live in discrete groups that have adapted to local conditions. There are few published data of woodland caribou in Northeastern B.C. Information is lacking on the number of caribou, their seasonal movements, their habitat requirements, and their interactions with other species. Logging, seismic activity, pipeline construction, oil and natural gas drilling, hydro-electric dams, and prescribed burning have all impacted habitat in previously undeveloped areas. The manner and rate at which these activities are changing habitats far exceeds our growth in knowledge of caribou ecology. Given this combination of few data and rapid habitat alteration, resource managers cannot know the impact of these habitat changes. We believe that this jeopardises the conservation of viable caribou populations.

Rangifer, Special Issue No. 9, 127-130

Introduction

This paper discusses management issues relating to woodland caribou (*Rangifer tarandus caribou*) in Northeastern B.C. We define a "group" as a geographically distinct association of caribou with limited genetic exchange with other groups. We use "population" to refer to the collection of all caribou in Northeastern B.C.

The first section, *Northeastern B.C.*, is an overview of the area and its physiographic and forest variability. Next, we discuss some of the distinct habitat features of the Northeast. *Caribou in Northeastern B.C.* presents caribou numbers and potential herd distributions and discusses some of factors that influence their ecology. Finally, we consider the *Issues of Caribou and Resource Management.*

Northeastern British Columbia

We refer to Northeastern B.C. as that area of B.C. drained by the Liard and Peace Rivers (including those rivers collected by Williston Lake). This area represents approximately 25% of the Provincial land-base, has approximately 25% of the ecoregions (10 of 43), and 25% of the ecosections (26 of 110) described for the Province (Demarchi, 1993). These figures indicate the high physiographic variation in Northeastern B.C. For example, peaks in the Rocky Mountains are at 2900 m, and the Alberta Plateau is at 350 m.

Meidinger & Pojar (1991) describe five biogeoclimatic zones for the Northeast: Boreal White and Black Spruce (BWBS), Spruce-Willow-Birch (SWB), Engelmann Spruce-Subalpine Fir (ESSF), Sub-Boreal Spruce (SBS), and Alpine Tundra (AT).

Predominant tree species in the BWBS are white spruce (*Picea glauca*), black spruce (*Picea mariana*), trembling aspen (*Populous tremuloides*), or lodgepole pine (*Pinus contorta*) depending on site conditions. Wide, meandering rivers are a prominent feature of the BWBS landscape. The alluvial habitats along these rivers are often 75 m lower than the surrounding uplands creating a separation of "alluvial" and "upland" forest systems. White spruce and balsam poplar (*Populous balsamifera balsamifera*) predominate the nutrient rich alluvial sites, and trembling aspen, pine, white spruce, and black spruce form mixed forests on the uplands.

In the north, there is a transition from the BWBS in the valleys to the SWB upslope. The SWB is characterised by open white spruce, lodgepole pine, subalpine fir (*Abies lasiocarpa*) forests with large areas of willow (*Salix* spp.) and scrub birch (*Betula glandulosa*) (Meidinger & Pojar, 1991). The

SWB has a history of extensive burning both by wildfires and by fires prescribed to convert areas of conifers to grasslands.

The ESSF occurs in the south above the BWBS valley bottoms. Lower and mid-elevational forests of Engelmann spruce (*Picea engelmannii*) are more continuous than forests in the SWB (Meidinger & Pojar, 1991). In contrast to the SWB, fire occurs infrequently in the ESSF; hence, the ESSF has older stands which support arboreal lichens - an important winter food for caribou.

A portion of the SBS reaches northward from central B.C. along Williston Lake to adjoin the BWBS. Hybrid white spruce (*P. engelmannii* x *glauca*) and subalpine fir predominate the forests of this zone (Meidinger & Pojar, 1991).

Distinctive Habitats

There are a number of habitats that are distinctive because caribou use them (data from projects listed below) or because these habitats are scarce in the Northeastern and their importance to caribou is not known. Examples of these distinctive habitats include the following:

- large, undeveloped landscape units (>120 000 ha);
- patches of white spruce surrounded by extensive areas of black spruce or mixedwood;
- large, alluvial systems;
- older, coniferous stands with arboreal lichens;
- dry pine sites with terrestrial lichens;
- remote alpine caribou calving areas, and
- wind-blown alpine tundra with terrestrial lichens.

The large, undeveloped landscape units are a particularly noteworthy habitat in Northeastern B.C. Only four landscapes that have timber that is considered "commercially viable" by today's economic standards remain "undeveloped" (Ministry of Forests, 1992). All the other landscapes classified as undeveloped occur in the SWB, are sparsely forested, and have extensive burn patterns from wildfires or from fires prescribed to create grasslands. The undeveloped, forested landscapes provide a valuable opportunity to examine caribou ecology and broader conservation issues relating to landscape ecology, ecosystem function, faunal interactions, and the habitat connectivity.

Caribou in Northeastern B.C.

Child (1987) commented about caribou in the Northeast that "status unfortunately cannot be accurately described, as inventory generally is largely lacking for most [caribou] groups and too infrequent on some to establish reliable trends." With this limited information, he estimated that there were 4700 caribou in Northeastern B.C. and presented population trends for the three administrative units used by B.C. Environment:

Northeast Peace	-decreasing
South Peace	-increasing
Omineca	-stable

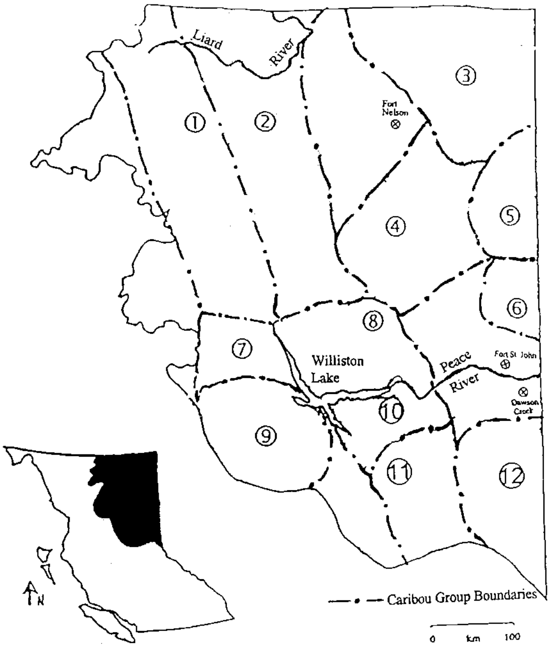

Fig. 1. Caribou Groups in Northeastern British Columbia. Group bondaries are estimated from radio-collar data and from field reports of caribou movment.

Four radio-collaring projects have gathered information about caribou groups in specific areas. In 1988, 10 collars were placed on caribou in the Graham River area (Group 8, Fig. 1), and in the following year, 10 caribou were collared in the Tumbler Ridge area (Group 12, Fig. 1). Twenty caribou in the Sikanni Chief and Profit River drainages were collared in the winter of 1990-91 (Group 4, Fig. 1). The fourth project began during the winter of 1990/1991 under the Peace-Williston Fish and Wildlife Compensation Program. Twenty-nine caribou in the Omineca Mountains were collared (Group 7 and Group 9, Fig. 1).

Movement patterns of Northeast caribou appear to be variable. The three classes of movement patterns described by Terry (1992) for caribou in east-central B.C. apply in the Northeast: migrators, non-migrators, and wanderers. Progress reports (B.C. Environment, unpubl.; Williston Wildlife Compensation Program, unpubl.) and information from people involved with the projects (R. Backmeyer, pers. comm.) suggest that there may be as many as 12 caribou groups in Northeastern B.C. (Fig. 1). The bounding of these 12 groups is subjective and should be tested with an expanded radio-collaring program.

Knowing which groups are distinct and how the caribou move throughout the Northeast has implications for resource management. For example, if the estimate of 12 groups is accurate, all caribou habitat requirements should be maintained in each of the 12 areas. If, on the other hand, there are fewer groups and caribou make long movements among areas, management should maintain connectivity and habitat on a broader scale.

An understanding of the ecology of different caribou groups also is important for management. Stevenson (1990) describes two ecotypes of woodland caribou in B.C.: Northern and Mountain. The Northern ecotype lives where snowfall is low and winter either in mature lodgepole pine and lodgepole pine/black spruce/white spruce forests or on wind-blown slopes in the alpine. In the winter, these caribou crater for terrestrial lichens. The Mountain ecotype occurs where snowfall is high and feeds primarily on arboreal lichens in the ESSF (Stevenson, 1990).

The Northeast may have both ecotypes. Some caribou groups winter on high elevation ESSF and alpine ranges while others use lower elevation lodgepole pine and lodgepole pine/black spruce/white spruce forests (B.C. Environment, unpubl.; Peace/Williston Compensation Program, unpubl.). Northeast caribou feed on arboreal lichens, terrestrial lichens, or a combination of both. The implications for management with the different ecotypes are discussed by Stevenson (1990).

Interactions with other species also are part of caribou ecology. In some areas of the Northeast, caribou live with 7 ungulate species and 7 predatory species. Competition or predation undoubtedly are important, but it is not clear as to their role as regulating or limiting factors in caribou populations (see Boutin, 1992). Unlike other areas of B.C., moose have long been present in the Northeast (Hatter, 1950 in Bergerud & Elliot, 1986). This is in contrast to other areas of the Province where wolf predation associated with changing moose populations is suggested as a limiting factor on caribou (Bergerud & Elliot, 1986). Regardless of the specific interaction between caribou and other species, the reduction of habitat and the increase in human access intensify those interspecific interactions by concentrating species in smaller areas or by increasing predator's search efficiencies.

Issues of Caribou and Resource Management

There are many resource-based industries in Northeastern B.C. that impact caribou habitat: forestry, oil and gas, pipeline and utility corridor construction, agriculture, mining, and hydro-electric. There have also been management activities that affect caribou populations such as access development, prescribed burning and wolf removal. Current concerns of caribou management focus on logging, access development, seismic activity, and pipeline construction because of the rapid and continual expansion of these operations across the land-base.

Caribou populations are at risk of decline in Northeast B.C. because the rate of habitat change is greater than the rate at which managers are gaining knowledge about caribou. This means that managers have insufficient local information upon which to base resource decisions. The aim of the four radio-collaring projects has been to get data on caribou seasonal movements and habitat use. Project sites were chosen because of previous or pending habitat losses from hydro-electric dams, logging, mining, or oil and gas development. However, poor funding limited the scope of most projects.

Clearly, if viable populations of caribou (and other fauna) are to be conserved, resource managers must improve their knowledge of local ecology. This should be done with a combination of monitoring projects to track population numbers and distributions and research that investigates the impacts of human activities on caribou ecology.

Research is part of the solution for improved caribou management. Another part should come from the implementation of innovative and adaptive resource management strategies. Adaptive management means that a variety of management strategies are employed as part of industrial operations. The aim is to learn how disturbances, such as resource extraction, affect ecological systems by setting defined, measurable goals, trying different management actions and monitoring the outcomes (Peterman, 1979). The types of disturbances are varied to observe changes in the results. For example with logging, of all the silvicultural systems available, clear-cutting has been used extensively. On appropriate sites, other silvicultural systems should be used to increase the variability of management actions on the land-base. As the results are monitored, practices are adapted to achieve management objectives. This is done to provide greater options in the future by mitigating against the possible negative consequences of having nothing but clear-cuts and even-aged plantations.

Conclusion

The issues of caribou management in Northeastern B.C. are similar to management concerns in other jurisdictions; however, advancements in the understanding of Northeastern B.C.'s ecosystems are not keeping pace with the rate of industrial development. A combination of approaches is required that includes scientific studies and innovative, adaptive resource management.

Government agencies, industry, and other interested parties should be working to understand and manage the habitat for woodland caribou (and other flora and fauna) rather than hoping the species will adapt to the changes because of some inherent ecological plasticity.

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Brief communication

Introduction to the Mountain Caribou in Managed Forests Program

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The following group of papers focusses on the woodland caribou (*Rangifer tarandus caribou*) of southeastern and east-central British Columbia. These animals, often known as "mountain caribou", inhabit mountainous terrain in which the winter snowpack is commonly 2 or 3 meters deep. Terrestrial forage lichens are absent from most habitat types. Shrubs are used by caribou in early winter, but are usually buried under the snowpack by midwinter. During most of the winter, mountain caribou feed on arboreal lichens. Arboreal forage lichens are abundant only in late-successional stands. Thus, the problems of integrating caribou habitat management and forest harvesting differ from those in the boreal forest, where good terrestrial forage production often occurs earlier in forest succession. In the range of mountain caribou, as in other areas, forestry activities also have the potential to increase disturbance and human-induced mortality, and to alter predator-prey relationships.

The Mountain Caribou in Managed Forests (MCMF) program was begun in 1988 by the Ministry of Environment in Prince George to address the question: *Can forest stands be managed, through silvicultural systems and habitat enhancement techniques, to sustain both timber harvest and mountain caribou habitat over the long term?* An interagency Technical Working Group, based in Prince George, oversaw caribou studies (described by Terry *et al.*, this issue.) and habitat management trials (described by Armleder & Stevenson, this issue.) aimed at developing stand-level strategies that would be applicable throughout the range of mountain caribou. That work has resulted in preliminary recommendations (Stevenson *et al.*, 1994).

By 1990, the need to address issues of landscape-level habitat management for caribou at a provincial level had become apparent. A provincial MCMF Committee was formed to develop consistent habitat management strategies for caribou. That group, described below by McKinnon, oversaw the work reported by Simpson *et al.*

The MCMF program has been supported by many funders and participants. Major participants that have provided continuity throughout the program are B.C. Ministry of Environment, Lands and Parks, B.C. Ministry of Forests, and Wildlife Habitat Canada. As well, specific subprojects have been funded by the B.C. Habitat Conservation Fund, Canada-B.C. Forest Resources Development Agreement, Canada-B.C. Partnership Agreement on Forest Resource Development, Mica Wildlife Compensation Program, Revelstoke Reservoir Compensation Program, and several forest companies.

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Early Winter Habitat Use by Mountain Caribou in the North Cariboo and Columbia Mountains, British Columbia.

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Abstract: Winter habitat use was compared between two mountain caribou (*Rangifer tarandus caribou)* populations in British Columbia. Regional differences were apparent during November and December. Radio-collared caribou inhabiting the gentle plateaus of the northern Cariboo Mountains, near Prince George, B.C. primarily used mid-elevation balsam-spruce stands on moderate slopes (<30%). In contrast, radio-collared caribou in the North Columbia Mountains, near Revelstoke, B.C. used low elevation hemlock-cedar stands and relatively steeper slopes (>30%). To adequately address habitat requirements of caribou, forest management plans should incorporate varying regional and seasonal habitat use patterns. Hypotheses on observed differences in habitat use are discussed.

Key words: *Rangifer,* winter habitat, forest management

Rangifer, Special Issue No. 9, 133-140

Introduction

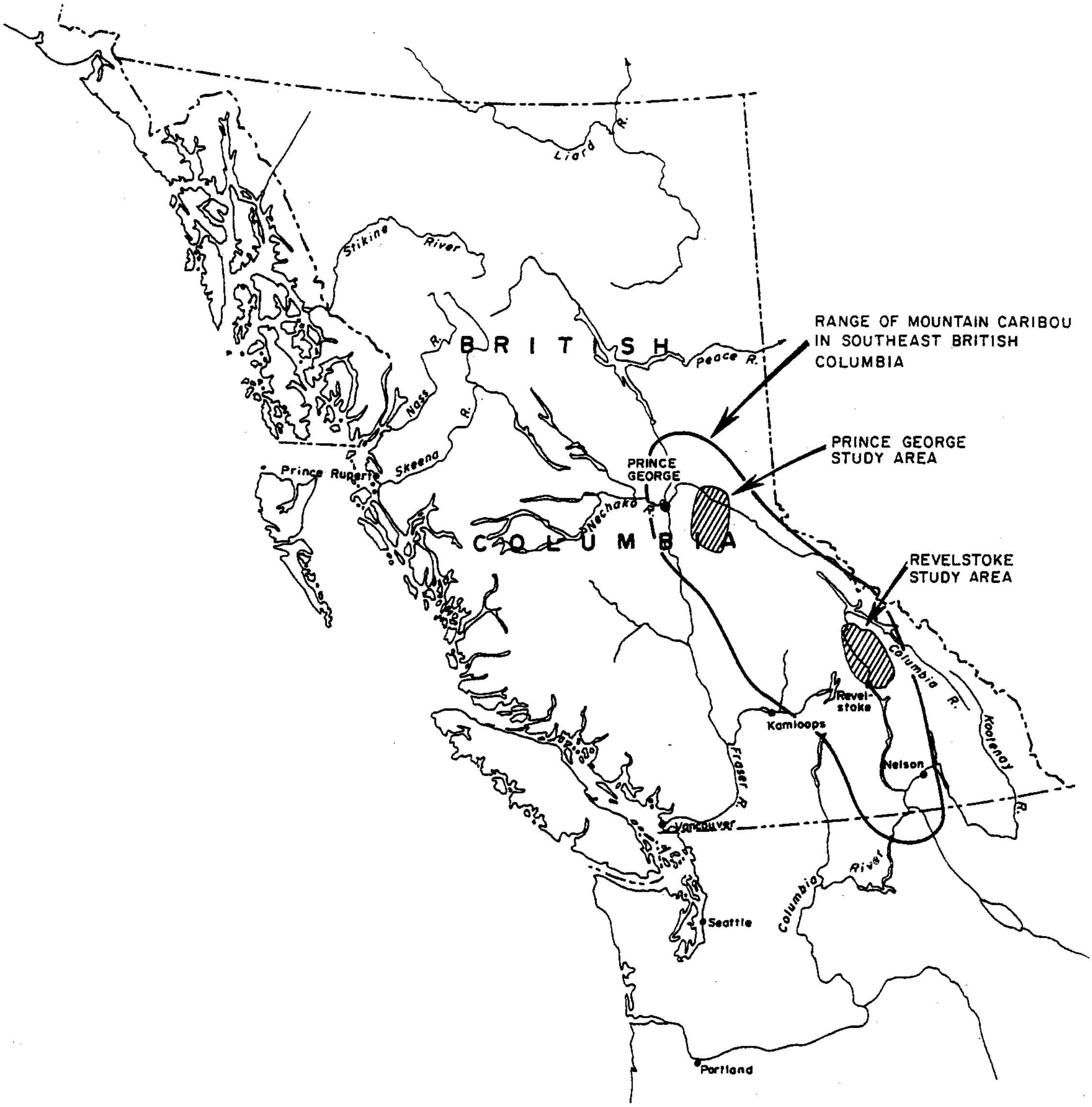
Woodland caribou (*Rangifer tarandus caribou*) that feed on arboreal lichens in winter have been identified as an old-growth dependent species (Ministry of Environment B.C., 1989). Because arboreal lichens (*Bryoria* spp. and *Alectoria sarmentosa*) are used by caribou as winter forage and are most abundant on mature trees, clear-cut harvesting of mature high-elevation forests has been perceived as incompatible with maintaining winter habitat and caribou populations (Stevenson & Hatler, 1985). The early winter period (Nov-Dec) may be a particularly critical period because of low forage availability. During these months the majority of arboreal lichens accessible to caribou are found on windfallen trees and as litterfall (Simpson & Woods, 1987; Rominger & Oldemeyer, 1989). During early winter, caribou must search for these uncommon lichen sources plus understory vegetation that is not buried by snow. Clear-cut harvesting of mature low-elevation forests that grow on very productive sites may also be incompatible with maintaining winter habitat for caribou because these closed canopy stands provide reduced snow depths and accessible understory vegetation.

In response to forest harvesting conflicts in mountain caribou winter range, radio-telemetry studies have been undertaken to provide forest and wildlife managers with habitat information to help integrate the habitat requirements of caribou into forest management plans. Because forest management strategies should account for regional variation in caribou habitat use patterns, we present data to highlight differences between early winter habitat from two areas with similar biogeoclimatic sequences: (1) North Cariboo Mountains, near Prince George, British Columbia; (2) North Columbia Mountains, near Revelstoke, British Columbia.

Study Area

The Revelstoke core study area is located in the Columbia Mountains (51°N,118°W) and includes the northern portion of the Selkirk Mountains east of the Revelstoke Reservoir and the Monashee Mountains to the west (Fig. 1). Topography is typically rugged with steep sidehills and narrow valleys. Elevations range from 610 m (valley bottom) to 2700 m. Treeline is situated at approximately 1980 m. The lower slopes of the Columbia Mountains are in the wet-cool Interior-Cedar-Hemlock (ICHwk) biogeoclimatic subzone (Ketcheson *et al.*, 1991). These forests form a closed canopy and are dominated by western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja placata*). Douglas fir (*Pseudotsuga menziesii*), western white pine (*Pinus monticola*), and white birch (*Betula papyrifera*) are present on drier sites. Dominant shrubs include falsebox (*Paxistima myrsinites*), black huckleberry (*Vaccinium membranaceum*) and western yew (*Taxus brevicola*). On wetter sites where the trees are larger and canopies more open, devil's club (*Oplopanax horridus*) is dominant with minor amounts of douglas maple (*Acer glabrum*), thimbleberry (*Rubus parviflorus*), and red-osier dogwood (*Cornus stolonifera*) (Ketcheson *et al.*, 1991). Mid slopes of the Columbia Mountains are in the very wet cold Engelmann Spruce-Subalpine Fir (ESSFvc) subzone where closed canopy forests are dominated by engelmann spruce (*Picea engelmanni* x *glauca*) and subalpine-fir (*Abies lasiocarpa*). Mountain hemlock (*Tsuga mertensiana*) can also be found in association with subalpine fir on some sites (Coupe *et al.*, 1991). At higher elevations subalpine fir grows in clumps forming an open canopy subalpine parkland.

The core study area east of Prince George is situated at the very north end of the Cariboo Mountains (53°N,121°W) and is characterized by gentle rolling plateaus. Elevations range between 750 m and 2000 m with treeline at about 1800 m.



RANGE OF MOUNTAIN CARIBOU IN SOUTHEAST BRITISH COLUMBIA

PRINCE GEORGE STUDY AREA

REVELSTOKE STUDY AREA

Fig. 1. Location of study areas: North Cariboo Mountains, Prince George; North Columbia Mountains, Revelstoke, British Columbia.

The lower slopes of the Northern Cariboo Mountains are also in the wet-cool variant of the ICHwk subzone. As in the Columbia Mountains, the ICHwk near Prince George is dominated by western hemlock, western red cedar and spruce. Understory shrubs include black huckleberry and devil's club. Mid slopes of the Cariboo Mountains contain closed canopy wet cool Engelmann Spruce-Subalpine Fir (ESSFwk) forests with *Rhododendron albiflorum* and *Vaccinium* spp. common in the shrub layer. Upper slopes are dominated by a wet cold (ESSFwc) subzone where shrubs are less abundant but support a rich herbaceous layer. At higher elevations subalpine fir also grows in clumps forming an open parkland. High elevation snowpack depths average 1 m during Nov-Dec and reach 2-3 meters by late winter (Mar-Apr) in both study areas.

Methods

Cariboo Mountains, Prince George, B.C.

This analysis was confined to portions of the Yellowhead population(s); specifically, Sugarbowl Mountain, Bearpaw ridge, and a section of the North Haggen winter ranges because these had ICH habitats available to caribou. Twenty radio-collared caribou were located approximately once a month from March 1988 to Feb. 1992 using a fixed wing aircraft. In March 1992, 5 additional adult female caribou were collared in the core study area (Sugarbowl-Raven Lake) and located once a week during the early winter period 1992-93. Variables recorded at each radio location included elevation, aspect, slope, and forest cover type using leading tree species.

North Columbia Mountains, Revelstoke, B.C.

Twenty-two collared caribou were located once a week from March 1992 to February 1993 using a fixed wing aircraft. An additional 14 caribou were collared in March 1993 which provided a total of 36 caribou that were monitored weekly for at least one year. Variables recorded at each radio location were similar in both study areas.

Caribou sinking depth (CSD) and a ski pole penetration (PP) (22 kg force) in the snow were measured in both areas. The following regression equation [CSD=5.3 + .76(PP); r^2=.84; $S_{y.x}$=3.4; n=76] was used to predict mean caribou sinking depths in Revelstoke.

Results and discussion

Use of Elevation bands

Caribou were located in significantly different elevation bands in the two study areas (X^2=213.8; df=8; P<.001). During November and December 52% of 403 telemetry locations in the Columbia Mountains

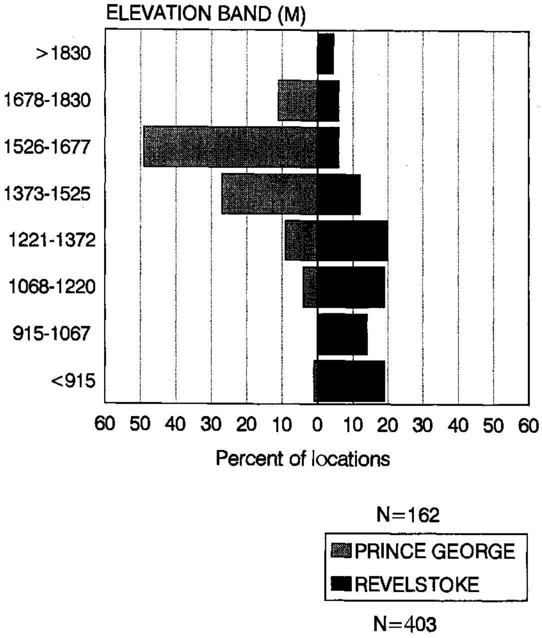


Fig. 2. Percent of caribou locations in each elevation-band during the early winter (Nov-Dec) nearPrince George, and Revelstoke, B.C. Samplesize (N) is number of locations.

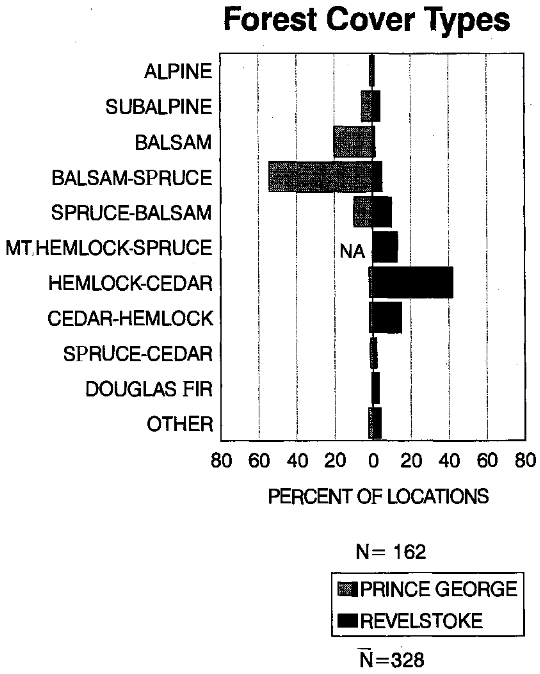


Fig. 3. Percent of caribou locations in each forest cover type during early winter (Nov-Dec) near Prince George, Revelstoke, B.C. (na = not available).

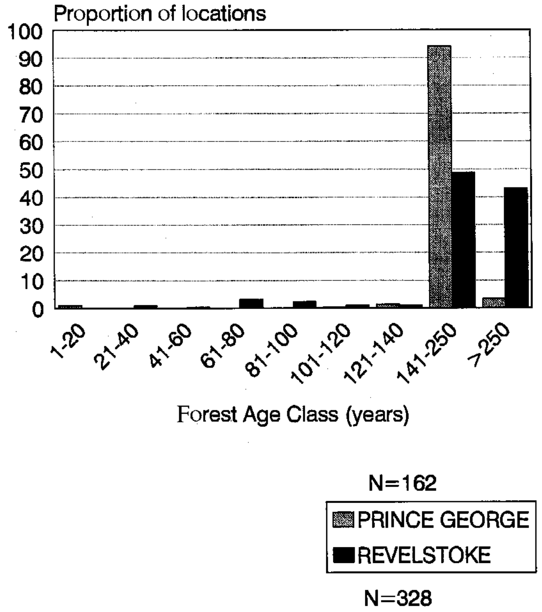


Fig. 4. Percent of caribou locations in each forest age class during the early winter (Nov-Dec) near Prince George, Revelstoke, B.C.

were located below 1220 m. Approximately one-third (32%) between 1221 and 1525 m, and the remaining 15% above 1525 m. In contrast, the majority (49% of 162) of radio-collared caribou in the Cariboo Mountains were located between 1526-1677 m (Fig. 2).

Forest Cover Types
Caribou in the Columbia Mountains used forests with significantly different species composition than those in the Cariboo Mountains (X^2=228.2; *df*=10; *P*<.001). In the Columbia Mountains 67% of the caribou locations were in forests dominated by western hemlock and western red cedar whereas less than 5% of radio-collared caribou in the Cariboo Mountains were in the ICH. Over half (54 % of 162) of the radio-collared caribou near Prince George were located in balsam-spruce stands and another 21% in balsam stands (Fig. 3).

Regional variation in the use of forest cover types partially reflected differences in elevation bands used. Caribou use of forest cover types in the northern Cariboo Mountains were similar to habitat use patterns reported by Seip (1992) in the Quesnel Highlands which has similar topographic and winter conditions. Caribou use of ICH stands near Revelstoke is consistent with more rugged areas of the province where caribou have also been reported to use low elevation ICH habitats extensively (Simpson & Woods, 1987; Servheen & Lyon, 1989; Rominger & Oldemeyer, 1989).

Forest Age
Caribou used forest age classes 8 (140-250 yr) and 9 (>250 yr) almost exclusively in both study areas (Fig. 4). Over 90% of the radio locations in the Cariboo Mountains were in 141-250 year old forests. In the Columbia Mountains 47% of the locations occurred in forests between 141 and 250 yrs and 42% in forest older than 250 years. Caribou used forests younger than 140 years old infrequently in both study areas.

Aspect
Caribou use of aspects varied between years in both study areas (Cariboo Mountains, X^2=15.1, *df*=4, *P*=.004; Columbia Mountains, X^2=11.2, *df*=1, *P*=.001). In the Cariboo Mountains warmer aspects were used to a greater extent in 1990 (79% of locations) and 1992 (62% locations); in the Columbia Mountains 65% of the locations were on warm aspects in 1992 and 45% in 1993 (Fig. 5.1). Caribou also used aspects significantly different (*P*<.001) between early and late winter periods (Fig. 5.2). Although all aspects were used, there was greater use of warmer aspects (S, SW, W, SE) during the early winter (50-79%) compared to late winter where caribou shifted to cooler (N, NE, E, NW) aspects.

Although reasons why this apparent shift occurs remains unclear, warmer aspects may be used to a greater extent in the early winter because they have relatively less snow and may provide accessible understory vegetation compared to northerly aspects. The shift to cooler aspects in the late winter may be related to greater snow depths that provide "lift" to facilitate arboreal lichen foraging.

Slope
Caribou use of slope classes was significantly different between the two study areas (X^2=114.5, *df*=4, *P*<.001). In the Cariboo Mountains, the majority of caribou were located on 16 to 30% slopes (59% of 162), 26% were located on 31-45% slopes, and the remaining 2% on slopes steeper than 45%. In the Columbia Mountains, caribou were more evenly distributed among the slope classes with 30% of the locations between 16 and 30%, 27% between 31 and 45%, and 38% on slopes greater than 45% (Fig. 6).

Caribou use of steeper slopes likely reflects the steeper terrain available in the Columbia Mountains. In the Cariboo Mountains, use-availability analyses indicated significant selection for moderate slopes (16 to 30%) slopes (Terry, 1993). Because slope often dictates operability and the feasibility of ground-based versus cable harvesting systems, ground-based partial cutting systems may not be an option over large portions of caribou winter range in the Columbia Mountains.

Use-Avoidance of Low Elevation Forests: Suggested Hypotheses
Although few data are available to address *why* caribou in the Columbia Mountains use low elevation forests and those in the Cariboo Mountains appear to avoid them, we suggest three factors that may be involved: (1) snow conditions; (2) food availability; and (3) predation. Because snow characteristics and forage availability are likely interrelated as are snow depth and predator abundance, these variables are not considered mutually exclusive.

Snowpack and Caribou Sinking Depths
It has been suggested that caribou move from high elevation habitats to lower elevations to avoid deep soft snow (Antifeau, 1987; Seip & Stevenson, 1987; Simpson & Woods, 1987). Early winter snowpacks at high elevations in the Cariboo Mountains, however, are quite similar to snowpacks in the Columbia Mountains (Table 1). Average caribou sinking depths in the Cariboo Mountains (43 ± 6 cm) are also similar to caribou sinking depths in the Columbia Mountains (40 ± 13 cm, unpubl. data) and suggests additional factors are needed to adequately explain early winter habitat use in these two regions. Although predicted caribou sinking depths were significantly less at 915 m than at 1525 m (Friedman Test, $P < .05$) during two winters near Revelstoke (Fig.7). and suggests caribou avoid deep snow, we have observed movement to lower elevations occurs before sinking depths at higher elevations become restrictive indicating that snow may not be the primary factor influencing caribou movement to lower elevations in the Columbia Mountains. The dynamic relationship between snow depth and forage availability (both understory vegetation as well as arboreal lichen accessibility) likely interact to produce the observed patterns.

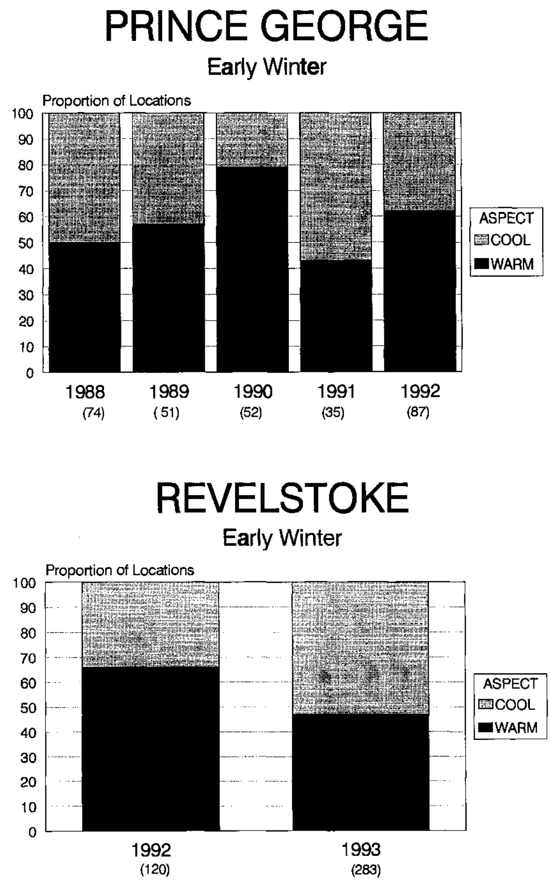


Fig. 5.1. Percent of caribou locations for each aspect class (warm vs cool) during early winter near Prince George, and Revelstoke, B.C. Sample sizes in brackets.

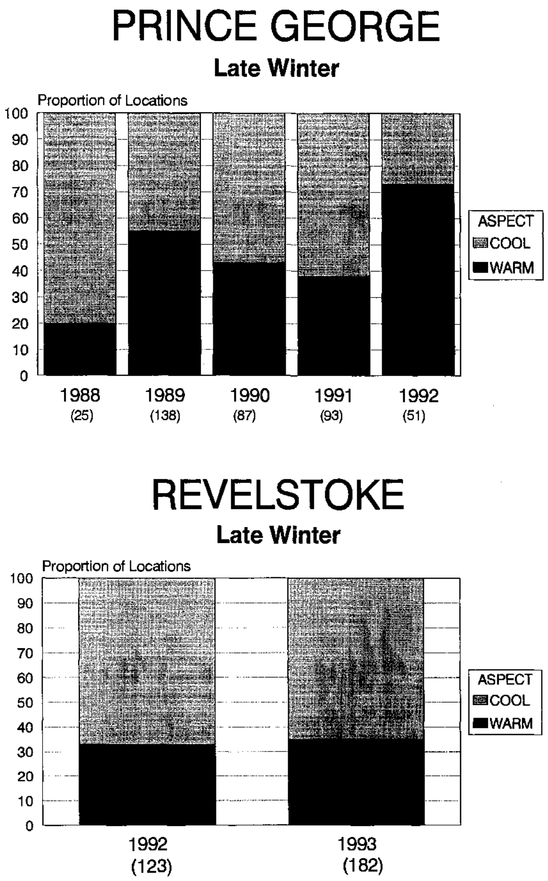


Fig. 5.2. Percent ofcaribou locations for each aspect class (warm vs cool) during late winter near Prince George, and Revelstoke, B.C. Sample sizes in brackets.

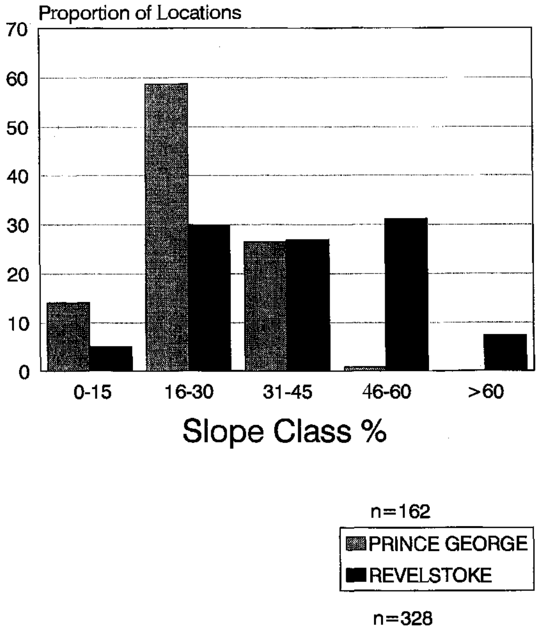


Fig. 6. Percent of caribou locations in each slope class near Prince George and Revelstoke, B.C.

Table 1. Comparison of average snowpack depths and density for Prince George and Revelstoke, British Columbia.

Location	December 30 Snowpack (cm)	 Density (%)	March 30* Snowpack (cm)
Prince George	182 (153-240)	27 (19-34)	223 (136-317)
Revelstoke	175 (134-252)	30 (24-35)	307 (210-429)

numbers are averages with range in brackets.
snow course - Prince George: Bearpaw Longworth 1740 m (1989-1993).
snow course - Revelstoke: Mt. Revelstoke 1830 m (1978-1993).
* 30 year normals (1961-90).
Source: B.C. Snow Survey. Ministry of Environment Lands and Parks.

Forage Availability

At lower elevations in the Columbia Mountains, falsebox provides caribou with an accessible food source in addition to the arboreal lichen available as litterfall and on windfallen trees (Simpson & Woods, 1987; McLellan & Flaa, 1992). In the southern Selkirk Mountains, microhistological analysis of feces also revealed falsebox to be a significant forage source during the early winter (Rominger & Oldemeyer, 1990). Because arboreal lichen is low in crude protein (Antifeau, 1987; Robbins, 1987) falsebox may provide caribou with a protein supplement to offset a low protein lichen diet. In contrast, this alternative forage source is not available in the ICH forests in the Cariboo Mountains and may be a factor related to their infrequent use. Although other shrubs such as willows (*Salix* spp.) and *Vaccinium* spp. are available they are sparsely distributed and forage intake in these habitats may be seriously constrained.

Predators

Predator avoidance may influence habitat use patterns and seasonal movements of caribou (Bergerud, 1983; Simpson & Woods, 1987; Seip, 1992). Wolves (*Canis lupus*) are the primary predator of caribou in most areas of B.C. and have been reported as a significant limiting factor for northern caribou (Bergerud & Elliot, 1986; Bergerud & Page, 1987) and some mountain caribou populations (Seip, 1992). Historically, wolves have been rare in the Columbia Mountains reflecting relatively low prey populations of other ungulates including moose (*Alces alces*), deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) and perhaps difficult hunting conditions due to deep snow. If wolf populations have been and continue to be relatively sparse, caribou may be able to use valley bottoms in the Columbia Mountains without a significant risk of becoming prey.

Population status of wolves in the northern Cariboo Mountains is poorly documented, however, pack activity is known to exist (Watts, pers. comm). Although wolf predation in the southern Cariboo Mountains (with similar terrain) has been implicated as a significant limiting factor (Seip, 1992), adult mortality rates of caribou in the northern Caribou Mountains has been relatively low (5-8%). Historic and possibly current wolf predation in the northern Cariboo Mountains may have either eliminated the use of low elevation forests in early winter as a viable strategy or presently represent a high predation risk.

Summary

Estimates of habitat availability will be required to assess habitat selection. The preliminary information presented, however, demonstrates that caribou use different forests and foraging strategies in different parts of British Columbia. Forest management planning and habitat protection guidelines should reflect the importance of low elevation hemlock-cedar stands in the Columbia Mountains whereas mid-elevation balsam-spruce stands should be targeted for protection or special management in the

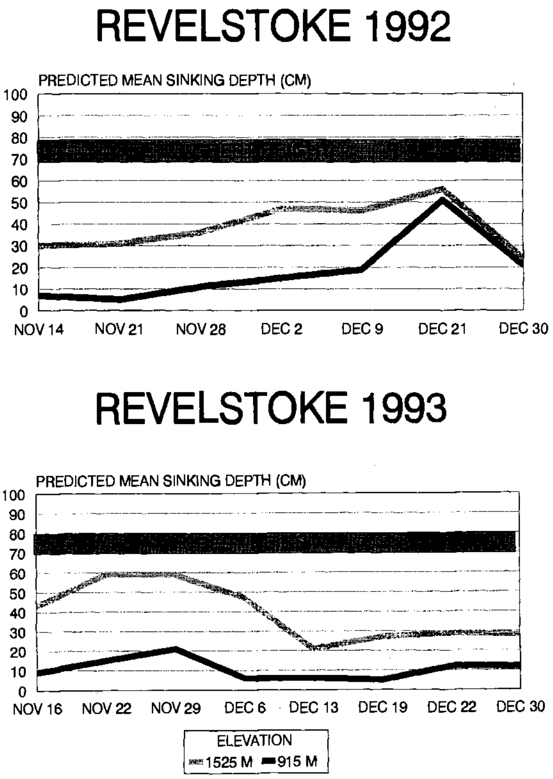


Fig. 7. Predicted mean caribou sinking depth (cm) for each week during the early winter period (Nov-Dec) in Revelstoke, B.C. 1992-93.

Cariboo Mountains. Landscape level planning should include movement corridors linking high and low elevation habitats in both areas.

The extent to which silvicultural systems such as partial cutting can be used to manage for both timber and caribou will also differ between regions. The steeper slopes of the Columbia Mountains may reduce the amount of area suitable for partial cutting. Managing for snow interception and understory production of shrubs such as falsebox will be relatively more important in the Columbia than Cariboo Mountains.

Acknowledgements

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Using Alternative Silvicultural Systems to Integrate Mountain Caribou and Timber Management in British Columbia

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Abstract: Even-aged forest management using the clearcutting silvicultural system as it is currently applied threatens mountain caribou habitat in British Columbia. Since neither complete preservation nor maximum development of timber resources are socially acceptable alternatives, forest managers are anxious to find integrated management options. We describe alternative silvicultural systems currently being tested, including single-tree and group selection. All the treatments have the goal of periodically extracting viable timber volumes while perpetually retaining stand characteristics necessary for caribou. The effects of these logging prescriptions on lichen biomass and growth rates are being tested. Alternative silvicultural systems may become part of a larger strategy to maintain caribou habitat in managed forests.

Key words: *Rangifer*, logging, forest management, arboreal lichens

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Introduction

Why do we need to consider alternative silvicultural systems to integrate mountain caribou (*Rangifer tarandas caribou*) and timber management? What is wrong with the status quo? A brief review of mountain caribou habitat requirements in British Columbia will help explain why the current application of the clearcutting silvicultural system is threatening mountain caribou habitat, and why alternatives are necessary.

Mountain caribou occur at low densities and range over large areas of east-central and southeastern British Columbia. Throughout the winter caribou use old forests and avoid immature stands (Simpson *et al.,* 1985; Seip, 1992). In early winter, as snow is accumulating to depths of 3 metres or more in the upper Engelmann spruce-subalpine fir zone (ESSF), caribou use the lower parts of the ESSF and the interior cedar-hemlock (ICH) zone, where the snow is not as deep. Most stands used by caribou in early winter are commercially valuable. Shrubs supplement lichen forage until snow burial makes them unavailable. As snow densities increase to levels that will support caribou, the animals move up in elevation and feed almost exclusively on arboreal lichens for the rest of the winter. In the late winter there is less conflict with forest management since more of the stands used by caribou at that time are non-merchantable.

Several types of silvicultural systems, or cycles of activities by which a stand is harvested, regenerated, and tended over time, are used in British Columbia. Nearly all ESSF and ICH forests are currently managed with only the clearcutting silvicultural system. Logging with that system removes the entire arboreal lichen food source, which is problematic because lichens are slow to disperse and slow to grow, even when a suitable substrate and microclimate exist. To attain a biomass useful to caribou, lichens take much longer than the 100 to 120 year rotation length normally used with the clearcutting system. Entire drainages could be virtually devoid of useful lichen bearing habitat after a number of logging passes and with normal rotation lengths.

Although space is thought to be the single most important habitat variable affecting caribou (Bergerud, 1980; Bergerud *et al.,* 1984), that space must contain suitable habitat providing the attributes specifically necessary in each season. In winter, that means having forests with available arboreal lichen forage. While caribou will travel across recent clearcuts, an area devoid of arboreal lichen food resources is not suitable winter habitat. Fragmentation of suitable habitat (space) by timber

Table 1. Mountain caribou partial cutting trials in the ESSF (adapted from Stevenson *et al.* 1994).

Study area	Stand age	Subzone	Forest District	Prescription	Planned volume removal	Actual volume removal[1]	Study components[2]	Year and season of treatment	Cooperators[3]; contact persons
George Cr. CP 32	200-300 yr	ESSFwk1	Prince George	overstory removal: - 35 cm diameter limit - feller-buncher - WCB variance to retain safe snags	45%	52%	AP,LA,W	winter 1989/90	WHC, SSWG,PGW, PGFD (S. Stevenson)
George Cr. CP 37	200-300 yr	ESSFwk1	Prince George	overstory removal: - 35 cm diameter limit - feller-buncher - WCB variance to retain safe snags	not available	52%	AP,W	winter 1990/91	WHC,SSWG, Rustad, PGFD (S. Stevenson)
Pinkerton	140-250 yr	ESSFwk1	Prince George	single tree selection: - Q=1.3 overstory removal: - 55 cm diameter limit partly feller-buncher, partly hand-felled	32%	AP,LA,LG,R,W		fall 1991 (to be completed summer 1994)	HCF, SSWG, Northwood, PGFD (S. Stevenson)
Lucille	200-300 yr	ESSFmm	Robson Valley	several prescriptions, all hand-felled: - single tree selection (STS) - irregular shelterwood - group selection sanitation cut	50% 50% 50%	44% 49% 69%	AP,LA,LG, CM,R	winter 1991/92	WHC, SSWG, RVFD, Mica (S. Stevenson, M. Jull)
Research Cr. CP 113-1	180-300 yr	ESSFwk1	Horsefly	group selection - 10 m diameter openings - 20 m diameter openings (.03 ha) - feller buncher - safe snags retained	30%	28%	LA,LG,CM,R	winter Dec-Jan 1990/91	CFR, HFD, SSWG, WELD (H. Armleder)

Study area	Stand age	Subzone	Forest District	Prescription	Planned volume removal	Actual volume removal[1]	Study components[2]	Year and season of treatment	Cooperators[3]; contact persons
Blackbear Cr TSL A43738	150-250 yr	ESSFwk1	Horsefly	group selection - .03,.13,1.0 ha openings - feller buncher - safe snags retained	30%	30%	LA,LG, DSS,R	summer Aug 1992	CFR, HFD,SSWG, WELD (H. Armleder)
Blackbear Cr. TSL A43738	150-250 yr	ESSFwk1	Horsefly - feller buncher	group selection - .03,.13,1.0 ha openings - feller buncher - safe snags retained	30%	30% DSS	LA,LG,R, V,CM, 1992	winter Nov-Dec WELD	CFR, HFD,SSWG, (H. Armleder)
Grain Cr. TSL A43737 BLK 1	180-300 yr	ESSFwk1	Horsefly	group selection - .03,.13,1.0 ha openings - feller buncher - safe snags retained	30%	30%	LA,LG ,R,V	winter Nov-Dec 1992	CFR, HFD,SSWG, WELD (H. Armleder)
Grain Cr. TSL A43737 BLK 1	180-300 yr	ESSFwk1	Horsefly	group selection - .03,.13,1.0 ha openings - feller buncher - safe snags retained	30%	30%	LA,LG,R, V,DSS	winter Dec-Jan 1992-93	CFR, HFD,SSWG, WELD (H. Armleder)

[1] Although volume removal >30% occurred in some management trials, this is not recommended for caribou habitat management.

[2] AP = air photo dot grid; LA = lichen abundance; LG = lichen growth rates; CM = canopy microclimate; V = detailed vegetation monitoring; R = regeneration; W = winter habitat measures/trailing; DSS = detailed snow survey (tentative).

[3] CFR = Cariboo Forest Region; HCF = Habitat Conservation Fund; HFD = Horsefly Forest District; Mica = Mica Wildlife Compensation Program; Northwood = Northwood Pulp & Timber Ltd.; PGFD = Prince George Forest District; PGW = Prince George Wood Preserving Ltd.; Rustad = Rustad Bros. & Co. Ltd.; RVFD = Robson Valley Forest District; SSWG = Silvicultural Systems Working Group; WELD = Weldwood of Canada Ltd.; WHC = Wildlife Habitat Canada.

harvesting may lead to higher levels of predation by introducing conditions that favour predators and by concentrating caribou into smaller areas.

The most promising stand level option that permits harvesting while potentially maintaining caribou habitat is the selection silvicultural system. The objective in using that system for caribou management is to retain, in perpetuity, a managed stand in a condition suitable for continued caribou use.

In this paper we review several major research initiatives that are exploring those alternative silvicultural systems and we describe how they might fit into a management strategy for caribou. Although research on alternative silvicultural systems in caribou habitat is ongoing in both the ESSF and ICH zones, we restrict our discussion to the ESSF zone.

Selection Silvicultural Systems

Selection systems designed to maintain mountain caribou habitat are being field tested in various study areas in British Columbia (Table 1). Both the single-tree and the group selection systems are being tested to explore the widest range of options for forest managers (Fig. 1). The single-tree selection system involves the removal of individual trees from the stand, and offers the flexibility of leaving trees with high lichen loads. The group selection system involves the removal of groups of trees, allowing more efficient logging and leaving much of the stand untouched until the next cutting cycle. Each system has its advantages (Table 2).

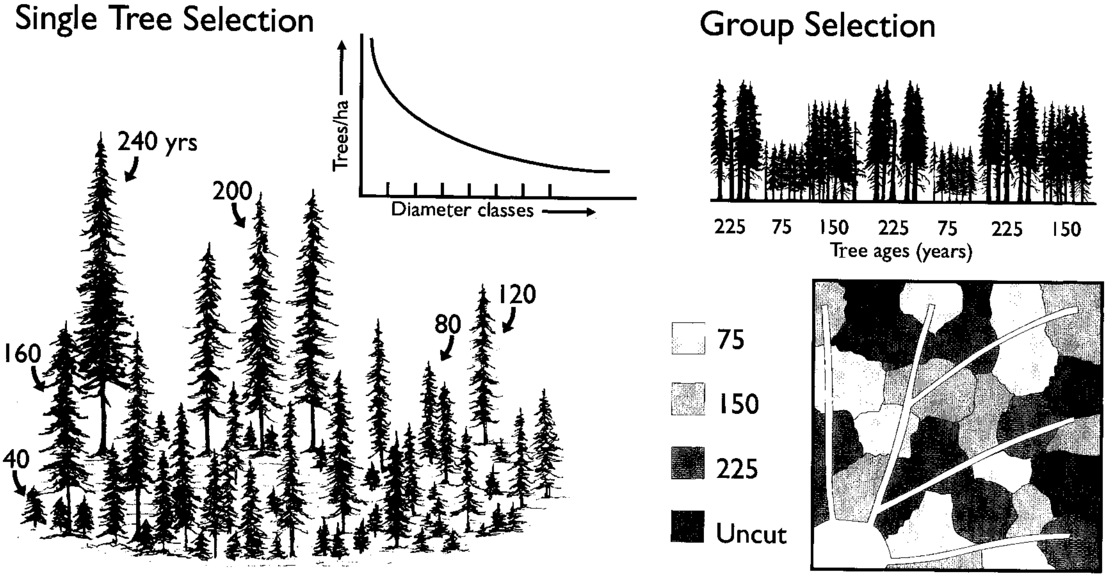
The selection systems being tested are intended to address the caribou habitat concern. For example, the timber volume removed is typically light so a significant proportion of trees remain for caribou and to ensure that the stand remains windfirm. Prescriptions are designed so that lichen-bearing trees are left in the stand.

The distribution of arboreal lichen biomass within a stand is highly variable. For example, surveys done on the trials in the Horsefly Forest District (Table 1) revealed that within species, larger trees (>30 cm dbh= diameter at breast height i.e. 1.3 m) have significantly (α=0.05) more arboreal lichen than smaller trees (10-30 cm dbh). Thus, harvesting just the largest trees is clearly not the best strategy for maintaining caribou habitat, and our prescriptions emphasize maintaining the tree size profile while harvesting timber.

Standing dead trees are common in these high elevation forests and often comprise 20% or more of the stems. Our surveys indicate that dead trees account for 12 to 35% of stand lichen biomass. In normal logging operations all dead trees must be felled concurrently with harvesting to protect worker safety. On some of our trials we obtained a variance from the Workers' Compensation Board of British Columbia (WCB) to retain safe dead trees by using fellerbunchers and grapple skidders, which enclose and protect the operators.

A variety of post-harvest silvicultural treatments are being tested to ensure that future trees will

Fig. 1. Examples of silvicultural systems suited to maintaining the stand characteristics required by caribou (Stevenson *et al.*, 1994).



replace those removed through harvesting and those lost to natural mortality. Both natural and artificial regeneration using various planting stocks, tree species, and site preparation options are being tested.

Methods of Testing Alternative Silvicultural Systems for Caribou

It is important to quantify the impact of timber extraction on lichen abundance. For the studies reported here, the photo reference manual of Armleder *et al.,* (1992) is used to estimate the abundance of arboreal lichen before and after logging. Growth rates of arboreal lichens are also being measured, since growth could be affected by changes to the stand microclimate caused by timber harvesting. To measure growth, lichen samples are placed in enclosures that allow ambient levels of temperature, humidity, and light while preventing contamination of the samples by wind-borne debris or losses through fragmentation. At intervals, the samples are brought into a laboratory and weighed in a humidity-controlled environment (Walker, 1996; Stevenson, 1993).

Direct use of the partially cut stands by caribou is difficult to quantify, because these animals live at low densities in remote areas. On some study areas, radio-collared caribou are available to provide some habitat use data, although probably not enough to allow quantitative assessments of treatment effects. Snow measurements are being taken on some of the trials to assess the hydrological impact of the timber harvesting prescriptions, and to gain insights on the possible impact of timber harvesting on the energy costs of locomotion for caribou through these habitats. Perhaps the most promising assessments of whether logged stands are still suitable caribou habitat will develop from trailing of caribou in managed and unmanaged stands, as in the studies described by Terry *et al.*, (1994).

Results

Although studies of selection harvesting in caribou habitat are still in progress, some useful insights have already been gained. The major factors contributing to loss of lichens due to harvesting are the removal of merchantable trees, the removal of snags, and loss of lichens from residual trees. In the group selection block at Research Creek (CP113), the proportion of lichens lost on felled trees was equal to the 30% of the area that was harvested. At George Creek (CP32), the proportion of lichens on felled trees (55%) was roughly equal to the 52% of the timber volume that was harvested. In both of those study areas, safe snags were retained during harvest. At Lucille Mountain, 43% of the lichens originally present was on living trees that were harvested, and an additional 27% was on snags that were felled during harvesting. That loss of lichens greatly exceeded the average of 45% of the timber volume harvested in the treatment units studied.

Some lichens are also lost from the trees that remain after selection harvesting, either from damage during logging or from increased exposure after logging. Those losses are greater in single tree selection cuts than in group selection cuts, and are greater on exposed sites than on sheltered sites.

Table 2. Comparison of advantages of single tree and group selection systems for mountain caribou habitat (Stevenson *et al.,* 1994).

Potential Advantages of Single Tree Selection	Potential Advantages of Group Selection
- more flexibility in selecting trees to harvest, therefore high lichen-bearing trees can be retained. - more flexibility in developing multi-layered stand structure on a micro level rather than producing series of even-aged clumps as with group selection - impact of logging homogeneously distributed throughout the stand - dispersed regeneration less likely to deter caribou use than even-aged clumps of regeneration - entire stand is structurally suitable for caribou use at any one time	- less damage to residual stems and less associated loss of lichens - snag retention a possibility with use of feller-buncher - logging costs lower than single tree selection - more options for post-harvesting silviculture available - influence of residual stand on regeneration can be varied through opening size selection - leaves much of the stand with no disturbance since logging only occurs in openings - typically smaller percent of cutblock in skid trails - risk of windthrow may be lower - better snow interception areas within stand

Residual trees assessed the summer after logging supported 26% less lichen than before logging at George Creek (CP 32), 8% less at Lucille Mountain, and about the same amount as before logging at Research Creek. Lichen abundance at George Creek has not been reassessed since 1990, but appears to be much lower than before harvesting.

Preliminary results of growth rate studies suggest that where selection harvesting results in drier, more exposed conditions, the two principal genera of forage lichens respond differently. Over time those differences could result in a shift from *Alectoria sarmentosa* to *Bryoria* spp. on some sites. In view of the observations of Rominger & Robbins (1994) that caribou prefer *Bryoria* spp. to *Alectoria sarmentosa*, such a shift might be beneficial. The impact of selection harvesting on overall lichen abundance over time is not yet clear.

Caribou or signs of caribou use have been observed in most of the selection blocks since harvesting was completed. During trailing studies, Terry & McLellan (1991) noted limited use of the George Creek (CP 32) block. The caribou appeared to concentrate their foraging activities along the edges of the block where lichen was available on windthrown trees.

At one single tree selection block (George Creek CP 32) heavy blowdown has occurred, leaving a stand that is unacceptable in terms of both caribou habitat and timber management objectives. Very little blowdown has occurred at Lucille Mountain or at the group selection blocks in the Horsefly Forest District. Blowdown at the other George Creek block (CP 37) and at Pinkerton Mountain has not been assessed, although some has been noted along landing edges and roadsides.

Discussion

We anticipate that, within the next 5 to 10 years, significantly more information will be available on the short-term impact of selection harvesting on the abundance and growth rates of the two principal genera of forage lichens for mountain caribou. There will also be more information on various forestry-related measures, such as logging costs, windfirmness, and short-term regeneration success, and further understanding of the use of selection blocks by caribou is likely. However, a thorough study of use by caribou would require a much larger area managed under selection systems, and an intensive monitoring program.

Some key questions cannot be answered in the near future. The long-term changes in stand structure that follow selection harvesting are likely to affect the abundance and species composition of arboreal lichens, use by caribou, and timber values. Long-term monitoring is needed to assess the effectiveness of the various possible selection prescriptions in maintaining both caribou and timber values.

Short-term results have indicated that high removal of timber volume, especially on exposed sites, can result in blowdown and in heavy losses of lichens from the remaining trees. For those reasons, no more than 30% removal of timber volume (including that removed from skid trails) is recommended in blocks managed as caribou habitat (Stevenson *et al.*, 1994).

Selection silvicultural systems are more costly to plan and implement than is the clearcutting silvicultural system, especially while initial experience is being gained. However, increased use of alternative silvicultural systems in some forest types is necessary to meet the changing demands of the public for integrated resource management, and is required by the proposed Forest Practices Code for British Columbia (B.C. Ministry of Forests, 1993).

Ongoing research on selection silvicultural systems in caribou habitat primarily addresses management at the stand level. However, implications for management at the landscape level must also be considered. The effectiveness of selection silvicultural systems in maintaining caribou habitat is uncertain and will continue to be uncertain for some time in the future. Furthermore, the impacts of forestry activities on predator/prey relationships and the effects of increased access on caribou are incompletely understood. We believe that those uncertainties can best be addressed through zoning of the landscape.

Some core caribou ranges should be set aside as no-harvest, no-access zones, to function as refugia in the event that integrated management strategies are unsuccessful in meeting the needs of caribou. In some areas, that need can be met largely in high-elevation areas where timber values are relatively low, although some low-elevation ranges and movement corridors will also be required. Where caribou use low elevations more extensively, larger no-harvest zones at low elevations will be needed.

Other parts of caribou range should be designated as special management zones, in which experimentation with selection silvicultural systems can continue. In some cases, clearcutting may be used within the special management zone, where selection harvesting is not feasible or where lichen biomass is not great enough that partial cutting is warranted. However, clearcutting must not compromise overall landscape-level habitat objectives in the special management zone. Access management to protect caribou is important in the special management zone.

Marginal caribou ranges may be managed according to ordinary policies of integrated management. However, studies by Seip (1990, 1992) suggest that to minimize the risk of increasing predation on caribou, managers should avoid enhancing habitat for moose in areas adjacent to caribou habitat.

The effectiveness of alternative silvicultural systems in maintaining caribou habitat is incompletely understood. However, those systems have the potential of becoming part of an overall strategy for successfully managing mountain caribou in British Columbia.

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A Mountain Caribou Strategy for British Columbia

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Abstract: Because of the declining population of mountain caribou in British Columbia and the increasing conflict between caribou management and timber harvesting, BC Environment recently has developed a new policy for mountain caribou management in the province. Three options were considered; 1) to manage habitats/populations to potential habitat suitability, 2) to manage habitats/populations to ensure that at least present levels are maintained and 3) to manage habitats/populations within a core area of the province only. The chosen strategy of managing habitats/populations to ensure that at least present levels are maintained is consistent with ministry goals and policies and will likely require that a network of protected areas, buffer areas and linking corridors be established. Initiatives to document existing mountain caribou distribution and to provide options for integrated caribou/timber solutions to management conflicts are ongoing. Successful implementation of this caribou management strategy will require the active participation of the Ministry of Forests since the protection of habitat is a shared responsibility.

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Concerns over logging of caribou ranges began to surface in the 1960s. Recommendations for moratoriums, reserves, extended rotations for high elevation forestry and modification to logging prescriptions in caribou range were common in the 1970s. As the demand for timber increases, so does the potential for conflict between habitat and timber management (Seip, 1987). In response, biologists, foresters and researchers within the Ministry of Environment, Lands and Parks, the Ministry of Forests and elsewhere have been looking for ways to maintain caribou habitat and populations in managed forest stands.

In 1988, the Mountain Caribou in Managed Forests (MCMF) Program was initiated within the Prince George area by the Wildlife Branch of BC Environment, the Ministry of Forests and the local Forest industry to address the issue of the potential conflict between mountain caribou and forest management. In the fall of 1990 the MCMF Advisory Committee met and identified the need to expand its membership to include all the southeastern portion of the province with similar forestry - caribou habitat related issues and concerns. The need to develop a consistent provincial strategy was clear.

The provincial version of the MCMF Committee has been inactive for over a year pending the development of a new committee structure which became necessary in light of the impending Forest Practices Code. In the interim the BC Environment component of this committee has met and continued to work on three main themes as follows:

1. Development of a management "strategy" for mountain caribou in British Columbia

Mountain caribou is classified as being "at risk" in British Columbia, (Harper *et al.*, 1994) and a clear management policy statement from BC Environment was needed to help prevent this ecotype of woodland caribou from becoming "threatened" or "endangered" in the province. By clearly articulating a management "vision" for Mountain Caribou, BC Environment is intending to provide support for its efforts within the provincial MCMF Committee as well as within larger land-use planning processes.

BC Environment as part of the Ministry of Environment, Lands and Parks is responsible for maintaining environmental quality through management and protection of the province's land, water, air and living resources (BC Wildlife Branch). It does this primarily in two ways: resource stewardship and regulatory action. In order to develop a provincial management strategy for mountain caribou it was necessary for BC Environment to look at mountain caribou management in the context of the mandate, goals and strategic objectives of Ministry as well as external pressures such as those exerted by the public at large, whether locally, provincially, nationally and internationally.

A number of federal and provincial policies and strategic plans are relevant to the conservation of mountain caribou in British Columbia and have been considered: eg. A Wildlife Policy for Canada (Wildlife Ministers Council of Canada, 1990), Strategic Plan of the Ministry of Environment, Lands and Parks (BC Environment, 1993), Maintaining British Columbia's Wildlife Heritage - Provincial Wildlife Strategy to 2001 (BC Environment, 1993). To summarize these initiatives, there currently are two main thrusts to wildlife policy in British Columbia:

a) Conservation of biodiversity - the variety of different ecosystems, species, and genetic stocks - and not just the birds and land mammals that traditionally have been termed "wildlife", and

b) Conservation of species and ecosystems threatened by human activities.

Taken together these provide considerable impetus for a concentrated effort to conserve mountain caribou and their habitats in the province.

Mountain caribou numbers are believed to have declined in many parts of British Columbia coincident with human development and habitat alteration. (Bergerud, 1974) The British Columbia population of woodland caribou is part of a western woodland caribou population classified as rare in 1984 by the Committee on the Status of Endangered Wildlife in Canada. (COSEWIC, 1993) In addition, mountain caribou are considered a species ecotype at risk in British Columbia and are currently Blue-listed (Harper *et al.*, 1994), (the Blue List includes vulnerable taxa that could become eligible to be considered for legal designation under the BC *Wildlife* Act as Endangered or Threatened.).

In response to the declining population of mountain caribou in British Columbia, three options for mountain caribou management have been considered by British Columbia Environment, as follows:

Option 1 Manage existing habitats/populations to present habitat suitability.

The option of managing to present suitability favours caribou over forest harvesting activities and may not be economically acceptable over wide areas. Adoption of this strategy conceivably would designate currently unused but suitable habitat as requiring either protected status or intensive integrated resource management. The option would be difficult to defend on a site specific basis and was rejected.

Option 2 Identify and manage caribou habitats/populations to ensure that at least present levels are maintained.

This option is consistent with ministry goals and policies and has been accepted as BC Environment policy with regard to Mountain Caribou Management. Although the objective here would be to maintain or enhance the current levels of caribou populations, it is recognized that the strategy of total protection is not possible for all areas used by this wide-ranging species. Solutions which provide an integrated management approach to conflict resolution will be sought, where possible. Although a system of protected areas will no doubt be a part of the solution, conservation of mountain caribou over the long term will require an integrated caribou/forestry strategy over a large area of British Columbia.

Option 3 Identify and manage caribou habitats/populations within a core area of the province only.

This option represents a further erosion of mountain caribou range in British Columbia and accepts the extirpation of some local populations of mountain caribou which are not in the core area. Some of these populations such as the southern Purcell herd are unique in being at the extreme southern edge of the world distribution of *Rangifer tarandus.* (Stevenson, 1985) These localized populations represent important genetic pools which would be lost to the species at large if the populations are allowed to become extirpated.

Adoption of this management option could be expected to result in a loss of genetic variability and extirpation of isolated groups of mountain caribou throughout its current range in British Columbia, and has been rejected. Ultimately adoption of such a policy could lead to the eventual downgrading of the status of mountain caribou in British Columbia to either endangered or threatened. If this were to occur, the Ministry's Provincial Wildlife Strategy to 2001 requires that a recovery plan be completed within two years of such designation.

2. Caribou distribution and habitat mapping

In order to provide a data base on which management decisions with regard to habitat protection and integrated management can be made, BC Environment is in the process of mapping known or expected mountain caribou distribution together with existing topographic, habitat and forest capability data throughout the range of mountain caribou in the province. From this it is BC Environment's intention to delineate areas which will require either integrated solutions to caribou/forestry conflicts or, in some cases, complete protection from the adverse effects of timber harvesting.

Identification of key caribou habitats can alleviate some conflicts since many core areas are located in non-merchantable or low value forest types - however many important caribou habitats occur within the merchantable forest and integrated management may not always be possible.

3. Integrated resource management

While the reservation of some areas from human activity will no doubt be necessary to protect mountain caribou, the strategy of total protection cannot reasonably be applied to all areas used by this wide-ranging species. In the final analysis conservation of mountain caribou populations in British Columbia will likely require an integrated network of protected areas, insulating buffer areas, and linking corridors; and the application of an appropriate mix of sound land management practices on the remaining land base. As a result, solutions which meet the needs of both managing mountain caribou and managing for timber production in southeastern British Columbia are preferred where feasible. Subalpine forests and highly productive low elevation cedar/hemlock forests present a particularly difficult challenge to resource managers. Habitat management for a large, wide ranging ungulate species dependent on old forest attributes and limited disturbance adds an additional layer of complexity to the challenge.

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Integrated Management of Mountain Caribou and Forestry in Southern British Columbia

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Introduction

The decline of mountain caribou (*Rangifer tarandus caribou*), particularly in the southern part of British Columbia, has been recognized for over two decades (see Bergerud, 1974). Mountain caribou are of special concern because they depend on old growth forests which are being removed by forest harvesting. Stevenson & Hatler's (1985) review documented the conflict between mountain caribou habitat requirements and forest management in British Columbia. Many recent studies in southern British Columbia, most using telemetry, were designed to determine caribou habitat requirements and limiting factors in particular areas. This paper is a summary of a larger report produced for the BC Ministry of Environment. More detailed information and data can be found in the original report.

Detailed ongoing work by the Mountain Caribou in Managed Forests (MCMF) program has contributed new information (e.g. Child *et al.*, 1989; Stevenson *et al.*, 1993). That program has completed a telemetry study and initiated habitat manipulation studies in the Prince George and Quesnel Highland areas (Terry & McLellan, 1991; Seip, 1992; Terry, 1993). Several sites have been experimentally harvested using silviculture treatments aimed at maintaining caribou habitat values while allowing commercial forestry activities. A similar program has been initiated near Mount Revelstoke and Glacier National Parks. The telemetry study is intended to identify those key habitats surrounding the parks which will be required to maintain the caribou now using the parks (McLellan & Flaa, 1993). A relevant project was initiated by the Revelstoke Forest District to assist planning for timber extraction in areas occupied by caribou. Computer modelling was used to estimate the long term effects of various caribou habitat conservation guidelines on timber supply. Using iterative processes, guidelines may be developed and tested in the model to determine if they meet the long term objectives for caribou habitat and to estimate the associated cost to the forest industry. Options are being sought which maximize the benefits to caribou while minimizing the impact on forestry (Nelson, 1993). A synthesis of the approaches used in the above projects will be helpful in developing guidelines for the province as a whole.

Wildlife inventory, radio telemetry, and forest management data for populations in the areas of north Thompson/Wells Gray Park (Antifeau, 1987; Seip, 1990), Revelstoke (Simpson & Woods, 1987; McLellan & Flaa, 1993), and the southern Selkirks/Idaho (Scott & Servheen, 1985; Warren, 1990; Wakkinen *et al.*, 1992), are useful for comparing habitat and population status. Habitat distribution and population data from isolated herds in the Monashee, Purcell and southern Selkirk Mountains is also used to provide information on the tolerance of caribou to habitat alteration (e.g. Simpson & Woods, 1987; Simpson, 1990).

The challenge is to develop workable guidelines that integrate the conflicting needs of the forest industry, which seeks to harvest older forests, and the needs of caribou which use large areas of old forests for food and shelter. The main concerns for caribou include loss of their winter food supply (arboreal lichens), fragmentation of useable habitat areas, human access and associated disturbance or mortality, and alteration of the predator/prey balance. These four concerns must be addressed in any guidelines which seek to preserve caribou populations in forests which are being harvested.

Forest values are low in the high elevation Alpine tundra (AT) and Engelmann spruce - subal-

Table 1. Caribou use and forest values in different elevation bands and biogeoclimatic zones.

Biogeoclimatic Zone	Timber Value	Caribou Use	Elevation
AT	Nil	Low - mod. (summer)	> 2000 m
ESSFp	Nil - low	High (Jan. - March)	1800 - 2000 m
ESSF	Poor - mod.	High (Jan. - March & summer)	1550 - 1800 m
ESSF	Mod. - good	High (Nov. - Dec.)	1350 - 1550 m
ICH	Good	Variable (Nov. - Dec. & May)	< 1350 m

pine fir parkland (ESSFp) biogeoclimatic zones (Table 1). However, within the Engelmann spruce - subalpine fir (ESSF) biogeoclimatic zone and particularly in the Interior Cedar Hemlock (ICH) biogeoclimatic zone, conservation of caribou habitat may conflict severely with forest management objectives.

Discussion and Recommendations

The emphasis for caribou management in B.C. has been on habitat conservation. The general premise is that if suitable habitat is properly distributed within caribou ranges then the populations will be maintained. The habitat distribution is important to maintain key winter food supplies and to enable caribou to avoid predators. Most predation occurs in summer (Seip, 1990; 1992; Compton *et al.*, 1990). Since summer habitats can also provide good late-winter range, emphasis should be on providing quality summer habitat. Compensatory management programs, such as predator control, should only be required where habitat objectives are not met due to human activities or uncontrollable events (eg. forest fires).

Knowledge of winter habitats and important foods, especially arboreal lichens, is relatively good and much research is ongoing to define methods of maintaining lichens in commercial forests. Knowledge of summer habitat needs and particularly of predator avoidance strategies of caribou, is relatively poor (Bergerud, 1983). The current habitat status for some populations has been described to provide guidance on what may be acceptable habitat distributions for caribou. Those analyses should be repeated using accurate digitally mapped habitat data. Similar analyses should also be completed for several other populations where the telemetry and habitat data are available.

Schreier *et al.* (1993) summarized a process used to define habitat management priorities for caribou and determine the consequences of various options. The recommended process corresponds to the approach used by Cichowski & Banner (1993) and is summarized in Fig. 1. That approach should be consistently applied to determine management priorities within the range of mountain caribou. It requires:

- a map based inventory of biophysical habitat units preferably accessible in digital form (GIS),
- clear definition of caribou values and forest values for habitat units which can be used to define high, moderate and low value zones,
- definition of:
  1. zones valuable to both caribou and forestry (conflict areas),
  2. zones valuable to caribou which are not valuable to forestry and
  3. zones valuable to forestry which are not valuable to caribou,
- definition of habitat objectives for caribou and forest management options to provide that habitat,
- assessment of the effectiveness of each option and the relative cost.

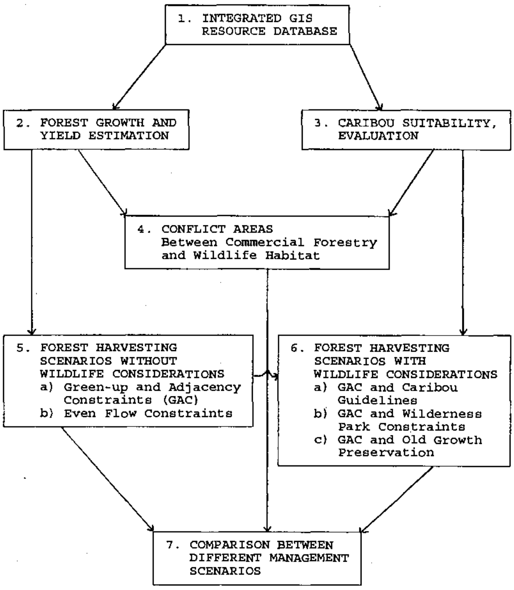

Fig. 1. Information needs and criteria used to define habitat management options for caribou habitat conservation (modified from Schreier *et al.*, 1993).

The habitat and population objectives for caribou at the landscape level are poorly defined. The lack of explicit objectives is mainly due to a lack of information on the amount of habitat needed to support caribou and the desired spacial distribution of suitable habitats. Recent censuses show that caribou are usually spread over large survey areas and occur at low densities compared to other ungulates. A large portion of each area is unused or rarely used by caribou. When unused habitats are deleted from the gross area, the density of caribou per suitable (occupied) habitat can be calculated. Gross densities (.01 - .08 caribou /km^2, Table 1) probably reflect the need for caribou to disperse over the landscape to avoid predators and allow time for slow growing lichens to regenerate in browsed areas. Net densities (0.2 - 0.5 caribou /km^2) more accurately reflect the actual carrying capacity of mountain caribou habitats (Table 1). The highest densities occurred near Prince George where areas occupied were mainly continuous unbroken old growth forest with only a minor proportion of ice, rock, avalanched or cleared areas (see Simpson *et al.*, 1994).

Examination of the habitat use patterns of 3 isolated caribou populations in the south Selkirk Mountains, south Purcell Mountains and Monashee Mountains suggest that caribou will use areas with up to 40% of the gross area in snow, rock, alpine tundra or second growth forest. Caribou maintained use of forested habitat units where up to 40% of the area was young forest or natural openings. Most high use habitats had ≥60% old growth forest but some areas with less old growth were occasionally used. Areas with no old growth were rarely used in any area. The minimum requirement of caribou in late-winter and summer appears to be 60% of the gross area supporting forests or forests complexed with other habitats and 60% of the vegetated land units should be old growth forest. High use land units can either be continuous forest, continuous forest broken by openings and younger age classes, or may be naturally occurring mixes of forest, meadows, wetlands, rock and avalanche paths.

The requirement for old growth forest appeared to be substantially less in early-winter and spring habitats. This might be expected since caribou use primarily shrubs and herbaceous forage, rather than lichens, in those habitats. Use by isolated caribou populations suggested that 20% of the available low elevation habitat (gross area) should be suitable for use by caribou. 25% was the objective set by the United States agencies for the endangered population in Idaho. Suitable habitats again included areas where ≥60% of the forest was old growth. This implies that caribou may survive in areas where special management zones totalling 20-25% of the available cedar-hemlock forest are located in areas needed by caribou and that 60% of those zones should be old growth forest. Overall the old growth conservation required for caribou at low elevations would total 12-15% of the potential forested habitat. In order for old growth areas to be accessible to caribou they must be located adjacent to late-winter/summer habitats.

Ideally, suitable habitat should be continuous or closely linked, however, caribou appeared willing to cross up to 5 km of poor habitat to reach high use old growth forests. Mature forest (60-120 years old) and shrubland (< 20 years) was commonly used for movement while immature forest (20-60 years) was rarely crossed based on examination of radio location points and habitat distribution (see Simpson *et al.*, 1994). Large man-made or fire created openings 10-15 km wide, have isolated caribou populations near Prince George (Narrow Lake, George Mountain) and may prevent caribou from accessing suitable habitats in the south Selkirks.

It is clear that habitat management planning for caribou must be done over large areas and consider not only the forested landscape but also the other habitats in between. The areas currently occupied by caribou, mainly along the transition from highland to mountain topography, suggest that fragmentation by natural features (high mountains, lakes, glaciers, etc.) may be beneficial to caribou by reducing their overall density and making it inefficient for predators to search for them. Much emphasis has been placed on managing winter habitat for caribou, particularly lichen bearing forest, however, spring and summer appear to be the seasons when most mortality occurs (Seip, 1990, 1992; Compton *et al.*, 1990). The high mortality noted in some populations, even at very low densities, suggests that predators are capable of maintaining caribou numbers below the food carrying capacity of their environment. Since favoured summer habitats usually provide abundant lichen forage and the factor limiting caribou numbers appears to be predator avoidance space (Bergerud & Page, 1987), management should focus on providing suitably dispersed summer habitat which will also function as late-winter habitat.

Fragmentation and road access are concerns primarily due to uncontrolled or illegal activities of people within caribou ranges. Human access and activities must be managed to ensure that caribou are not unnecessarily harassed and that they are not forced into marginal terrain where movement is difficult and the risk of accidental death, particularly in avalanches, is elevated.

It has not been shown that roads influence predator/prey relationships for mountain caribou. Based on the inspection of habitat distribution within areas currently occupied by caribou, openings, both man-caused and natural, occur in every caribou range. Predators of various kinds also occur on every caribou range and ungulates other than caribou are limited by deep winter snow, which is a characteristic of mountain caribou ranges. Provided that a suitable proportion of the range is maintained in old growth forest and provided that other prey species do not support very high predator numbers, caribou appear able to maintain stable populations. Examples in B.C. include the Revelstoke and Prince George populations which have been stable or increasing slightly in recent years.

Habitat management planning should be completed over large areas (3000 to 5000 km^2). Along the boundaries of administrative regions, management plans must be coordinated to ensure that habitat contiguity is maintained. Areas valuable to caribou which are not valuable to forestry have been identified in some regions. Current 1:250,000 scale mapping of management zones (I. Stewart - pers. comm.) identifies broad areas occupied by caribou but does not identify key high value habitats within those zones or the habitats unimportant to caribou.

Management zones should be prioritized based on the expected level of conflict between caribou habitat management objectives and other resource users, particularly forestry and winter recreation. Some caribou herds are dependant mainly on low conflict areas (eg. parks, non-productive forests). Contentious habitats important to those herds must receive a high priority for conservation or special management. Two good examples of top priority management zones are the upper Raft River area, and the Mackay River to Deception Creek area, used by the largely protected Wells Gray Park caribou herd. Linkage areas between secured caribou populations must also receive careful attention.

Analyses of forest landscape patterns within the range of various caribou populations have been completed using small scale mapping and visually quantified area estimates. They should be considered first approximations to estimate the actual habitat needs of caribou. More detailed planning using GIS analysis and larger scale mapping should be completed within the range of core caribou populations. Computer analytical tools have been developed by the Wildlife Branch, the Ministry of Forests and by various researchers to enable efficient processing of information. Using GIS modelling in the Kamloops region they were able to highlight high use caribou habitats in drier ESSF zones based on aspect criteria (D. Low - personal communication). The newly developed tools and information have the potential to improve the definition of caribou habitat management zones and greatly reduce the potential cost to forest harvest operations.

The desired landscape distribution of habitat types provides direction for planning caribou habitat conservation within large areas. The second level of planning requires definition of stand level management objectives. Caribou select particular site associations within cedar-hemlock and spruce-subalpine fir forests (Summerfield, 1985; Scott & Servheen, 1985; Idaho Panhandle National Forest, 1987; Terry & McLellan, 1991). After contiguous forested units (polygons) are mapped to provide linked seasonal habitats, the high use associations within those polygons should be the target for the 60% conservation of old growth forests. Some of the habitat characteristics important in summer and late-winter include:

- wet gentle to moderately sloping sites (sedge, sitka valerian associations)
- subalpine fir leading with heavy lichen loads especially Bryoria sp.
- open herbacious understory ie. not *Rhododendron* or *Azalea* associations.

Some habitat characteristics important in early-winter and spring include:

- dry moderate sloping sites *(Pachystima, Aralia* and *Vaccinium* associations),
- western hemlock leading with an open low shrub understory ie. not Devil's club or skunk cabbage associations.

Scott & Servheen (1985) probably provides the best assessment currently available of micro-site characteristics of mountain caribou seasonal habitats in the ESSF and ICH biogeoclimatic zones. That information was used to develop a cumulative effects model to predict the suitability of any land unit for use by caribou (Summerfield, 1985). An updated version of that model is being prepared by the US Forest Service (L. Allen-Johnson - pers. comm.). Recent work by the MCMF committee has identified stand level prescriptions and operational guidelines needed to maintain stand attributes important to caribou (Stevenson *et al.*, 1993). Trials are currently underway to test various prescriptions (H. Armleder - pers. comm.).

Recommendations

Population objectives for mountain caribou should be defined using all available information with consideration of minimum viable populations and contiguity.

Preliminary landscape objectives for the habitat distribution could be set using the approximate gross density estimates provided here (Table 2) or by completing recommended habitat distribution analyses for each population.

Table 2. Caribou density based on gross area within range and suitable habitat within range.

Location	#Caribou counted	Gross area (km^2)	# Caribou/ Gross area (#/km^2)	Suitable habitat area (km^2)	Caribou/ suitable area(#/km^2)
Prince George					
Captain-Otter	98	1100	.087		
Bear Paw-Dezaiko	300	2800	.11		
Sugarbowl	146	600	.24	320	.46
George	20	300	.067		
Narrow Lake	40	500	.08	300	.133
Haggen	214	1300	.16	820	.26
Quesnel Highland					
Bowron	4	1900	.0022		
Wells	19	1600	.012		
Stevenson	114	1500	.078		
Junction	23	1400	.017		
Horsefly	51	1100	.046		
Total	211	7500	.028		
Wells Gray	238	4800	.050		
North Thompson	187	4000	.047		
Revelstoke	350	7400	.047		
South Purcells	100	1400	.071	630	.158
South Selkirks	30	370	.081	220	.209

Note: based on BC Environment population estimates and 1:250,000 scale habitat mapping.

Suitable habitat which is not contentious should be mapped and assessed to determine its effectiveness in meeting the preliminary gross area landscape objectives (60% suitable and 60% old growth). These areas are key habitats but because they are not contentious, they do not require special management. Such areas may include non-commercial forest, parks and other protected areas.

Additional habitats, which are contentious and are required to meet seasonal habitat, movement or population linkage needs (core habitats and corridors), should be mapped and identified as special management zones.

Harvesting should only be permitted where the desired habitat distribution described above can be maintained in special management zones. Selected harvesting may be preferable at high elevations (see Stevenson *et al.*, 1993).

However, large openings in low elevation habitats may be beneficial to discourage use by moose and associated predators. Harvest prescriptions should be adjusted to meet local landscape objectives within larger landscape planning units.

Within special management zones, any permissible development should target the site associations used least by caribou. Important habitats should be located in close proximity to each other and never more than 5 km apart.

Harvest scheduling should ensure that mature forests that are useable by caribou, link special management zones at all times.

Human and vehicular disturbance on late-winter caribou ranges should be discouraged, especially where such activities will force caribou onto avalanche prone terrain. An integrated management program for snowmobiling near Revelstoke should be investigated to determine its success and applicability in other areas.

In some instances, where specific habitat objectives cannot be met due to other resource interests, it may be possible to maintain caribou through compensatory management. Potential special management programs, which are less desireable than proper habitat management, include:

- access control signs, physical barriers on roads or removal of roads,
- predator control through liberal public hunting or active professionally executed control programs,
- reduction in the numbers of other ungulates and associated predators through liberalized hunting regulations.

Such compensatory programs should only be considered where habitats are already below target levels, where catastrophic events (eg. fires, disease) alter the habitat values or where economically viable alternatives are limited. Careful site specific planning must be completed to ensure that key caribou habitats are identified and protected.

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Towards a Caribou Habitat Management Strategy for Northwestern Ontario: Running the Gauntlet

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Abstract: A management strategy for woodland caribou (*Rangifer tarandus caribou*) habitat is being developed in northwestern Ontario. This strategy is based upon a set of draft *Timber Management Guidelines for the Provision of Woodland Caribou Habitat.* These guidelines recommend maintaining a sustainable supply of winter habitat within large tracts of old forest, protecting calving areas and minimizing human disturbance. Due to the large temporal and spatial scale of caribou habitat management, an ecosystem-based approach is recommended. Public response to the strategy shows a strong dichotomy between environmental and utilitarian values among all the major stakeholder groups. The major issues raised by the public include security of industrial wood supply, quality of the knowledge base, level of awareness of caribou, economic impacts on remote communities, concern about environmental impacts and silvicultural know-how. The government is responding to these concerns as the strategy evolves. Current emphasis is placed on increasing awareness of the public, training resource managers in caribou biology, management and habitat planning, implementing interim habitat management prescriptions and studying the potential impact on wood supply. The final direction for a northwestern Ontario strategy to conserve woodland caribou habitat has yet to be decided, although a commitment has been made to strive for the conservation of woodland caribou populations and their habitat.

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Introduction

Northwestern Ontario is developing a strategy for managing woodland caribou (*Rangifer tarandus caribou*) habitat. This paper describes our progress and approach in developing and implementing this strategy. It represents a case study in caribou habitat management, and builds upon proposals previously documented by Racey *et al.* (1991). As such, it is not so much a scientific paper as a chronicle of activities and responses to those activities in pursuit of a management strategy.

The strategy was required to halt the documented northward recession of woodland caribou range in Ontario. This range recession has resulted from a variety of factors including changes in forest structure, predator-prey balance, disease and hunting (Darby *et al.,* 1989). Changes in forest and wildlife communities as a result of timber harvesting have been identified as major factors (Darby *et al.*, 1989; Racey *et al.,* 1991). Evidence to suggest the connection between caribou decline and timber management activities is summarized by Cumming and Beange (1993). The impetus for trying to manage woodland caribou habitat in the forested regions of northwestern Ontario arose from increased awareness of their presence across the landscape, and the realization that they were a resource that was neither being considered nor conserved by contemporary forest management practices.

Ontario has developed draft *Timber Management Guidelines for the Provision of Woodland Caribou Habitat* (Racey *et al.*, 1991; OMNR, 1993a), to both protect woodland caribou and permit timber management to take place. Whether these guidelines will work is an ongoing debate. However, we know that continuing to manage the forest in the traditional manner will not protect woodland caribou (Racey *et al.,* 1991; Cumming & Beange, 1993). In addition it was apparent it would be impractical to attempt to manage caribou on one Forest Management Unit (FMU) without regard for management on adjacent FMU's. The caribou management strategy is based upon the understanding that caribou couldn't be sustained on a single FMU and need to be considered at a regional scale, using a broader ecosystem-based approach. This is a new concept as all other wildlife and forest resources are managed on Wildlife Management Units (WMUs) or FMUs.

The increased concern for caribou occurred at approximately the same time as a change in the expressed corporate culture of the Ontario Ministry of Natural Resources (OMNR). A corporate shift towards sustainable development and an "ecosystem management" approach was reflected in a number of OMNR documents (Ontario Wildlife Working Group, 1991; Ontario Forest Policy Panel, 1993; OMNR, 1991). The OMNR articulated a new goal based on the concept of sustainable development (OMNR, 1991) partially based on the following policy principles:

> "... Human activity that affects one part of the natural world should never be considered in isolation from its effects on others."
>
> "... We must recognize the value of a diversified economy based on the preservation of the diversity of the natural world."
>
> "Our understanding of the way the natural world works - and how our actions affect it - is often incomplete. This means that we exercise caution, and special concern for natural values in the face of such uncertainty, and respect the 'precautionary principle'".

The challenge to northwestern Ontario resource managers was to develop a Caribou Management Strategy with the goal of maintaining caribou populations within their current range. The objective is to provide a long-term supply of caribou habitat while maintaining a viable forest products industry within significant portions of caribou range. This sets the stage for the gauntlet that must be run.

A gauntlet is two rows of people facing each other armed with clubs or other weapons with which they strike at an individual who is made to run between them. Like any emotionally charged and polarized issue, those trying to manage the issue are often caught in the middle (Fig. 1). In the case of woodland caribou in northwestern Ontario, the apparent solution to management problems may appear counter-intuitive; a paradox that confuses the stakeholders and frustrates managers. The apparent immediate solution, protection of existing habitat, does not recognize the spatial and temporal complexity of forested landscapes. Long term maintenance of habitat may require scheduled and large-scale habitat disturbance. Provision for long term wood supply and access may require initial investment in road construction and regulation of forest age class. Maintenance of diversity at the Provincial level may mean conservation of local areas of low habitat or wildlife diversity. Differing perceptions and demands among stakeholders, even when certain principles are agreed to, are the weapons that befall the management strategy as it is developed, as it matures, and as it is implemented.

Methods

A team of foresters, biologists and resource management specialists was empowered to develop a regional caribou strategy to guide habitat management and to undertake public consultation pertaining to wood-

Fig. 1.
The caribou gauntlet. To almost every proposed solution to the problem of managing woodland caribou there is a strongly bipolar response based upon an environmental or utilitarian perspective. There is either too much information too fast, or not enough information; concern over amount of wood available for harvest, but concern that the cuts are too big; desire to protect caribou, but not at the expense of moose.

land caribou in northwestern Ontario. This process involved the collection of background information, development of a habitat mosaic methodology based upon the draft guidelines, application of the guidelines to current Timber Management Plans, and consultation on all components of the strategy.

Background information on inventory and biology was collected to clarify the status of caribou in northwestern Ontario. Emphasis was placed on identifying caribou wintering areas (Timmermann, 1993a), and determining caribou presence in areas where inventory information was scarce or absent. The public was enlisted to report sightings of woodland caribou, particularly summer habitat. A special emphasis was placed on the remote tourism industry because of their access to, and use of, potential calving lakes. In addition, calving site surveys were conducted according to a set methodology (Timmermann, 1993b) on potential calving areas near locations of proposed timber harvest allocations. Past observations of caribou were compiled to augment contemporary inventory efforts.

A regional map of current caribou distribution and range was constructed based upon these data. This map formed the basis for discussions on the area which could be managed for woodland caribou and to identify the zone of continuous distribution.

A habitat mosaic development process was created using as its basis, the draft *Timber Management Guidelines for the Provision of Woodland Caribou Habitat* (Racey *et al.*, 1991; OMNR, 1993a). Mosaic development was based on the concept of identifying and documenting areas of present and future winter habitat. This was done by developing a schedule of allocation and harvest of the forest so a sustainable supply of large areas of mature winter habitat is provided. This approach recognizes the dual role of winter habitat in providing opportunities for caribou to space themselves from predators while still providing winter food resources (Racey *et al.*, 1991).

Caribou sightings and basic interpretive information on soils, landform, forest cover and contemporary forest ecology knowledge were used to identify and evaluate, current and future winter habitat. These current and future winter habitat blocks provided the framework around which the sustainable mosaic was developed. In areas with relatively few options for conserving winter habitat, emphasis was placed on protection of existing winter habitat. In areas where most of the forest was old, emphasis was placed on renewing large areas of future winter habitat while protecting large areas of existing winter habitat. Maintenance of a sustainable supply of large tracts of old forest containing suitable winter habitat required planned cutting of large areas (100 km^2 or greater) to provide for future habitat. This does not require clearcutting the entire allocation, but of operating in an area for a period of 5-20 years, regenerating the forest to winter habitat where ecologically feasible, abandoning all secondary and tertiary roads, and then leaving the area largely untouched until the next commercial rotation. Primary roads must avoid existing or future winter habitat blocks. Silviculture strategies would encourage management of non-winter habitat areas to restore the basic landscape structure and composition that was previously there, but not to enhance diversity beyond the level previously existing. This is quite different from the strategy for managing moose (*Alces alces*) that encourages the deliberate production and maintenance of a high proportion of forest edge habitat.

There were several objectives of the consultation and communication program. A communication strategy was developed to upgrade biological knowledge of resource management staff and to increase the awareness of the public of woodland caribou in northwestern Ontario. Materials to support the public education and consultation strategy were developed. This information included written and audio-visual products and a detailed communication plan to address the key issues that were anticipated to arise. Input was solicited from the public and timber industry on the proposed caribou strategy and the potential impacts of managing for woodland caribou.

Early in the process, communication took place with the forest industry to discuss potential issues and identify areas of significance to woodland caribou. Specific resource management planning teams were in place for the preparation of five year Timber Management Plans on the Trout Forest, and Brightsand Forest, and for a two year contingency plan for the East Caribou Forest (Fig. 2). Aspects of the caribou strategy were presented to the public during development of these plans, as well as during consultation relating specifically to the caribou strategy.

A concurrent planning process was the public review of the boundary for the 155 000 ha Wabakimi Provincial Wilderness Park. The role of parks as refugia in sustaining woodland caribou populations in northwestern Ontario was a major consideration in the boundary review.

Results

The southern limit of continuous caribou range in northwestern Ontario was delineated as a result of the compilation of all recent caribou sightings, inventory efforts and habitat surveys (Fig. 2). The area north of this line represents that portion of the

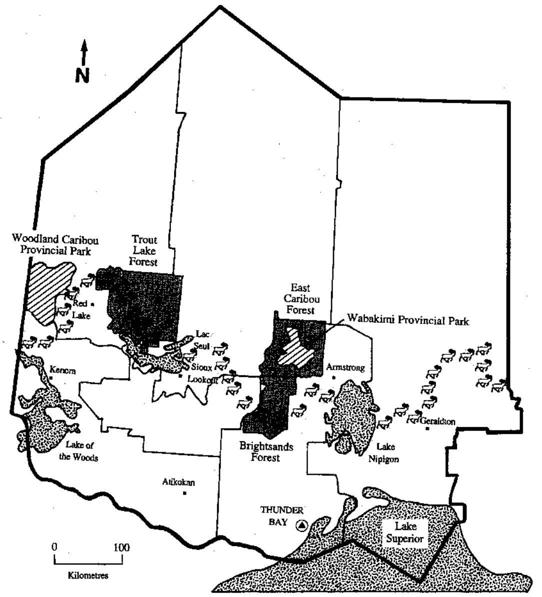

Fig. 2. Locations of the Trout Forest, Brightsand Forest, East Caribou Forest and Wabakimi Provincial Wilderness Park in northwestern Ontario. The best estimated "continuous distribution" line represents the southern-most limits of where we believe we could sustain woodland caribou using a habitat mosaic approach.

landscape most appropriately managed to maintain caribou habitat. The line also defines the zone in which caribou habitat mosaic planning should take place.

Most FMU's north of the line of continuous caribou distribution were involved in the mosaic development process to some degree, and mosaic development was achieved to varying degrees of completeness. Mosaic development was most urgent, and is most complete for those FMU's where timber management planning was currently under way. The process for habitat mosaic planning was customized for specific FMU's by recognizing the contributions of disturbance history, natural landscape features, existing access and refugia such as parks and reserves. Efforts were made to ensure compatibility and continuity of habitat mosaics across administrative boundaries. This regional mosaic is still incomplete, and work is continuing.

Education and communication documents prepared included a technical note on caribou biology and issues (Godwin, 1990), an 11 minute video on woodland caribou and forest management (OMNR, 1992), and three fact sheets pertaining to woodland caribou biology (OMNR, 1993b), the proposed caribou management strategy (OMNR, 1993c) and common questions and answers (OMNR, 1993d).

Twelve key messages which summarize the basis for and content of the strategy were assembled and relayed to the public during the education and consultation process:

1. OMNR is managing for maintenance of caribou and caribou habitat, as part of its ecosystem management approach in the Northwest Region.
2. Caribou are adapted to a fire-disturbed boreal ecosystem. They have different habitat requirements and differ biologically from white-tailed deer and moose.
3. Caribou occur now across much of the northern part of the region. Their range has receded northward over the past century. The primary causes of this recession include loss of habitat and a change in the predator (gray wolf (*Canis lupus*) and prey (moose/caribou) relationships resulting from forest disturbance and increased road access.
4. Current caribou range and the zone of continuous distribution are the basis for future caribou management. The caribou habitat management strategy is intended to stop the northward recession of caribou range in northwestern Ontario.
5. Timber management planning is now occurring within caribou range, and evidence indicates that a continuation of current (traditional) timber management practices will result in further loss of caribou range.
6. The Northwest Region of the OMNR is proposing to manage the forested land base within caribou range using a habitat mosaic approach. Large protected areas of mature forest growth will be balanced with large disturbed areas over the caribou range. Over a period of 50-100 years, this would approach the coarse landscape pattern created by wildfires. The effects of wildfire will also be incorporated into the management strategy.
7. Known critical habitat values will be protected during the planning process.
8. Typical application of the *Timber Management Guidelines for the Provision of Moose Habitat* (OMNR, 1988) generally results in a progressive harvest development pattern. Over time, this creates large disturbance areas associated with the developing road network, but without associated large contiguous undisturbed areas. A caribou habitat mosaic approach will result in a sustainable supply of large, relatively even-aged, older, forest tracts across the landscape, and designed to include winter habitat.

9. In current caribou range, moose numbers are unlikely to decrease. The existing balance of moose, wolves and caribou will be maintained, although there will still likely be an increase in moose numbers for a period of time in the vicinity of cutovers.
10. The OMNR wants public comment on these habitat management proposals.
11. A provincial caribou policy is being developed through public consultation. As part of that process, a regional caribou habitat strategy is being implemented [Subsequent to public consultation, a decision was made to defer policy development].
12. Caribou habitat management at the landscape level will change the pattern of traditional timber harvesting, and there may be measurable impacts on wood supply to the forest industry.

Public consultation took place in October through December 1993 with a large and diverse audience being reached and a large number of caribou sightings reported by the public (Table 1). The response from the public varied but revealed a dichotomy of perspectives on caribou management and the perceived impact (Table 2). The issues, as identified from public input, fall into the following broad categories where action is required to address the real or perceived problems.

Wood Supply

Wood supply concerns expressed by the forest industry revolved around the loss of merchantable volume in older stands fulfilling the need for caribou habitat, due to being withheld from harvest past their normal prescribed rotation age. There were concerns that wood utilization patterns would result in excess or shortage of veneer, sawlog or pulpwood depending on the size or make-up of the harvest block, and the specific product demands of the company doing the harvesting. There was also concern that the anticipated higher investment in road building due to bypassing accessible wood would result in more expensive wood and reduced competitiveness. The forest industry is concerned that caribou management will constrain flexibility and reduce opportunities for making best economic use of the forest. There were sincere, but unsubstantiated, concerns raised about the potential loss of jobs.

Table 1. Summary of public involvement related directly or indirectly to the caribou strategy. This involvement includes responses to proposals and provision of information.

	Event	No. of Events	No.of People Attending Events
Direct consultation	Open houses	11	441
	Caribou displays	20	464
	Staff training	15	268
	Comments / letters received	99	N/A
	Caribou sightings reported by public	423	N/A
Indirect consultation	Other resource management planning sessions	20	578

Knowledge Base

Knowledge about the caribou population and habitat resource is still limited with little prospect for significant improvement in the near future. The potential socio-economic impacts of de-emphasizing moose management for the sake of caribou and of altering the rules for allocation, harvest and regeneration are largely unknown or undocumented. There is no empirical evidence to suggest the proposed management strategy will be effective at maintaining woodland caribou where they now exist.

Awareness

Awareness of caribou biology, ecology and management principles is still very low among the general public, but increasing among resource managers and special interest groups. Comments from the public suggested many were overwhelmed by the quantity and complexity of information they received while, at the other extreme, some were dismayed by the limited information available on which to base their opinion. Unfamiliarity with the process of public consultation, policy development and current government priorities lead to mistrust and questions as to why the process was happening and how input would be used.

Local Needs

Local needs are perceived as being sacrificed for "city dwellers" far removed from northwestern Ontario, who will never experience the resource first hand. There is the perception that "ecosystem management" is not very tangible and will not provide local economic benefits. The concept of "ecotourism" is still in early stages of development.

Environmental Impacts

Concern over environmental impacts, both known and hypothesized, suggest to some that the Ministry

Table 2. Synthesis of public responses to the caribou strategy by stakeholder group, subdivided by key components of the strategy. Every component of the strategy seems to be perceived in both a positive and negative way by each of the stakeholder groups. Each group has a utilitarian (human-centred) and environmental (environmental ethics) perspective to its position.

Stakeholder Group strategy component	Environmental Perspective	Utilitarian Perspective
Forest Industry Size of cut	may create more "natural" landscape pattern; some companies want to be thought of as land stewards	increased cost of regeneration in remote cutovers would force harvesting of immature or unmerchantable products; pulp instead of sawlogs, hardwood instead of softwood etc. may increase access cost, and alter wood supply calculations resulting in reduced annual allowable cut, and potential loss of jobs public may view caribou as an excuse for larger cut size, this perception may have repercussions on the industry
Caribou vs moose	generally in tune to sustain all species, including woodland caribou	possible anti-logging repercussions if cutting patterns are perceived to be anti-moose
Location of "line"	where wood supply and access are not issues, the proposed management line for caribou makes sense and is generally accepted	line may be very inconvenient for certain timber management priorities in specific areas "lots of caribou" north of the line, and socio-economic factors should be primary consideration on where to manage caribou. Feel the line should be moved north in certain circumstances
Mosaic concept	may provide greater flexibility in applying silvicultural practices consistent with the ecology of the site; such as prescribed burning consistent with long range forest management planning principles; forces companies to look at entire forest over entire rotation	difficult to plan for with quality of existing inventory information requirements for 60-80 year projections and links to adjacent Management Units requires a variation from traditional Timber Management Planning Process; administrative limitations to planning and implementation of the mosaic may be situations where the necessary silvicultural prescription is much more expensive than the acceptable prescription that would have been used under the moose guidelines
Environmental Groups Size of cut	desirable if it may conserve caribou; have many concerns pertaining to site degradation, nutrient depletion, and impacts on other wildlife species	large clear cuts are ugly and are inconsistent with the general environmental position that small cuts with lots of edge are aesthetically pleasing and beneficial to wildlife
Caribou vs moose	caribou are part of the ecology of this portion of the boreal forest and should be conserved, even at the expense of moose moose will still be present on the landscape woodland caribou should be a priority because the number of caribou in the area would suggest they are "threatened"	some wildlife species that have their habitat conserved through moose habitat management will not be protected when managing for woodland caribou; want all species protected

Location of "line"	conserve caribou where they now occur should consider reintroduction and movements into areas previously occupied by caribou	disagree with partitioning of the environment into management zones; inconsistent with notion of managing ecosystems
Mosaic concept	long term planning for habitat is desirable, as is a commitment to try to sustain boreal ecosystems; question the similarity between a caribou habitat mosaic and landscape pattern created by wildfire recognize that no better approach to conserve caribou currently exists other than no timber harvest a natural fire pattern would provide a range of fire sizes	want to create a large fire driven ecosystem wilderness park to act as a control to the management strategy. This also serves their need for wilderness conservation; want park system to provide anchor to habitat mosaic
Outfitters Size of cut	large areas would be regenerating at a relatively consistent rate leaving the appearance of wilderness at an earlier age than if a large number of age classes and reserves were present in a relatively small area	large cutover blocks would destroy the perception of wilderness, particularly for fly-in operations
Caribou vs moose	do not want to see moose decline but would like to sustain caribou if moose hunting opportunities are not limited	want to try to maximize number of moose available to harvest and market no significant economic return from caribou
Location of "line"	conserve caribou where they are	would just as soon manage for moose, or sustain wilderness in all areas where remote tourism exists
Mosaic concept	eco-tourism opportunities for non-consumptive resource use are becoming more abundant; greater protection may be afforded to caribou calving lakes that also have tourist camps than afforded through the moose guidelines	would like to get greater protection around calving lakes and reduced access as offered in the caribou guidelines, but smaller cutovers as offered in the moose guidelines
OMNR Staff Size of cut	large cuts are acceptable if they sustain the species and ecosystem function of the forest concern over social, political and environmental implications of large cuts	may cause problems with wood flow and product availability would require re-examination of how wood supply calculations are made on the management unit level
Caribou vs moose	would generally prefer to conserve caribou in areas where they currently exist; sustain the function of the boreal forest ecosystem	moose targets may not be achieved, the moose program which has traditionally been a flagship of the wildlife management program is seen as threatened in some areas
Location of "line"	based on biological data in accordance with current corporate direction to maintain species where they now exist	concern of increased issues management and undue workload and criticism of OMNR
Mosaic concept	accept notion of the mosaic creating a landscape pattern of age class and patch size similar to that created by wildfire	requires planning beyond the traditional 20 year planning horizon; the administrative mechanisms do not readily allow for this major changes may be required to basic forest management principles; such as oldest first, normalization and estimation of maximum allowable depletion

should err on the side of caution (the precautionary principle). Environmental concerns over the impacts of large harvest areas on nutrient status, regeneration success, successional pathways, aesthetic value and wildlife population fluctuations have been expressed. These concerns appear to arise because of both ideological objections to large cutovers and specific concerns about environmental degradation. These environmental concerns manifest themselves in the perception that the mosaic approach does not mimic fire disturbance and will not be effective at sustaining forest composition and structure.

Silviculture and forestry

Silviculture and forestry practices required to produce forest stands valuable for caribou winter habitat have not yet been fully documented and tested. Questions exist as to how the forest industry will set and achieve targets in woodland caribou range. There is difficulty in extrapolating and envisioning the impact of practices applied at the stand level to responses at the landscape level. This is true particularly in light of the underlying, and often limiting, influence of landform and soil conditions. The interaction of silvicultural practices with lichen (*Cladina* spp.) ecology, successional pathways and hardwood magnification have all been identified as problems, but usually in a general sense and not specific to identified landscape units. Two questions arise repeatedly: can we adequately describe stand conditions and silvicultural objectives in a way meaningful for woodland caribou habitat, and do we have the tools and commitment to achieve these objectives under the current management, institutional and fiscal framework?

The caribou habitat mosaic developed for the Brightsand Forest centred on the documented calving areas on Seseganaga Lake. This is an irregular, island-filled lake dominating the northeast portion of the Management Unit. Existing wintering areas to the south were identified for protection as well as the timber along a chain of ridges and lakes connecting the two. The past logging history in the Unit left very few options for the protection of woodland caribou or the development of a mosaic other than a large protected area of winter habitat. In the Brightsand Forest caribou management will probably result in a reduction in opportunities for the harvest of timber, but the magnitude and duration are still to be decided.

In the Trout Forest the majority of timber harvest occurs in the southern end of the unit. Caribou wintering areas can largely be avoided in future allocations of timber for harvest at existing allocation levels. Anticipated higher demand for sawlogs from the unit in the near future may initiate some conflicts in resource use that do not now exist. There are still many options available for managing the Trout Forest for both caribou and timber. The approved 1994-1999 TMP for the Trout Forest implements the principles of caribou habitat management and maintains the options for long term mosaic development.

Management decisions for woodland caribou in the East Caribou Management Unit were heavily influenced by discussions on the role of Wabakimi Provincial Park. One position was that the park should act as a refuge for caribou to mitigate the impacts of forest management in the area around the park. Another argument was that there is no guarantee that the guidelines for caribou will work, and therefore the park should be expanded from 155 000 hectares to 1 250 000 ha. It was proposed that this would permit a natural, fire-driven ecosystem to sustain caribou habitat until we know if the guidelines are effective. Recommendations for park boundary expansion are being developed, with caribou being one of the major values considered. A preliminary mosaic has been developed based upon the existing park boundary. Timber management planning has been deferred, pending the outcome of the park boundary review. In the interim, caribou wintering areas are being protected in a contingency plan.

Discussion

In an ideal scenario, the OMNR would have comprehensive inventories in place before it initiated management programs. In the case of caribou, inventory information was being gathered and assembled at the same time as management issues and conflicts were being identified. As a non-game species in Ontario, there was not a comprehensive caribou data base of either populations or habitat. However, managers were comfortable with the initial level of information obtained from a number of conventional and non-conventional sources, such as observations from the public, searches of archival documents and quickly mobilized inventory efforts. Public reports of caribou sightings were very helpful in delineating caribou range; the public was very supportive and over 400 such reports were received. The Region was able to assemble a good estimate of the southern boundary of continuous caribou range which was significantly revised from that previously reported (Darby *et al.*, 1989).

The amount of inventory and habitat information required to initiate caribou management illustrates the dilemma of trying to manage species using a single-species management approach. We will never have the resources to collect meaningful biological data on all wildlife species for conservation purposes. It suggests that investment in management and inventory should be focused on a more "ecosystem-based" management strategy. In general, the broad habitat mosaic approach based upon winter habitat blocks (Racey *et al.,* 1991), is an attempt to sustain a landscape pattern at a scale similar to that created by wildfire - a rudimentary ecosystem management concept. Much more knowledge of stand and forest level composition, structure and function and how to manage for these attributes will be required to truly call this process a form of "ecosystem management". This strategy may more appropriately be described as a modification of timber management practices to conform to some basic landscape patterns associated with a natural environment. Expressed in this way, the maintenance of woodland caribou may be interpreted as an indicator that one aspect of ecosystem function, at the landscape level, has been maintained.

The probability (uncertainty) of success in sustaining woodland caribou in the face of timber management activities was questioned by environmental groups. It was fully recognized that our scientific, management and inventory information was incomplete and that the management strategy and projected impacts were based only upon best estimates from the available data.

Uncertainty about the prognosis for success of the proposed management strategy could not be adequately allayed at this point. However, it has been recognized, even by many critics of the strategy that it reflects the only real alternative other than the prohibition of forest management within caribou range or accepting further loss of caribou range. Experience and knowledge we now have suggests we won't know for up to 40 years if attempts to create winter habitat blocks have been successful. The only proof accepted by critics will be empirical evidence of previously harvested forest stands becoming reoccupied by woodland caribou in the winter. In the absence of such empirical evidence, we must always recognize the risk associated with an untried management activity. However, we wouldn't be following the "precautionary principle" if we continued using management practices we know will fail to sustain caribou.

Very difficult management decisions will have to be made. Should caribou be allowed to disappear from the commercial portion of the boreal forest by continuing with current management practices which we know will lead to the demise of caribou (Cumming & Beange, 1993)? Should a huge fire-driven wilderness park be established to conserve caribou in case the proposed management strategy should fail to achieve its objectives? Should the boreal forest be divided up into a very large controlled experiment?. Adaptive management would have us manage woodland caribou based upon the best information and knowledge available, and be prepared to modify those management practices as more, and better information becomes available. A more active approach would be to design specific, paired treatments on the landscape with a rigorous assessment schedule to monitor effectiveness.

Adaptive management using ecosystem management principles may ultimately force us to challenge the limits (validity) of established forest management practices. There are still institutional and procedural barriers to implementing a caribou habitat management strategy. Our official planning framework is still very much based on featured species management and 20 year planning horizons at the FMU level. Caribou management requires a new look at established forest management planning principles such as the calculation of maximum allowable depletion, the "oldest first" rule, and the definition of a "normal forest". It stimulates managers to synthesize information from stand level concepts and silvicultural effectiveness in order to visualize the results at the landscape level.

Analysis of public input showed that most stakeholders supported the concept of sustaining caribou on the land base. Public reaction to the proposed habitat management strategy was clearly split between two philosophies: environmental and utilitarian. For example, environmental groups expressed strong support for efforts to maintain caribou but strong resistance to the use of large cutovers to achieve that end. A proposed alternative as well as insurance against the uncertainty of the strategy was the use of large protected areas such as parks to protect or "anchor" caribou range in the commercial forest. This alternative would exclude logging within the parks. The forest industry also indicated support for the concept of sustaining caribou, but expressed major concerns about bypassing accessible wood, increased access costs and loss of wood supply. Outfitters and members of the remote tourism industry generally welcome the added protection to calving lakes, and increased access control, but did not like the idea that we might not be trying to maximize moose in these areas or the aesthetic implications of large operating blocks for timber harvest. Representatives of remote communities in the north expressed concern that attempts to conserve caribou may constrain their ability to utilize other resources.

These opposing views have led to polarized positions in the search for solutions. It is generally accepted that caribou could be sustained by halting timber management and allowing a fire-driven ecosystem to exist. It is also generally accepted that we could continue managing timber according to traditional means if we accepted the recession of caribou range beyond that zone of immediate economic interest. Neither of these highly polar views supports the proposed caribou management strategy which is based upon the best understood science, the concept of sustainable development and which attempts to integrate timber management with the conservation of caribou. These opposing views form the Gauntlet that must be run by the resource managers in considering the full range of environmental, social and economic factors when natural resource management decisions are made. Our management challenge is to reconcile these differences to provide the economic benefits while not compromising our natural resource base.

Increased public awareness of woodland caribou in the boreal forest of northwestern Ontario is evident in the past few years by portrayals in popular magazines (Taylor, 1993; Addison, 1993). Stakeholders involved in TMP advisory teams now routinely discuss the implications of timber and caribou management.

The open houses and information sessions were successful in increasing public awareness of the presence of caribou, caribou biology and habitat requirements. There was also increased awareness of the fact that maintenance of caribou on the landscape would require significant changes to timber management practices. Comments ranged from profound, well-reasoned arguments in support, against or supporting modification of the proposed strategy to comments revealing an emotional reaction to specific, perceived concerns. Comments received from the open houses allowed us to set priorities to respond in three major ways: 1) further efforts in education and awareness, 2) improvements in information and knowledge base, and 3) revisions to the proposed strategy and guidelines. Efforts to implement these responses are now under way.

Caribou habitat mosaic development forces forest managers to look beyond traditional 20 year planning horizons at forest growth and access over the rotation of the forest. It also requires them to consider the impacts of their management of the Forest Management Unit within the greater context of the forest landscape as a whole. This approach is essential to the concept of managing and sustaining ecosystems across the region. It could, in effect, be a first positive step in the direction of "ecosystem management".

Caribou management requires commitments to be made over vast tracts of land over long periods of time. Therefore, it is desirable that we strive toward the basic ecosystem management principle of sustaining composition, structure and function of the forest at all scales. Caribou management can be delivered within an integrated resource management approach as part of a broader ecosystem management framework. This is the over-riding philosophy that will allow both the sustainability of the resource and the inherent utility of the resource to be managed. However, the concept of sustainable development suggests that the first allocation of the resource is to the resource itself, which is an essential component of the "precautionary principle"

Conclusions

In the case of woodland caribou, the complex interaction of habitat, predators, and populations was very difficult for the general public to understand. As all jurisdictions slowly move toward ecosystem-based management, resource management agencies must find a way to communicate and increase the awareness of these concepts among the public. The public has to be involved and the public has to be informed in order to play its essential role in resource management. The public will always have a valuable role in defining appropriate balance between economics, protection of specific resource values and long term environmental health.

Stakeholders identified wood supply and lack of information on impacts of caribou management as the most significant issues. The first stage of caribou strategy development was necessary just to isolate and focus on these issues. The OMNR now has a clearly defined set of tasks to resolve before further decisions can be made on the caribou strategy. These tasks include a comprehensive analysis of the impact of caribou management on industrial wood supply, bringing together stakeholders to identify and reconcile opposing perspectives, refining the caribou strategy and implementing an interim caribou management approach as a precautionary measure. In addition, the need for better and more comprehensive inventory and habitat information was clearly identified and actions are being taken to meet these needs.

Caribou habitat management requires large-scale, long-term management of the boreal forest, and the opportunities for doing rigorous scientific studies of the effectiveness of the management techniques are very limited. Some form of adaptive management is required. We must use the best management and scientific knowledge currently available to initiate habitat management, but have appropriate active and passive monitoring programs in place to allow managers to respond to new knowledge and adjust their management practices accordingly. Our first attempts will not be perfect.

We must maintain our focus on sustaining caribou populations and habitat within the context of ecosystem-based management, within an environment of constant change and while addressing a gauntlet of public concerns and perceptions. These concerns and perceptions that caribou and caribou managers face are examples of a larger problem: trying to trade off utilitarian and environmental concerns pertaining to resource allocation and conservation. This will be one of our biggest challenges as we practice, implement and refine ecosystem-based management in support of sustainable development.

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Managing for Caribou Survival in a Partitioned Habitat

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Abstract: Forest management guidelines for woodland caribou (*Rangifer tarandus caribou*) in Ontario need to be re-examined in light of the finding that caribou partition habitat with moose (*Alces alces*), partly to find virtual refuges from predation by gray wolves (*Canis lupus*). Forest-wide guidelines seem inappropriate for a species that is widely scattered and little known. Management should concentrate on and around currently used virtual refuges to ensure their continued habitability. Cutting these areas may force the caribou into places with higher densities of predators; winter use of roads might bring poachers, increased wolf entry, and accidents. A proposal for 100 km^2 clear-cuts scheduled over 60+ years across the forest landscape would probably minimize moose/wolf densities in the long run as intended, but because of habitat partitioning might forfeit any benefits to caribou in the short-term. Sharply reducing moose densities near areas where caribou have sought refuge might incline wolves to switch to caribou. Cutting beyond caribou winter refuge areas should aim at maintaining current moose densities to prevent wolves from switching prey species. Operations level manipulation of the forest around each wintering area should provide winter habitat for the future, while treatment replications with controls across the whole forest would provide reliable knowledge about which approaches work best. The remainder of the forest should be managed to maintain suitable densities of all other species.

Key words: forest harvesting, guidelines, habitat partitioning, moose, gray wolf

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Woodland caribou ecology has progressed to a stage where useful generalizations are available to managers. Perhaps most widely recognized is Bergerud's (e.g., 1974a, 1985a, 1992) insistence that predation is the crucial factor to consider in managing caribou populations. Support for his position has come from numerous other authors (Gauthier & Theberge, 1986; Edmonds, 1988; Elliot, 1989; Hayes *et al.*, 1989; Seip, 1989). The consensus is that only plans minimizing predation will succeed in perpetuating caribou populations.

One of the most common causes of increased predation has been the presence of alternate prey species, especially the moose. Simkin (1965) suggested that caribou in Ontario declined because higher wolf densities resulted from immigration of moose after 1900. He was followed by other authors, mostly in British Columbia (e.g. Bergerud, 1974a; 1985a; 1985; Bergerud & Elliot, 1986; Seip, 1985; 1990; 1991; 1992). In view of these studies, agreement has grown that the goal of caribou management in the presence of moose and wolves should be to reduce moose densities and keep them low. Following this logic, Racey *et al.* (1991) described forest management guidelines for northern Ontario aimed at minimizing the suitability of newly harvested forest areas for moose to reduce the density of wolves that might prey on caribou.

But ecology of woodland caribou in Ontario differs in some respects from ecology described in most other places (except, perhaps, Wells Gray Park; Seip, 1990). Survival of caribou in the face of apparent competition from moose appears to depend on habitat partitioning in the patchy forest (Cumming *et al.*, 1996). The question arises, "what difference should the knowledge of habitat partitioning make to management strategies for caribou survival?" In this paper, I examine that question in the Ontario context to critique guidelines presented by Racey *et al.* (1991) and to present alternatives. The question has application outside Ontario since similar management alternatives require resolution in any place with habitat partitioning between caribou and some other prey species in the presence of shared predators. Furthermore, the problem necessitates drawing implicitly or explicitly on a range of basic issues to address the single problem of managing landscapes for caribou survival.

General questions

What is the goal of management?

Management goals must relate to the size of the population to be managed. Darby *et al.* (1989) estimated 15 000 woodland caribou in Ontario, an estimate slightly higher than the 13 000+ estimated by Simkin (1965). These figures give the appearance of a substantial number of caribou at least holding their numbers, and, perhaps, increasing slightly. But timber management guidelines are necessary only for the portions of commercial forest of northern Ontario where caribou live. The size of the area to be managed is difficult to estimate because the southern limits to caribou distribution remain indefinite. By inspection (Fig. 1, Cumming & Beange, 1993), it would seem to be at least 1/4 of the commercial forest or about 100 000 km^2. Darby *et al.* (1989) reported data that would have allowed differentiation between caribou populations in the commercial forest and those farther north in Ontario, but they did not make use of the information. Cumming & Beange (1993) estimated only about 800 caribou in the actual commercial forest area. Some 13 000 caribou living in the Hudson's Bay Lowlands, 800 caribou in parks and 400 in a timber reserve are irrelevant for purposes of designing timber management guidelines. Management for sustained yield of 15 000 caribou would be quite conceivable; the goal for managing 800 caribou must be to ensure survival. The landscape scale planning proposed by Racey *et al.* (1991) would be suitable for 15 000 caribou, but stand level planning is necessary to ensure survival of 800 animals.

What is the planning/management area?

The idea of dividing the forest between areas where moose are featured species and areas where caribou are featured ignores the reality that even in those parts of the boreal forest inhabited by caribou, the portions actually used by caribou are relatively small. Cumming & Beange (1987) found <10% of the forest used by caribou in winter. Even the 20% projected by the draft guidelines would imply vast expanses with no apparent use by caribou. Some justification might be found for retaining a row of 100 km^2 polygons next to caribou wintering areas to keep moose and wolf densities low near caribou, following the logic of Racey *et al.* (1991), but large unused areas would remain. Furthermore, pockets of caribou might be located south of that line, or might return, or be re-introduced there.

Areas to be managed specifically for woodland caribou should be those with caribou potential. Although the draft guidelines discuss potential habitat, they do not distinguish it from habitat currently used. Present winter habitat can be determined by mapping tracks in snow from the air (Cumming & Beange, 1987); potential areas can be found by combining satellite imagery available for fire prediction purposes with Forest Resources Inventory data (Antoniak, 1993). Thus, it should be possible to delineate both currently used stands and areas of caribou potential from the forest in general. These areas, rather than everything north of a prescribed line, should be the areas designated for special caribou management.

What is the general management strategy?

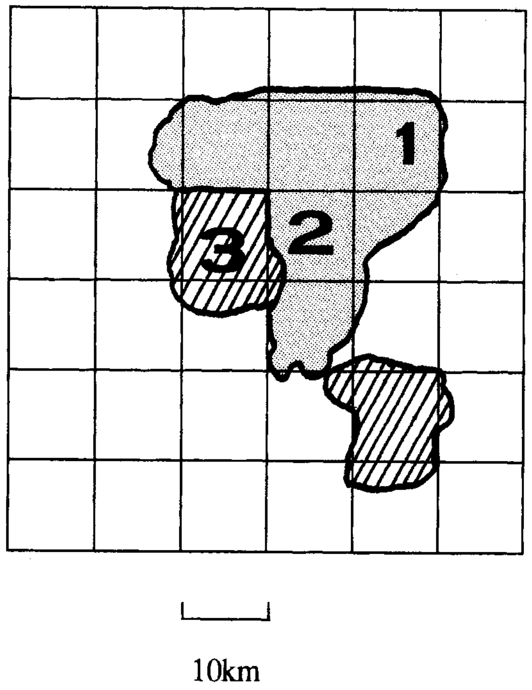
In their review of woodland caribou biology, Darby *et al.* (1989) overlooked a striking difference between caribou in Ontario and those described elsewhere. Bergerud (1985a, p. 221) referring to British Columbia states, "Winter ranges are more variable for caribou than (ranges) at any other season", but Cumming & Beange (1987) provided evidence that caribou in Ontario return to the same general areas each winter, much the way white-tailed deer (*Odocoileus virginianus*) use winter yards (Taylor, 1956). The behaviour is probably dictated by the patchy nature of the forest where ground lichen stands supply food for caribou. These forest types are found only in definable locations (Antoniak, 1993). Once caribou locate such places they live there throughout the winter and return annually for many years. Nearly all the wintering areas located by Cumming & Beange (1987) are still in use (Cumming & Beange, 1993); caribou have been known to occupy one area each winter since at least 1956, and they were reported in the same vicinity by a Conservation Officer in 1910. Thus, these are traditional wintering areas that should not be ignored in management plans. Their presence allows managers to avoid dispersing their efforts over vast areas and, instead, concentrate them on the stands currently used by caribou, and those with future potential.

Racey *et al.* (1991) agree with Bergerud (1985a) that caribou will easily shift from a currently used wintering area to a new one: "Caribou have evolved to shift their range in response to fire and can likely shift it in response to logging." (p. 113). This statement assumes that caribou have suitable alternate range. Schaefer & Pruitt (1991) showed that on a small scale and short time period caribou were not able to shift their range in response to fire. Cumming & Beange (1993) showed similar evidence for cutting. It may be that all suitable winter range (i.e. available food and few predators) is already occupied. At any rate, it would seem imprudent to base the future survival of caribou on the assumption that caribou will be able to shift their range and survive.

These wintering areas may be more important than just food sources if Cumming *et al.* (1996) are correct in their contention that caribou use them as virtual refuges also. If that is true, destruction of the refuge, or any disturbance that forced caribou to leave it, might increase predation risks to levels that could terminate the local caribou band. Where a patchy habitat provides the possibility of virtual refuges the first and most important management step for preserving caribou appears to be ensuring that these refuges remain habitable for caribou.

Unfortunately, the guidelines to maintain a patchy forest would not assure continuation of wintering areas that are currently providing refuge for caribou (Fig. 1). Prescriptions for a matrix of harvest and leave blocks, as proposed by Racey *et al.* (1991), might, or might not, delay harvesting areas currently used by caribou. Eventually these areas would certainly be cut, hoping that suitable habitat had been prepared by the scheduled cutting somewhere else. Such dependence on extensive management is not reliable enough where caribou survival is at stake. More specific direction must be applied to localized areas to maximize benefits of forest management planning for caribou.

Management of caribou wintering areas is much like managing for old forests (Harris, 1984). Racey *et al.* (1991) maintain that 20% of the forest should be in caribou winter habitat at any one time. Thus, they propose cutting 20% of the timber in each of the age categories 0-20, 20-40, 40-60, 60-80, and 80-100, similar to the example provided by Hunter (1990, p.69). However, as Hunter (1990) points out, the trouble with this approach is that it occupies so much forest land, in this case, all the commercial forest north of the yet-to-be-determined line dividing caribou forest from moose country. A reserve system would tie up much less forest land.



▒ Existing Winter habit (which may or may not be occupided)

☐ Other forest types in a variety of age classes providing summer and calving habitat

▨ Block allocated for harvest in next five years

Fig. 1. Management at the landscape level may not ensure survival of caribou with partitioned habitat. If caribou were currently wintering in Area 1, the distant cutting would do them no harm. If they were using Area 2, adacent cutting might cause disturbance, reduce moose densities, incline wolves to switch from moose, and lead individual wolves along ecotones directly to the caribou. If caribou were using Area 3, cutting would probably cause caribou to leave and that would likely result in the demise of the local caribou band (Cumming & Beange, 1993)

Specific questions

Should virtual refuge areas be cut?

Cumming & Beange (1993) provided evidence that forest harvesting in caribou wintering areas resulted in the caribou leaving. In 3 places where portions of wintering areas were cut, caribou did not use those areas again for 12 years. Thus an important requirement for retaining virtual refuge areas would be to exclude them from forest harvesting until the caribou prove that suitable alternate stands are available by moving to them. However, reserving wintering areas themselves from cutting might not be enough. Cumming & Beange (1993) reported 2 monitored areas that caribou abandoned even though actual harvesting activities were 1 and 3 km distant. Nearby disturbance that drives out the caribou would eliminate the benefits of these special patches as effectively as would cutting them. Therefore, in addition to prohibiting cutting in areas occupied by caribou, the same prescription would have to be extended to a buffer zone surrounding them. On the basis of this one example, it appears that a buffer against disturbance from forest harvesting would need to be at least 3 km wide.

Another possible threat associated with forest harvesting might be the presence of roads through wintering areas. Whether or not traffic by itself has any effect on caribou, roads might increase incursions by wolves, provide access for poachers, and introduce the possibility of road kills. Caribou mortality would probably increase reducing the value of these areas as refuges.

What is the significance of fire?

Since the time of Cringan (1957) the role of fire in caribou ecology has remained controversial. Some biologists have emphasized the destructive power of fire (e.g., Scotter, 1972) while others have pointed out its necessity for renewing conditions that will support lichens (e.g., Miller, 1979). Racey *et al.* (1991) recognize the threat of fire in blocks of mature timber providing winter habitat and suggest that their protection from fire will have to be made a priority. Support for this view has been provided by Schaefer & Pruitt (1991).

Espousing the view that fires in the past have been good for caribou, Racey *et al.* (1991) model their forest management guidelines on these fires. They claim that to do so requires 100 km^2 harvest cuts. Although some fires undoubtedly exceeded 100 km^2, many smaller fires must have accompanied them. A better mimic of natural conditions would be to cut areas of varying sizes. Furthermore, it does not follow from the observation of early fires producing caribou range that they did so in the best way. In a 32000 km^2 study area, Cumming & Beange (1987) found the overall gross area used by caribou was 9% of the forest north of the Canadian National Railway (where there has been little recent disturbance by humans) and 6% to the south. Over 90% of the range produced by fire is not being used. Specific management directed at caribou wintering areas and their surroundings should be able to do better.

What procedures will minimize predation on calving grounds?

The importance of calving refuges to caribou has long been established (e.g., Bergerud *et al.,* 1984; Bergerud, 1985b; Bergerud *et al.*, 1990). But disagreement remains concerning what constitutes a calving ground for caribou in Ontario. Racey *et al.* (1991) suggest that calving sites may be dispersed "in isolated or secluded bogs, fens or in mainland forest stands" and that "a much higher proportion of Ontario's caribou may give birth to calves in this type of site and collectively they may be more important than islands or lake shorelines" (p. 110). This statement has implications for management strategy. If caribou use the entire forest for calving, a matrix of cutting areas would seem to be the only way of maintaining some calving grounds. But if most caribou calve on islands and shorelines a series of shoreline reserves could protect all of them. Racey *et al.* (1991) support their assertion by referring to studies in Newfoundland (Bergerud, 1974b), northern Quebec (Brown *et al.*, 1986) and Manitoba (Shoesmith & Storey, 1977; Darby & Pruitt, 1984 - only the latter suggested that most caribou calve inland). On the other hand, Racey *et al.* (1991) overlooked five references specific to caribou in Ontario, all of which agree that caribou calve on islands or along shorelines (Bergerud, 1974a; 1985b; Bergerud *et al.*, 1990; Cumming & Beange, 1987; & Simkin, 1965). Simkin (1965), with a research assistant and two native trappers, searched for caribou calving grounds by canoe, and by foot up to 1 km inland (Simkin, pers. comm.), during four summers, and supplemented these ground surveys with two helicopter flights. He concluded that caribou cows with calves, at calving time, were found only on certain types of islands and similar shorelines. Future research may support the views of Racey *et al.* (1991), but current information does not warrant protection of the entire forest for calving.

Even a designation of islands and shorelines as caribou calving areas is not specific enough for recommendations concerning management of summer habitat. At the present state of knowledge, managers cannot predict in advance which islands and shorelines caribou will use. Summer habitat has to be within migration distance of suitable winter habitat (or vice versa), but travel distances between winter and summer range vary greatly (from 26 to 80 km, mean 46 km (Cumming & Beange, 1987). In abundantly watered northern Ontario, many lakes will not be used. Bergerud *et al.* (1990) show that summer presence of caribou can be discerned along shorelines, even where sand beaches are not available. Summer reconnaissance should be undertaken to determine which lakes require shoreline protection for caribou cows with calves. Once these lakes have been identified, the recommendations for reserves put forward by Racey *et al.* (1991) seem adequate: shoreline reserves ranging from 400-900 m varying in size and shape to suit individual sites should be designated. As Racey *et al.* (1991) point out, care needs to be exercised to ensure that narrow reserves do not become "traps" for vulnerable animals in areas easily searched by predators (a consideration common among caribou biologists but not yet addressed by theory, Holt, pers. comm.).

What measures are necessary to retain travel corridors?

With winter and summer grounds protected, final consideration for year-round caribou habitat protection must include routes followed by caribou moving between winter and summer ranges. For some caribou bands, this is not a problem.

Cumming & Beange (1987) reported 1 caribou band that did not move at all. Similarly, the caribou described by Cumming *et al.* (1996) rarely ranged outside the area occupied in winter to find summer habitat (unpublished data). However, many other caribou do move substantial distances, and for these the travel routes between summer and winter refuge areas may be the most hazardous portions of their habitat.

But prescriptions to minimize predation along these routes are difficult to specify. In some cases, the travel area is so diffuse that it can scarcely a be called a "route" (Cumming & Beange, 1987). In such circumstances, the best course would be to remove the entire travel area from the forest land base as some kind of reserve. If that is not possible, the alternative would seem to be scheduled cutting to retain some standing tree cover along the way at all times. In places where the travel route is well defined, prescriptions can be more specific. Racey *et al.* (1991) suggest a 2 km wide corridor of (mainly) conifers >3 m height. This provision should be adequate in most places.

How can winter predation be minimized?

Possibly, the most controversial recommendation of the guidelines proposed by Racey *et al.* (1991) concerns their method for minimizing winter predation. Since direct wolf control would be publicly unacceptable in Ontario, the draft guidelines propose forest harvest scheduling to form matrices of 100 km^2 cut and uncut blocks. The provisions would be applied throughout the entire >100 000 km^2 of the northern commercial forest occupied by caribou. The objective is to keep moose densities low so that their biomass would not support high enough wolf densities to threaten caribou. This strategy should be successful in producing poor moose habitat since it is designed to approximate the opposite of that produced by moose guidelines (Ont. Min. Nat. Res., 1988) . Over the long term, numbers of moose should decline, and with them numbers of wolves, thus reducing the threat to caribou.

However, Racey *et al.* (1991) give no consideration to the short term. As Holt & Lawton (1994) point out short-term effects may differ markedly from those of the long term. Forest harvesting generally produces clear-cut areas where escape cover for moose has been removed and road access for hunters improved (Eason, 1989). A dangerous situations might arise if this practice were carried out in mixed-wood stands with relatively high moose and wolf densities. Eason (1989) reported a reduction from 0.40 - 0.27 moose/km^2 in the first 2 years after such an area was cut, due mainly to hunting. If this scenario were re-enacted adjacent to a caribou wintering area, prey switching would be almost inevitable (Bergerud, 1983). With their normal prey base greatly reduced and no time for numerical response, wolves could be expected to show a functional response by turning to caribou.

Perhaps these short term effects could be avoided. Two possibilities explored by Eason (1985, 1989) were to prescribe block cuts rather than clear cuts or prohibit hunting after the area had been cut. These alternatives might prevent a sharp decrease in moose numbers but they would leave the elevated densities of moose that Racey *et al.* (1991) are trying to avoid. A gradual decrease might be achieved by cutting blocks near caribou wintering areas and then gradually liberalizing hunting over a period of several years. That way moose numbers might be reduced without the short term adverse consequences. Unfortunately, such a carefully timed reduction of moose densities would require more intensive management than currently practiced in Ontario. Intensive management of this kind, though a desirable objective, appears a possibility far in the future.

A final possibility for avoiding dangerous short-term reductions of moose near caribou might be to leave uncut buffers around caribou wintering areas. But documented long range movements of wolves (Fritts *et al.*, 1984) suggest that such a buffer would have to be very wide; translocations in Minnesota to distances of 50-317 km were largely unsuccessful at keeping problem wolves out of livestock production areas. Establishing wide enough buffers to keep out hungry wolves would amount to reserving large tracts of land from forest harvesting.

Any efforts short of the careful management explored in these options would run the risk of abruptly decreasing moose densities, with consequent prey switching by wolves, and heightened predation on caribou. Few, if any, caribou might remain to benefit from planned long term reductions in predation.

The solution would seem to be to avoid reducing moose densities. Caribou are surviving with current moose densities; presumably they could continue to do so in the future if, as recommended earlier, currently used virtual refuges were retained. As long as moose remained at current levels, more practical buffer widths should prove effective (Fig. 2). Unpublished data for 7 flights during 3 winters in a recent study of a small wintering area (40 ha, as *per* Jones & Sherman, 1983) showed only 3 wolf tracks inside the caribou wintering area (2 in year 1, 1 in year 2), 6 within the first surrounding kilometer, 7 in the second, and 6 in the third (B. Hyer, pers. comm.). The 19 tracks in surrounding areas represent wolves that could have preyed on caribou if they had chosen to do so. Since they rarely entered the caribou occupied area, it seems unlikely that wolves beyond 3 km would be so inclined. Therefore, as long as moose densities remain about the same, the 3 km buffer width recommended for protection from forest harvesting disturbance would seem sufficient for protection from predation also, as long as moose densities remain unchanged. Managers must manage wolf motivation, not travel ability.

In view of the uncertainty of present knowledge, the safest course of action in managing for caribou survival would seem to be maintenance of moose densities at about present levels. If they should accidentally increase, they could always be reduced by more liberal hunting seasons.

How should the rest of the forest be managed?
If moose densities are best kept at present levels, cutting in the forest outside caribou wintering areas could follow moose guidelines (Ont. Min. Nat. Res., 1988). However, in these locations there seems no reason to specialize on moose. The far north areas which are virtually the only places where caribou still survive are too remote from human populations centres to be considered prime moose management areas. In these places, management for species richness might be more suitable than management for featured species. Such an objective would not imply increasing numbers of species beyond those originally present. It means attempting to maintain all the species found in the area at suitable population levels. But these approaches are not mutually exclusive. "The two management systems can also be used together to insure species richness while favouring selected species in specific locations for particular purposes." (Thomas, 1979, p. 17). A combined system might be best in view of the complexities already discussed. A general objective would be to manage the forest for species richness; specific objectives might then include managing for caribou where site conditions permit, and for moose where site conditions favour them. Species richness could be retained by managing for a "diversity of diversities" (Hunter, 1990). The objective would be to diversify not only forest types, but also cut sizes as discussed earlier, by prescribing many small cut areas, a substantial number of larger cuts, and a few very large harvest areas. These could be arranged to retain all current caribou wintering areas, produce experimental new ones, encourage high moose densities in suitable places remote from caribou, and retain all other species native to the boreal forest.

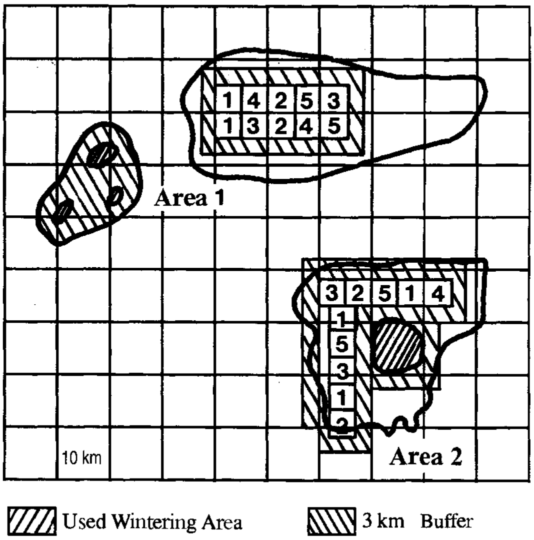


Fig. 2. Proposed forest management strategy for winter caribou refuges in partitioned habitat. Area 1 is a complex of small currently used wintering areas with a 3 km buffer; since no adjacent potential sites are available, replicated operations-level treatments for stand renewal are carried out on a nearby area (numbered small squares represent treatments or controls). Area 2 is a single currently used wintering area surrounded by a larger potential area with treatments; numbers represent same treatments as in Area 1 to allow determination of within-site and between-site variation.

A basic question - is the use of guidelines appropriate?

The analysis thus far assumes that forest harvesting guidelines to benefit woodland caribou are acceptable and necessary. But perhaps a more fundamental questions needs to be asked: in view of the known wide dispersion of caribou and uncertain state of knowledge concerning their ecology, is the writing of guidelines the most appropriate approach to habitat management? Walters & Holling (1990, p. 2060) point out that "every major change in harvesting rates and management policies is in fact a perturbation experiment with highly uncertain outcome, no matter how skillful the management agency is in marshaling evidence and arguments in support of the change" Walters & Holling (1990) maintain that this "passive adaptive" approach to management is only one step better than evolutionary or trial and error management. Using the best data available at the time, the passive adaptive approach constructs a single best estimate or model for response (in this case, the guidelines) and bases subsequent decision choices on the assumption that this model is correct. Walters & Holling (1990, p. 2064) warn that although some might argue that we can "learn from experience" (in this case, improving the guidelines as better understanding becomes available) "there is a long history of sad experience with the false premise that it is possible to 'learn by doing' through sequential application of different policies to whole systems". Furthermore, this approach may lead to overlooking opportunities for improving system performance in the future.

Walters & Holling (1990) emphasize that the balance between knowledge gained and risks incurred often does not favour experimental disturbances in single, unique, managed systems, but they point out that this conclusion changes drastically for a collection of similar units (lakes, distinct populations, areas). The semi-isolated bands of caribou still scattered across northern Ontario constitute such a collection. A key question then, according to Walters & Holling (1990), is how large an experiment to conduct. Again, Walters & Holling (1990) put the problem concisely: "The challenge is to develop a nested experimental design that will permit clear separation of the effects of as many of these changes as possible, so that a sensible balance of management tools and policies can be developed" (p.2065). An alternative caribou management proposal along these lines would attempt to provide future winter habitat for caribou, not by general guidelines, but by a series of replicated experimental perturbations located in potential caribou habitat near presently used stands. For example, where ground lichens are being lost due to crown closure, a variety of treatments might be attempted to set back succession without opening the canopy enough to affect snow conditions.

This scheme would be similar to the reserve system proposed for retaining old Douglas fir (*Pseudotsuga menziesii*) forests by (Harris, 1984).The "core" reserve of old forest would be the area currently used by caribou. Surrounding the core would be a series of stands harvested in long rotations (perhaps 100 years) using the experimental cutting techniques that would provide answers on how best to produce new caribou habitat (Fig. 2). Currently used caribou habitat would receive maximum protection for as long as necessary while active adaptive cutting alternatives attempted to produce replacement winter habitat.

Summary of strategies for managing caribou habitat in a partitioned forest

A sound management strategy for caribou survival in northern Ontario must begin with the virtual refuges that allow the caribou to survive apparent competition with moose. These areas, with at least 3 km buffers, should be located and reserved from forest harvesting and from road-use during winter. Without such immediate action, the time would soon come when the only caribou remaining in the forested portion of northern Ontario would be those in 4 national and provincial parks. Since these parks are separated by hundreds of kilometers, caribou habitat would be fragmented and caribou numbers reduced to levels approaching minimum population sizes. Saving the smaller caribou bands outside the parks would allow individual caribou to trade among bands, greatly enhancing the genetic viability of the whole local group. In places where caribou wintering areas are sufficiently large and close so that boundaries of winter reserves overlap, consideration should be given to removing the entire area from the commercial forest land base, either through establishing more parks or by declaring them caribou habitat areas. Reserves should also be placed around calving lakes and along travel routes.

Having taken care of the most immediate and dangerous threat to caribou, management should turn to activities that would replace currently used caribou wintering areas when they become no longer habitable though successional changes. To achieve this objective, currently used wintering areas should be mapped and designated "areas of concern" where habitat renewal would be attempted through specialized forest harvesting. Once alternate areas proved sufficiently attractive for the caribou to move to them, original wintering areas could be cut.

No one can predict with certainty that recommendations will ensure the future of caribou, but following these suggestions should contribute toward continuation of woodland caribou populations in their ancestral forest habitats into the next century, and, hopefully, beyond.

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A Cooperative Industry - Government Woodland Caribou Research Program in Northeastern Alberta

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Abstract: Rapid development of large scale logging and increasingly intensive petroleum exploration and development in northeastern Alberta prompted the establishment of a cooperative research program to investigate various aspects of woodland caribou (*Rangifer tarandus caribou*) biology. The ultimate goal of the program is to develop an effective plan that will ensure the long term survival of caribou while allowing for renewable and non-renewable resource development. There are three parts to the program. Part I began early in 1991 and makes use of conventional radio telemetry as a means of recording various parameters of general caribou biology. The study area encompasses approximately 4000 km2 of low relief, boreal mixedwood forest. Preliminary results from 2500 radio locations (involving 50 individuals) indicate that woodland caribou inhabiting the study area are non-migratory and are strongly associated with some of the more scarce peatland forest types present in the area. Investigations to document the basic biology and ecology will continue for another two years. Part II began in early 1993 as a part of a two-year investigation into the disturbance effects of petroleum exploration and development on caribou movements and behaviour. One objective of this study is to develop a predictive model useful in determining the cumulative effects of varying intensities of disturbance on caribou. Part III began in early 1994 with a proposed three-year investigation to determine the mechanism of spatial and temporal separation of caribou and moose in the study area. These relationships may indicate the means by which caribou minimize the impact of wolf predation on their populations in northeastern Alberta. Results will be applied to industrial land use and specifically to large scale forest harvesting planned for the area. The research program is supported through cooperative funding contributed by 24 petroleum companies, 1 forest company, 2 peat companies and the Alberta Departments of Environmental Protection and Energy. The research aspect of the program has been developed and implemented by staff of the University of Alberta, Alberta-Pacific Forest Industries, the Alberta Fish and Wildlife and Forest Services and the Alberta Environmental Centre. The program also incorporates a public information and liaison function. Newsletters, information videos, brochures and public consultation are the means used to accomplish this task.

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Introduction

In the 1970's, considerable concern was expressed across North America about declining woodland caribou (*Rangifer tarandus caribou*) numbers and distribution (Bergerud, 1974 and others). Agricultural and industrial encroachment along with human settlement gradually encroached on caribou range in the north-eastern United States and in Canadian provinces along the southern boreal forest fringe to the Rockies.

Trends in woodland caribou populations in the remainder of their range vary across their distribution in accordance with a variety of factors. Speculation that Alberta caribou have suffered a significant decline in their occupied range over the past 50 years is an issue currently being debated. (Bradshaw & Hebert, 1994). However, recent large scale commitments of wood to the forest industry and oil and gas to the petroleum industry has placed this species in a very vulnerable position.

In west-central Alberta during the late 1970s and early 1980s, considerable effort was made to investigate a declining population of caribou (mainly the mountain ecotype). Logging was resulting in deterioration of the winter range of these animals. Wolf predation, native hunting, poaching and highway vehicle collision were implicated in a steady decline of these caribou (Edmonds, 1986).

Although woodland caribou status in Alberta overall was poorly documented at that time, the concern generated by the study resulted in a closure of recreational hunting in 1981 and the development of restrictive industrial land use regulations relative to caribou range.

These restrictions were modelled after general knowledge of ungulate biology and energetics. The emphasis was aimed primarily at minimizing exposure of caribou to disturbance or other factors which potentially increased mortality during mid and late winter.

Industrial operators found the land use restrictions onerous and considerable conflict resulted. Attempts have recently been made to resolve the conflict through the establishment of regional industry/ government working groups.

The following outlines the development of the group working in northeastern Alberta.

Development of the Northeast Region Standing Committee on Caribou

Northeast Alberta is an area of relatively flat boreal mixed-wood forest, much of which is occupied by woodland caribou. Alberta government land use restrictions on occupied range were aimed largely at minimizing potential adverse effects on caribou by actions of the petroleum exploration and development industry. Restrictions related primarily to industrial access and timing with the intent of reducing caribou exposure to hunting or harassment and to disturbance which potentially cost caribou increased energy drain in late winter. As well, there was an effort to prevent improvement of predator (wolf) efficiency via limiting seismograph line clearing or snow packing during winter.

Efforts by industry to comply with these restrictions lead to considerable conflict with regulatory agencies. The conflict lead to much discussion between government and industry. A decision was eventually reached to approach the problem through local cooperative working groups. As a result, the North East Region Standing Committee on Caribou (NERSC) was initiated in mid-1991 as an attempt to address the conflict in the northeastern part of the province. The committee originally consisted of members of several petroleum companies, one forestry company and staff representing the government regulatory agencies. The objective was to illicit a better understanding of restrictions and foster a cooperative approach to addressing the integration of caribou needs and industrial objectives.

NERSC was originally and still is co-chaired by a member each from government and from industry.

Very early in its evolution (fall 1991) it was learned that flexibility in land use regulations would not be possible until further information was known about caribou in the region. It was decided therefore that NERSC would act as facilitator for caribou research designed to answer the questions required to assure the long term survival of caribou as well as integrate industrial activity on caribou range.

Funding to initiate research originally resulted from direct participant donations of dollars, facilities and staff time. The Alberta Fish and Wildlife Service's Wildlife Trust Fund is used as the bank for the project.

From it's beginning in mid-1991 to the present, NERSC has continued to evolve with additional membership and the development of sub-committees for funding, public information and liaison, provincial coordination in addition to caribou research.

NERSC has produced two videos and a brochure, describing NERSC and its research program. Periodic newsletters are produced with a mailing list of 200.

The NERSC program is presently funded by a combination of industry donations of dollars, equipment and facilities; government input in the form of aircraft rental, staff time, equipment and facilities; and the University of Alberta in the form of student, student support and equipment. Donations and funds have been supplemented by significant grants from the Alberta Recreation, Parks and Wildlife Foundation and the Canada-Alberta Partnership Agreement in Forestry. Total NERSC funding to date is approximately $450,000 which includes an assessment of non-monetary contribution values. We anticipate funding sufficient to complete the program will be available.

As in any major research program, information useful for management application does not materialize until well into the program. This year however, we expect the findings to date will be sufficient to make preliminary adjustments to regulations affecting industry. A sub-committee to review this issue was recently established and recommendation will be submitted by mid-1994.

The NERSC Research Program

The NERSC research program has three basic components. The initial thrust was designed to investigate the basic biology and ecology of caribou in northeastern Alberta. Radio telemetry was the primary tool used.

Since field work began in early 1992, radio tracking, aerial census for numbers and recruitment, mortality retrieval, as well as vegetation and habitat information on an Arcinfo Geographic Information System (GIS) is providing an increasingly clearer picture of caribou numbers, distribution, seasonal movements, habitat preference, mortality and recruitment rate of these animals. Our GIS is presently working with about 3000 radio locations (from a total of 57 radio-collared animals), detailed access mapping and several vegetative/habitat mapping parameters including a detailed forest-peatland classification. Thus far, our caribou are relatively sedentary within general wetland complexes and show very significant preferences for specific treed-bog habitat types.

Density, mortality and recruitment rates determined to date are indicative of a stable or slowly declining population (although our sample sizes are still relatively small). The picture will improve, as we plan this aspect of the program to continue for another two seasons.

The second aspect of the NERSC Program is an investigation of the effects on caribou of industry-caused sensory disturbance. Monitoring caribou reaction in the form of behaviour and distance moved from simulated seismic explosions is the main mechanism of this study. This two year investigation will be completed in mid-1994. Results of the study will allow the development of a model to predict the probability of caribou encountering disturbance factors. This will be useful in establishing limits for specific industrial activity conducted on critical caribou range.

We will be reviewing the results of these two programs in the near future to determine how we might modify the access and timing restrictions presently imposed on industrial operators.

The third aspect of the program is designed to investigate the complex relationship between caribou and moose relative to wolf predation. The literature indicates that spatial and/or temporal overlap of range by caribou and moose exposes caribou to wolf predation which may be the primary factor limiting caribou population growth (Bergerud & Elliot, 1986; Seip, 1990). Understanding this relationship is critical in the design of large scale habitat disturbances such as the logging planned by Alberta Pacific Forest Industries which has rights to much of the timber in northeastern Alberta.

Field work on this aspect began in late 1993 with the selection of a suitable study area. Radio collaring of caribou was completed in early 1994. Moose and wolves will be captured as conditions allow.

The subsequent field work, data collection and analysis will be conducted largely by students from the University of Alberta, Department of Zoology and Animal Science. It is anticipated that this investigation will be completed in 1997.

Results will hopefully clarify the antipredator strategies used by caribou in northeast Alberta and will be applied to industrial land use regulations with particular emphasis on forest cutting design to maximize caribou survival over the long term.

NERSC As A Cooperative Program

The success of NERSC as a effective, cooperative government-industry research program is a result of genuine commitment of its members and very hard work by many involved in the planning, research, funding and the public information effort.

The establishment of a working group such as NERSC first requires a strong will on the part of senior government regulators to rely on a cooperative approach to problem solving by affected stakeholders. It then requires a few key persons in both government and industry who can instill confidence in all involved stakeholders. The subsequent building of trust and commitment requires demonstrated progress toward problem solving and considerable feed-back to assure that serious efforts are being made. Incorporation of a public information system is also essential to assure acceptance and accountability beyond the direct stakeholders.

An important and essential element involved in the success of NERSC is the extent of funding and the diversity of funding sources. It has been demonstrated that project funding is easier to obtain if stakeholders are seen to be financial contributors, partly as an indicator of support for their expressed concerns and commitment to problem solving. The leverage value of stakeholder contributions in expanding the "pot" is very substantial and should not be underestimated. It is therefore very useful to orchestrate funding efforts around the cooperative theme.

The ultimate objective of NERSC is to facilitate the development of specific management programs which will effectively address the needs of caribou while integrating resource extraction to the extent possible. Whether this is possible on a large scale and will meet the long term goals is open to speculation. However without an organization like NERSC, the long term survival of woodland caribou in the northeastern Alberta boreal forest would be much less probable.

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Industry:

Alberta Energy Company Ltd., Alberta-Pacific Forest Industries, Alberta Recreation, Parks and Wildlife Foundation, Amoco Canada Petroleum Company Ltd., Anderson Exploration Ltd., Bow Valley Energy, Canada-Alberta Partnership Agreement in Forestry, Chevron Canada Resources Ltd., Home Oil Company Ltd., Husky Oil Operations Ltd., ISH Energy Ltd., Lakeland Peat Moss Ltd., Lakewood Energy Inc., Mobil Oil Canada, Mark Resources Inc., Northstar Energy Corp., Nova Corporation of Alberta, Paramount Resources Ltd., Pensionfund Energy Resources Ltd., Petrorep (Canada) Ltd., Pinnacle Resources

Ltd., Rio Alto Exploration Ltd., Sun-Gro Horticulture Canada Ltd., Triton Canada Resources Ltd., Universal Explorations, Wascana Energy Inc.
Government:
Alberta Energy Department - Minerals Division
Alberta Environmental Protection
    - Alberta Fish and Wildlife Service
    - Alberta Environmental Center
    - Alberta Lands and Forest Service
    - Regional Coordination Services
Energy Resource Conservation Board
University of Alberta
    - Department of Zoology and Animal Science
Other Funding Agencies:
    - Alberta Recreation, Parks, and Wildlife Foundation
    - Canada-Alberta Partnership Agreement in Forestry

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Successful and unsuccessful attempts to resolve caribou management and timber harvesting issues in west central Alberta

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Abstract: Research studies of woodland caribou in west central Alberta began in 1979 in response to proposed timber harvesting on their winter ranges. Using results from initial studies, timber harvest guidelines were developed. A recent review of these guidelines, and the assumptions on which they were based, has resulted in a renegotiation by government and industry of timber harvesting on caribou range in west central Alberta. Caribou range in west central Alberta overlaps many jurisdictional boundaries: federal and provincial lands, four Forest Management Agreement Areas, three Alberta Land and Forest Service Regions and two Alberta Fish and Wildlife Service Regions. This jurisdictional complexity in combination with other factors such as total allocation of the timber resources, high levels of petroleum, natural gas and coal extraction activities, a high level of concern by public groups for caribou conservation and recent understanding of woodland caribou needs for abundant space has made resolution of caribou/timber harvest conflicts exceedingly slow and often relatively unproductive. This paper reviews 10 years of trying to resolve conflicts between timber harvesting and caribou conservation through meetings, committees, integrated resource planning, policy papers and public consultation. We describe what might be learned by other jurisdictions that are trying to resolve similar caribou/timber harvesting issues. We conclude with an overview of recent timber harvest planning initiatives on caribou range in west central Alberta.

Key words: *Rangifer*, woodland caribou, timber management, landscape planning, habitat management, conflict resolution, Alberta

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Introduction

As in many other jurisdictions (Darby & Duquette, 1986; Cichowski & Banner, 1993; Stevenson, 1991), maintaining woodland caribou (*Rangifer tarandus caribou*) populations in commercial forests is a complex issue in west central Alberta (WCA). Various factors contribute to this complexity. In WCA virtually all timber resources on caribou winter range have been allocated to forest products companies. In several cases more than one company has been awarded harvesting rights on a given winter range (up to three companies on one range). Annual allowable cut calculations have been made without consideration of caribou habitat requirements. A considerable amount of timber harvesting has occurred on caribou winter range in WCA, and there are demands for continued harvesting as these ranges are largely composed of merchantable and operable timber lands. Our current data (Hervieux *et al.*, 1993) indicate that on at least some winter ranges in WCA, caribou prefer highly merchantable mature and overmature forest stands, especially during deep-snow winter conditions. In addition to removing critical habitat for caribou, the current timber harvesting strategy (patterns of small, dispersed cut and reserve blocks), has considerable potential to increase the distribution and abundance of other ungulate species (moose, elk, white-tailed and mule deer) on caribou range. An increased prey base may result in increased predator numbers (Seip, 1991), primarily wolves, and a corresponding increase in predation rates on caribou. Other factors including petroleum and natural gas exploration and production projects, coal mining, human recreational activities, and the occurrence of a primary highway on caribou range all increase the challenges involved in managing caribou populations in WCA.

The intent of this paper is to provide a description of past and present attempts to integrate caribou population and habitat management with timber harvest planning in WCA. Together with reports such as Racey *et al.* (1991) and Stevenson *et al.* (1991), we hope that a description of our activities in WCA may be of some value to those facing similar issues in other areas.

Background on WCA caribou and industry

Initial caribou studies in WCA (1979 - 1984) described a migratory mountain caribou population and a more sedentary forest-dwelling population (Edmonds & Bloomfield, 1984). Both populations were below the probable food based carrying capacity of their range and had high adult and calf mortality primarily related to predation and man-caused factors (Edmonds, 1988; Edmonds & Smith, 1991). The migratory population calves, summers and breeds in mountainous areas that have protected status (Jasper National Park, Willmore Wilderness Park, etc.). However these caribou winter on multiple use lands in the foothills that are available for industrial, recreational and other human activities. Their year-round range encompasses about 15,000 km^2 which includes summer range in British Columbia. The forest-dwelling, non-migratory population inhabits about 1600 km^2 of unprotected, multiple use provincial lands on the eastern edge of the foothills. We currently estimate 400 - 500 mountain caribou using three winter ranges (Redrock Creek, Prairie Creek and A la Peche) and 60 - 100 forest caribou use the Little Smoky range (Fig. 1). Caribou range in WCA is primarily lodgepole pine (*Pinus contorta*) and lodgepole pine/spruce (*Picea* spp.) forest, greater than 80 years of age, interspersed with relatively small muskegs that provide terrestrial and arboreal lichens.

Two of the three mountain caribou winter ranges have had some timber harvesting since completion of the initial caribou studies in 1984. About 15% of the Redrock winter range and 10% of the A la Peche winter range has been impacted by first-pass logging. Negotiations over further logging within those two winter ranges and within the other two unlogged ranges have been ongoing since the mid-1980's.

Early timber management guidelines

Increased emphasis on understanding WCA caribou populations and habitat in the late 1970's and early 1980's was triggered by demands for new major logging entries on to the Redrock and A La Peche winter ranges. Special timber management plans were quickly developed in an attempt to mitigate the affects of those logging programs on caribou. A main emphasis was to protect areas of forest for the production of terrestrial and arboreal lichens. Also, those plans were composed of measures that did not deviate greatly from standard ground rules for timber harvesting in Alberta and as a result had negligible affect on the annual allowable cut. A description of the range specific plans follows.

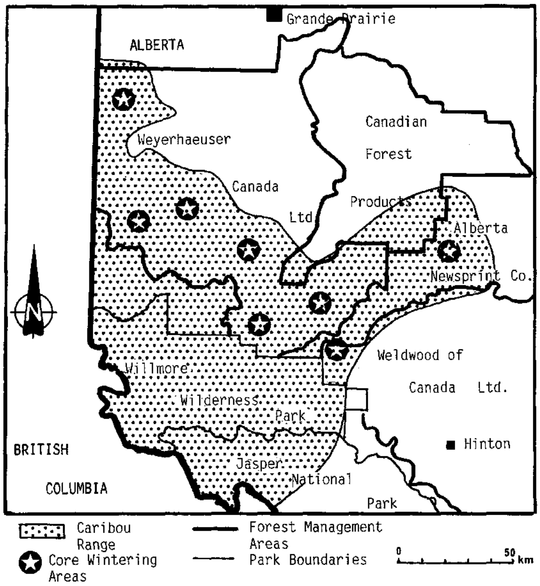

Fig. 1. Woodland caribou distribution and location of Forest Management Agreement Areas in west central Alberta.

Redrock Creek

Using 4 years of radio telemetry relocation data (up to 11 collared caribou) and some winter ground tracking, a Redrock winter range was delineated. This winter range was then subdivided into several zones based on the apparent importance of parts of the range to caribou (Procter and Gamble Cellulose, 1989). As a result of this zonation process, 60% of the winter range was made available for logging with a two-pass system. The remaining winter range was deferred from timber harvesting for 80 years, at which time a two-pass system would be initiated. The areas subject to this 80 year deferral were small (2.6 km^2 to 74.0 km^2 in size) relative to caribou travel patterns. Most of the deferred areas contained little or no merchantable timber volumes (meadow complexes, rocky ridges, younger pulp stands).

In Alberta two-pass logging involves laying out a series of first-pass cut blocks and second-pass reserve blocks in a checker board pattern throughout all operable, merchantable timber. Block size can vary to a maximum of 60 ha. Reserve blocks are harvested once timber regeneration in adjacent first-pass blocks has reached 2 - 3 meters in height . A timber rotation age of 100 years was established for the Redrock area. A goal of the Redrock plan was to use cutblock sizes that mimiced natural openings with the hope that caribou would use the cutblocks for foraging, travelling and other activities.

A La Peche

The A La Peche winter range was delineated using radio telemetry relocation data from 8 collared caribou collected over 3 years and four years of winter ground surveys. A three-pass system (with a 120 - 150 year rotation) was planned for about two-thirds of the range and in the remainder a two-pass logging system would apply. The three-pass system was to be used in areas known to produce terrestrial and arboreal lichens. A three-pass system involves a pattern of cut blocks, reserve-one and reserve-two blocks being laid out in a checker board pattern throughout the operable, merchantable timber. Harvest of reserve-one and then reserve-two blocks would require that regeneration had reached 2 - 3 meters in adjacent harvested blocks. Cut blocks could be up to 60 ha. in size and were to approximate the shape of natural forest openings (narrow and winding). The intent of this three-pass system was to leave about one-third of the area available as a foraging area, with perhaps another one-third available as travel/security cover.

Other winter ranges and reflections on early guidelines

The prospect of timber harvesting in the Prairie Creek and Little Smoky winter ranges (Fig. 1) remained a contentious issue during and after early work in Redrock and A La Peche. Throughout much of the 1980's, Alberta Fish and Wildlife Division field staff argued that portions of the Prairie Creek and Little Smoky winter ranges, 194 km^2 and 450 km^2, respectively, should be subject to a 30 year deferral from timber harvesting. A moratorium was sought to provide a reserve of effective habitat for caribou populations and to provide an experimental control in view of the unpredictable results of logging in Redrock and A La Peche winter ranges.

To date a timber harvesting moratorium for Prairie Creek has not been agreed to by senior levels in government. Much of the timber within Prairie Creek is at or past typical rotation age; government and industry timber managers felt that harvesting was required. In 1989 the Alberta Forest Service and the Fish and Wildlife Division agreed to a 30 year deferral for timber harvesting within a central portion of the Little Smoky range; an area that contained timber which was younger on average than preferred rotation age. Timber harvesting has continued to expand into the Redrock and A La Peche ranges as per the original caribou management plans.

Since development of these plans in the mid 1980's Alberta Fish and Wildlife Division field staff have had growing concerns that they were inadequate for the long term habitat needs of resident caribou populations. It was also becoming difficult to explain to an increasingly knowledgeable public how our plans might work. In view of new research and proposals being presented by various workers (Bergerud *et al.,* 1984; Bergerud & Page, 1987; Darby *et al.*, 1989; Seip, 1990; 1991) it was felt that the two and three-pass logging systems being used in Redrock and A La Peche would prove unsatisfactory in many ways. We had placed too much emphasis on maintaining foraging habitat and had not given enough consideration to the effects of increases in alternate prey and concentrating caribou into the remaining areas of useable habitat. Two factors that would possibly subject caribou to increased rates of predation on the winter range. Caribou habitat management no longer seemed clear or straight forward and the era of committees, working groups and policy statements began.

Committees, plans and processes

Over the past decade, concern that we had not adequately addressed issues relating to timber harvesting (and other industrial/recreational activities) on caribou range has resulted in a variety of government, industry and public initiatives in Alberta. These initiatives were started at local, regional or provincial levels and overall have attempted to develop a consensus on how to manage caribou herds and ranges. The following list discusses each major process in chronological order, to provide some insight on how issues have and haveaddressed in Alberta.

1984. The Fish and Wildlife Division produced the "Status of the Fish and Wildlife Resource in Alberta" (Paetkau, 1984). A report endorsed by the Provincial Government which argued that existing caribou populations and ranges in the province should be increased or at least maintained. This report provided an overall frame work for Fish and Wildlife Division activities, however, it had little affect on the allocation/management of timber and other resources.

1986. The Fish and Wildlife Division produced the "Woodland Caribou Provincial Restoration Plan" (Edmonds, 1986), a report which discussed ways to stem an apparent decline in provincial and especially WCA caribou populations. Few of the recommendations listed in the plan were adopted. Some aspects, especially discussions of wolf management, resulted in considerable public debate.

1987. Caribou were listed as endangered under the Alberta Wildlife Act.

1989. The West Central Alberta Caribou Technical Committee was formed. This was an ad hoc group of representatives from industry, government and public interest groups who attempted to exchange information and seek possible solutions to issues relating to industrial activity on WCA caribou ranges. After several years of meetings, no consensus had been reached and the group has disbanded. However, knowledge level of caribou biology and resource industry's requirements for operation was greatly increased.

1989. The Fox Creek/Knight and Berland Integrated Resource Plans were initiated. Part of a provincial scale planning frame work, these plans identify broad land management priorities in and around the Little Smoky and A La Peche ranges. In 1993 a Kakwa plan similarly began to set management priorities for parts of the Redrock and Prairie Creek ranges. All of these plans are ongoing and have yet to produce products.

1991. Alberta Forestry, Lands and Wildlife with Alberta Minerals Division produced the "Procedural Guide for Petroleum and Natural Gas Activity on Caribou Range" (Alberta Forestry, Lands and Wildlife, 1991). This is a policy paper which sanctioned general protection procedures for provincial caribou populations and habitat in relation to oil and gas development. Oil and gas development is to occur on caribou ranges so long as the "integrity" of caribou habitats and populations are maintained. What habitat and population integrity means, and how to insure it, has been left to industry and government field staff to determine. This policy paper did result in the formation of five government/industry committees which are to develop range specific operating plans for oil/gas and in some cases timber harvesting activities. Several of the committees have developed oil/gas guidelines, but in some cases these guidelines have been contested by some companies.

1991. A working group of Alberta Forest Service and Fish and Wildlife Division staff was formed to develop provincial timber management guidelines for caribou range. No consensus could be reached and the group disbanded after 18 months of periodic meetings.

1991. Alberta Fish and Wildlife Division released a provincial management plan for wolves (Alberta Fish and Wildlife Division, 1991). This policy paper requires that prior to wolf management, regional data sets must clearly indicate that wolf predation is a primary factor limiting ungulate populations.

1991. The Alberta Forest Products Association (various companies) completed a dialogue with the Alberta Environmental Network (public interest groups) on caribou/forestry issues. Agreement was reached on a list of factors which might limit caribou populations in the province.

1993. By this time all Forest Management Agreement holders had formed local public advisory boards and local Fish and Wildlife/Forest Service/Industry committees to, at least in part, resolve caribou/timber harvesting issues at the local level. No specific plans have been finalized yet.

1993. Alberta Fish and Wildlife Services released a provincial plan, the "Strategy for the Conservation of Woodland Caribou in Alberta" (Alberta Fish and Wildlife Services, 1993). This plan proposed general caribou management prescriptions on a range by range basis. Using a risk assessment process it was argued that two-thirds of the provincial caribou population could be maintained; largely herds in protected areas and in areas of low current conflict with industry. Industrial activity on remaining ranges would proceed with the possibility of some attempts to mitigate negative affects on caribou. The report did recognize unique aspects of mountain caribou in WCA and suggested that timber harvesting rights be purchased back from industry to protect some winter ranges. Upon its release, this plan was strongly criticised by government agencies, public groups and by industry. This criticism lead to abandonment of the draft plan and the formation of a new stakeholders committee (Alberta Caribou Conservation Strategy Development Committee) to recommend a provincial policy for caribou management activities.

Overall, the last decade of committees and process in Alberta have produced few results that address specific management issues on caribou range. To a certain extent, key decisions have been left to government and industry field staff, with little policy frame work available to help resolve disputes. Although progress has been slow, the debate about industrial activity on caribou range has become more focused. A decade ago the overall knowledge level among the various stakeholder groups was low. We were all doing our own thing and talking past each other. Now most stakeholders have had an opportunity for input and have adopted a true problem solving perspective. The current stakeholders committee process will hopefully work towards a much needed provincial overview as to objectives, priorities and management options for caribou populations.

Current timber harvest planning on WCA caribou ranges

A deficiency of our early timber harvesting plans was that we did not give adequate consideration to how much useable and effective habitat would be available for caribou populations into the future. To correct this situation we are now trying to develop a timber planning system that uses a landscape perspective to specifically consider the issue of caribou habitat supply and quality through time. Most local government and industry staff generally agree that timber harvesting will occur on most or all WCA caribou ranges subject to the following general principles.

1. Each winter range will again be delineated using current information. We will outline landscapes that now are or have the potential to be good winter habitat areas for caribou, that are large enough to support existing or target caribou populations (see below), that are relatively undisturbed and that allow for some management flexibility. Using these criteria we have increased or are negotiating increases in the sizes of several winter ranges; Redrock from 329 km^2 to 920 km^2, Prairie Creek from 194 km^2 to 560 km^2, A la Peche from 600 km^2 to 970 km^2 and Little Smoky from 450 km^2 to 1600 km^2.
2. Each range will be described as to current habitat supply and quality (stand types and ages). We will attempt to project future caribou habitat supply/quality in view of natural forest succession. This information will be reviewed to determine how timber harvesting, in the absence of wildfire, could be used to renew caribou habitat through time. The rationale being that harvesting could occur in given stand type/age classes as the availability of those habitats increased through forest succession and thus maintain winter ranges in a state similar to current composition.
3. We will strive to not unduly reduce the near term availability of any one stand type or age class in our sequencing of timber harvest.
4. Timber harvesting would be brought onto caribou winter ranges in a manner to, as much as possible, avoid fragmenting the range with cut blocks and areas of regenerating timber. We would try to take as much timber as possible out of as small an area as possible while still addressing other important management issues (eg. watershed and fisheries protection, stand regeneration).
5. In the near term, timber harvesting would stay out of presently defined range core areas, as recommended by Cichowski & Banner (1993) and Darby & Duquette (1986).
6. We would be careful that the proportion of a winter range harvested at any one time was not so large as to unduly constrain the resident caribou population with regard to the area available for dispersion to avoid predators and seekout forage and optimal snow conditions. As noted by Stevenson (1991), it is not obvious how to determine the amount of range a caribou population requires. We propose that two methods might be used to tackle the issue. First, we could try to leave enough useable habitat to allow the population densities of resident caribou to emulate caribou densities reported in literature (eg. Seip, 1991) for apparently stable populations. Second, by way of an impact assessment we might determine what the consequences of a planned logging entry would be on existing caribou population densities and decide if that change (increase) was acceptable. Both of these techniques would require an estimate of current caribou population size and agreement on population goals for each range.

The principles listed above are general. Specific planning and operational criteria still need to be agreed upon for several of the principles. Some criteria and decisions will be arbitrary. Timber harvest planning in view of the above discussion is beginning on a range by range basis in WCA. For example, our original plans for Redrock have been abandoned and a re-assessment for the A la Peche and Little Smoky ranges is required. Not all of the identified timber volume in those ranges was harvested under the old plans; providing an opportunity for a new approach. In Redrock we will meet further timber harvesting needs by accelerating the initiation of reserve block harvesting within the current layout area. Subject to agreement on a new harvest sequencing plan, no further harvesting will occur outside of this layout area for one or more decades thereby avoiding further habitat fragmentation of the Redrock range. Within Prairie Creek a relatively small harvesting area is being identified well away from the current core use portion of the winter range. Local government and industry personnel have agreed to develop sustained yield timber calculations for both Redrock and Prairie Creek ranges that specifically take into account a caribou habitat supply analysis. This will be a major achievement.

Conclusion

Despite slow progress over more than a decade, there are encouraging aspects to our management activities in WCA. Although some WCA caribou populations may only be approximately stable (Edmonds & Smith, 1991), we still have functioning caribou populations and habitats to work with. Also, caribou conservation is clearly a shared goal between government, industry and the public. It seems that we have side stepped absolute gridlock and are now discussing alternate strategies in a risk/benefit framework. A major issue will arise if addressing long term caribou habitat supply has significant affects on near term timber supplies (i.e. annual allowable cut) for industry. If such an issue occurs, it will require resolution at senior levels.

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Section 3.

General papers

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The recent record of climate on the range of the George River Caribou Herd, Northern Québec and Labrador, Canada

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Abstract: Records from permanent meteorological stations in and around the range of the George River Caribou Herd have been analyzed for the 1950-1991 period in order to identify climatic factors potentially influencing the numbers, condition, and distribution of caribou. Winter conditions identified include a significant temperature decrease over the period and some years of extreme snowfall. Spatial variations in snow cover may be responsible for shifts in winter range. Indications are that summer climate has not varied significantly, but spring and summer conditions may not have been particularly favourable for plant productivity in the summer range of females and calves. Climatological observations more representative of the summer range are needed for a better understanding of ecological relationships there.

Key words: Bioclimate, climate change

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Introduction

Climate or, more specifically, climate variability and change has been proposed as a significant and sometimes principal factor in the population dynamics of caribou (e.g. Vibe, 1967; Miller *et al.*, 1982; Meldgaard, 1986). It has been suggested that recent climatic events and trends may have contributed to the present state of the George River Herd of woodland caribou (*Rangifer tarandus caribou*) (Messier *et al.*, 1988; Crête & Payette, 1990; Couturier *et al.*, 1990; 1996). This herd, which currently ranges over an area of about 400,000 km² in northern Quebec and Labrador (Fig. 1), experienced a more than 30-fold increase between the late 1950s (Bergerud, 1967) and the mid 1980s (Couturier *et al.*, 1990). Recent surveys place current numbers at about the same level as in the 1980s, i.e. approximately 700,000 animals, with substantial evidence for declining recruitment and poor condition of the animals (Crête *et al.* 1996; Couturier *et al.*, 1996; Huot *et al.*, 1994; Russell & Couturier, 1994).

As described by Couturier *et al.* (1990), the current range of the George River Herd extends from the southern limit of the open boreal woodland (*taiga*) across the forest-tundra zone and to some extent into the tundra, particularly in northern Labrador (Fig. 1). The calving ground of the George River Herd is located near the height of land in the northeast. A separate caribou population, the Rivière aux Feuilles Herd, is identified with a calving area west of Ungava Bay and has a winter range that overlaps with that of the George River Herd (Couturier *et al.*, 1990). Major differences between these two herds have been found by Crête *et al.* (1990) in the composition and relative abundance of forage plants on their respective calving grounds and the resulting diet of lactating females. In the areas surveyed, the proportion of ground cover represented by forage plants of all kinds was 31% in the George River calving area, compared with 78% in the Rivière aux Feuilles area. The relatively poor condition of cows in the George River Herd reported by Huot (1989) has been attributed to these differences (Crête *et al.*, 1990; Huot *et al.*, 1994).

Climatic conditions determine to a large extent the composition of the vegetation, its productivity in the growing season, and its accessibility to foraging animals in winter. The climatic record from stations in and around the range of the George River Herd should indicate whether there have been any widespread climatic events or trends that might have significantly affected range conditions during the recent period of population growth,

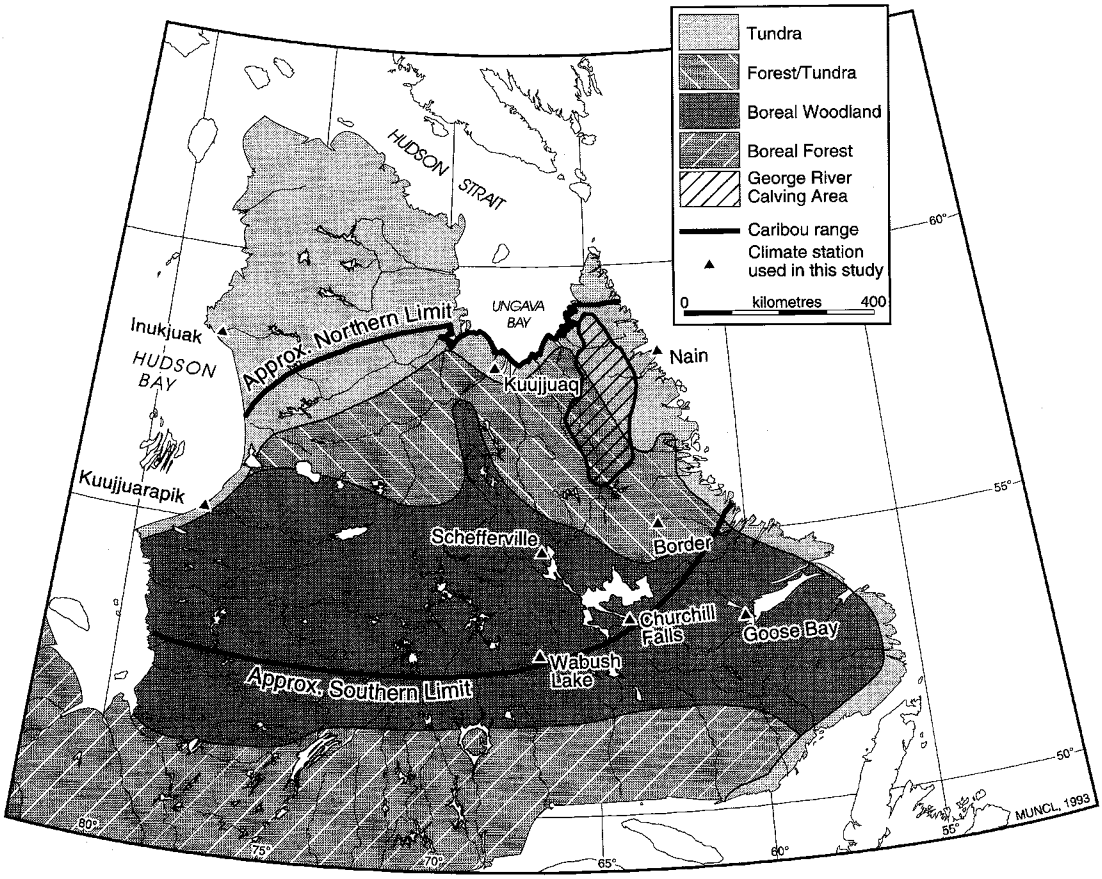


Fig. 1. Northern Quebec - Labrador, showing the location of climate stations used in this study, with bioclimatic zones according to Hare (1950) and range limits of the George River Herd according to Couturier *et al.* (1990).

subsequent leveling off and possible decline of the George River Herd. Such an analysis was carried out for northern Québec by Crête & Payette (1990) using records from two northern stations which they attempted to link to the longer record from Québec City and to black spruce krummholz heights near the tree-line. Their general conclusion was that the climate of the region was warmer during the first half of the 20th century, with consequent impacts on the caribou range through deeper winter snow and more frequent forest fires. By contrast, they inferred a trend toward a regional cooling in the latter half of the century which they associated with improved conditions and rapid growth of the George River Herd (Crête & Payette,1990).

We have conducted an analysis of the climatic record from northern Québec and Labrador for the 1950-1991 period from the standpoint of caribou bioclimate. This paper reports on the methodology and main findings. A more general review and analysis will be presented elsewhere. It is assumed, with some qualifications, that the various climatic factors reported in the literature as being important to reindeer and caribou elsewhere (e.g. Leader-Williams, 1988) are likewise relevant to the George River Herd.

Method

Nine climate stations located within or around the range of the George River Herd provided the basis for the analysis (Fig. 1). Standard climatic summaries (normals) for the 1951-1990 period were available from seven stations with uninterrupted records (Table 1). Digital data were available from the Canadian Climate Archive for 1950 through 1991. Five of the stations have complete records for the full period of analysis (Table 1). Nain has a short and interrupted record starting in 1970. The data available for Border were limited to the 1965-1978 period of manned observation there, although an automatic station has operated there more recently.

The selection of appropriate variables was made from consideration of what conditions are known

Table 1. Permanent Stations used in this study, with 1951- 1990 mean values for selected variables. (Source: Atmospheric Environment Service)

Station	Inukjuak	Kuujjuaq	Kuujjuarapik	Schefferville	Wabush Lake	Churchill Falls	Goose Bay
Year Established	1921	1947	1925	1948	1960	1968	1941
Summer (JJA) Temperature (C)	7,4	9,4	9,0	10,6	11,5	11,8	13,2
Annual Rainfall (mm)	251,1	262,0	387,1	402,2	476,0	497,9	557,3
Degree-day above 5C	333	492	556	604	741	745	995
Winter (DJF) Temperature (C)	-22,7	-21,9	-20,8	-21,6	-20,4	-19,9	-15,4
Degree-day below 0C	3395	3222	2891	3071	2779	2727	1955
Annual Snowfall (cm)	175,4	270,5	238,2	415,0	455,0	481,0	463,8
Snow on ground end of March (cm)	49	66	53	85	92	119	83
Days with Freezing precip.	8	9	10	12	11	13	14
Prevailing wind							
speed (km/h)	20	16	17	17	14	15	16
direction	W	SW	SE	NW	W	W	W

to be unfavourable for caribou, but in the knowledge that standard meteorological observations can only approximate the biophysical reality of the caribou range. For summer (June, July, August), the assumption is that sunshine, heat, and moisture are positive factors through their relationship to primary production, with allowance for different microclimatic responses to regional climate in the various vegetation and landscape types. The negative side of a warm summer is increased potential for insect harassment, unless mitigated by wind (Helle & Tarvainen, 1984; Walsh *et al.* 1992). The principal variables for summer are therefore air temperature, precipitation, and wind.

In winter (September to May, for the purpose of this analysis), deep snow, frequent thaws and icing make foraging and movement difficult (Pruitt, 1959; Leader-Williams, 1988). A cold winter and delayed spring can also be a major factor affecting reproductive success. As Verm (1977) concluded from a study of white-tailed deer, delayed emergence of new shoots leads to poor lactation in females, resulting in significantly lower birth weights and reduced survival of neonates. On the other hand, evidence presented by Miller & Gunn (1986) indicates that healthy calves can tolerate the direct effects of severe spring weather quite well. For the September through May period, then, the variables of interest include temperature, total snowfall, snow depth measured on the last day of each month, and total rainfall and frequency of freezing rain events.

Descriptive statistics were calculated from each station record for the 33-year period. Frequency distributions were calculated and used to distinguish "favourable" and "unfavourable" conditions. A conservative measure was used, namely the tail portions of the frequency distribution exceeding two standard deviations (2σ). For each bioclimatic year (defined as June through May), a particular variable was counted as unfavourable if its value exceeded the 2σ criterion. Both individual and composite scores were then considered for each station over the period. In order to assess the degree of spatial variability in conditions across the region, correlations were carried out between pairs of stations using the series of yearly values. Finally, in order to assess the possibility of climatic change, the data series were smoothed using a 5 year running average and examined for trends.

Results

Winter Range Conditions

Because of its location, Schefferville is the station that is most representative of the winter range area. Kuujjuarapik lies at the western limit, while Border, Churchill Falls, and Wabush Lake coincide approximately with eastern and southern limits (Fig. 1). Interstation correlations were carried out on seasonal temperatures and snowfall by year among the following: Churchill Falls, Kuujjuarapik, Schefferville, and Wabush Lake (Table 2). For midwinter temperature, the correlations were all high and significant ($p < 0.01$). Correlations of total winter snowfall among the same stations were generally low and, with one exception, not statistically significant.

Midwinter (December through February) temperatures for Schefferville averaged -26.3°C (Fig. 2a), and the running mean shows a significant ($p < 0.05$) negative trend over the period. This decline is seen to varying degrees the other winter temperature records from the region, though not all meet the test of statistical significance. It is clear, however, that there is no evidence in these records for a regional warming.

Average winter snowfall at Schefferville was 415 cm, accounting for 52% of the annual precipitation. The depth of snow on the ground at the end of March averaged 85 cm for the period. No long-term trend is evident in snowfall, although there were consistently higher than average amounts from 1971 through 1983. As reported by Barr & Wright (1981) the Schefferville meteorological instrument site was relocated in 1970 to an airport site, with the potential for an artificial enhancement of the snow catch as a result of runway clearing operations. Nevertheless, the record shows a decline beginning in the mid-1980s (Fig. 2b), while Churchill Falls and Wabush Lake also showed a decrease in winter snowfall through the mid-1980s.

Winter rainfall at Schefferville averaged about 150 mm, was higher in the late 1960s, declined by half in the early 1970s, then increased in the early 1980s and remained consistently high through the end of the period. Schefferville had an average of 12.1 ($\sigma = 6.6$) winter days with freezing rain over the 1950-91 period (Fig. 2c). The frequency of such events showed a pronounced decrease from the early 1970s onward. By contrast, freezing rain events reported at Kuujjuarapik, Churchill Falls, and Wabush Lake increased in frequency from the mid-1970s to the mid-1980s, while the record from Goose Bay shows no significant trend.

Table 2. Interstation correlations (*r*) for winter range of the George River Herd. The upper value in each pair refers to winter temperature and the lower to total annual snowfall.

	Kuujjuarapik	Schefferville	Wabush Lake
Churchill Falls	0.68^{**}	0.94^{**}	0.94^{**}
	0.01	0.21	0.48^{*}
Kuujjuarapik		0.86^{**}	0.82^{**}
		0.01	0.11
Schefferville			0.92^{**}
			0.61^{**}

* Significant at p=0.05

** Significant at p=0.01

Particularly severe recent winters can be identified from the Schefferville record. The 1971-72 winter was one of widespread cold over all of northeastern Canada. 1957-58 and 1968-69 were significant for freezing rain at Schefferville, but were not exceptional at the other stations. Total winter rainfall amounts were high in 1957-58, 1968-69, 1983-84, 1988-89, and 1990-91. The 1976-1977 winter saw significantly above average snowfall at Schefferville and Border, but near average at Kuujjuarapik and Goose Bay. In the winter of 1980-81, all of the stations in the southern part of the region had above average snowfall except Churchill Falls, although Kuujjuarapik was only slightly above normal. 1988-89 is distinctive in that all of the winter range stations had negative snowfall anomalies in the 20 to 30% range.

Calving area and summer range

There are no stations in or near the plateau area east of the George River, which is the calving grounds and summer range for cows and calves of the George River Herd (Huot *et al.* 1994). The closest inland station, Border (465 m a.s.l.), had a relatively short record and only recently has been reestablished as an automatic station. Nain and Kuujjuaq are at coastal locations east and west of the area, but only Kuujjuaq has a complete record of observations for the 1950-1991 period. Schefferville can be included because of its elevation (522 m a.s.l.) and relative proximity to the southwest part of the summer range. Interstation correlations for summer temperature and precipitation (Table 3) indicate that Nain and Kuujjuaq have dissimilar summer regimes. Neither coastal station represents the interior plateau area as well as Schefferville; however, from consideration of its latitude and location near the tree-line, Kuujjuaq (Fig. 3) will serve to illustra-

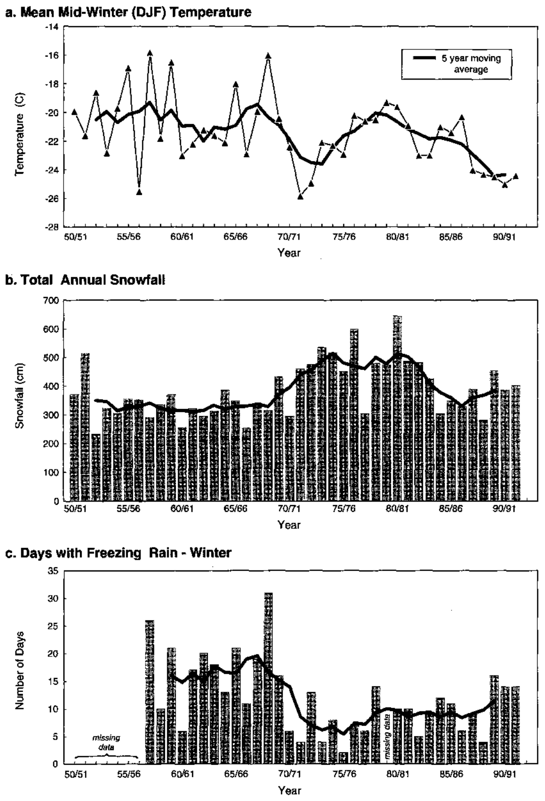


Fig. 2. Winter temperature, snowfall, and frequency of freezing rain recorded at Schefferville, Quebec, 1950-91, representing conditions on the winter range of the George River Herd.

te conditions on the summer range in comparison with Border and Schefferville.

Kuujjuaq had a mean summer temperature of 9.4°C over the 1950-91 period. The mean summer temperature at Border was 8.9°C for the shorter period of record there, compared with 10.4°C at Schefferville. Summer temperatures throughout the region were slightly lower in the late 1960s and early 1970s, but there has been no long-term trend (Fig. 3a).

Average summer precipitation at Kuujjuaq was 168 mm (σ =40 mm), compared with 254 mm (σ=80 mm) at Border and 258 mm (σ=67 mm) at Schefferville. Kuujjuaq showed a slight decrease between the 1970s and 1980s (Fig. 3b), while Schefferville experienced a decline of about 20% between the mid 1970s and the late 1980s.

The number of days during the June neonatal period with combined subfreezing temperatures and strong winds (speed > 20 km h^{-1}) doubled at Kuujjuaq between the mid-1970s and mid-1980s, with the summer of 1986 being a particularly extreme one in this regard (Fig. 3c). Comparable data are not available from Border for this period, but because wide regional spatial coherence generally exists in temperature patterns and to a lesser extent in winds, it is likely that similar conditions were experienced there.

Summary

From the frequency distributions of all measures, summer and winter, taking into account only those years in which a variable equals or exceeds two standard deviations, a rough assessment was made of years that were presumably unfavourable for caribou. These years are identified in Table 4. Only rarely did more than one variable exceed the criterion, so most of the unfavourable years represent ones in which, for example, winter snow was excessive *or* freezing rain was frequent, not both. Generally, severe winters are more frequent than severe summers, though this is to some extent an artifact of the method and the fact that precipitation data tend to be positively skewed. For the summer range, represented here by Kuujjuaq, it seems that there were more unfavourable years in the second half of the period. For the winter range, best represented by Schefferville, the period of the mid-1960s through the mid-1970s was unfavourable. Kuujjuarapik, at the western limit, experienced such conditions about a decade earlier.

Discussion

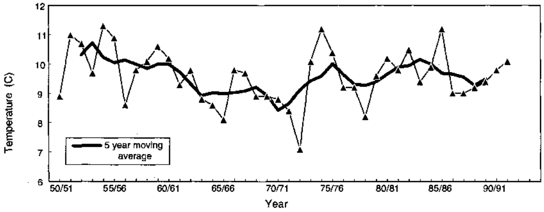
The results presented here are based mainly on data from seven meteorological stations, most of which are on the periphery of the George River range. Correlation analysis in this study as well as more rigorous analysis elsewhere (Jacobs, 1989) indicates that the seasonal temperatures and temperature trends evident in such records are representative of conditions in the study area. Thus, the decline in winter temperatures since the 1960s that was found to be statistically significant at Schefferville is valid as to sign, if not magnitude, for the region as a

Table 3. Interstation correlations (r) for summer range of the George River Herd. The upper value in each pair refers to summer temperature and the lower to total summer precipitation.

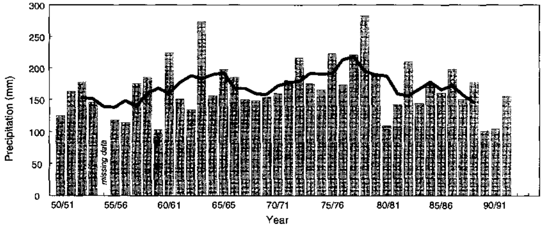
	Kuujjuaq	Nain	Schefferville
Border	0.76**	0.80**	0.90**
	0.25	0.21	0.65*
Kuujjuaq		0.50*	0.80**
		0.03	0.18
Nain			0.67*
			0.08

* Significant at p=0.05.
** Significant at p=0.01.

a. Mean Summer (JJA) Temperature



b. Total Summer (JJA) Precipitation



c. Wind and Frost Days - June

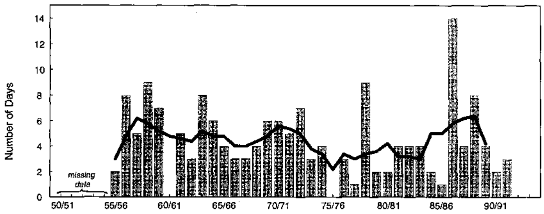


Fig. 3. Summer temperature, precipitation, and days with combined windspeed > 20 km hr^{-1} and temperature < 0°C recorded at Kuujjuaq, Quebec, 1950-91, as an indication of conditions in the summer range area of the George River Herd.

whole. This is consistent with other studies of regional temperature trends in Canada (Gullett *et al.*, 1992). Likewise, the absence of any trend in summer temperatures in the station records can be confidently applied to the region as a whole. These results may be compared with those of Crête & Payette (1990), who inferred from the Québec City record a regional cooling in both seasons since the 1950s, compared with the preceding half-century.

Snowfall and rainfall data cannot be so easily extrapolated beyond the vicinity of the reporting stations, and snowdepth data are even more subject to spatial variability (Jacobs, 1989). Crête & Payette (1990) found that they could not extrapolate precipitation trends from the Québec City record, as they did for temperature. Pruitt (1959) recognized the large spatial and temporal variations in the characteristics of snow cover over caribou range. He argued that for purposes of explaining caribou winter range conditions, "...conventional snow data as reported by the existing net of meteorological observatories are not only insufficient but may actually be misleading" (Pruitt, 1959:1759). With that in mind, one should be cautious in how the snowfall record from these few stations is interpreted. Winter precipitation totals at Schefferville were relatively high from 1974 through 1983, with the 1980-81 amount nearly twice the period average. From this evidence, Couturier *et al.* (1990) inferred stressful conditions on the winter range in that year, as well as for a number of years in the 1974-83 interval. The fact that most other stations in the area had above average snowfall in 1980-81 lends support to that argument, despite previously mentioned concerns about the effects on the record of the relocation of the Schefferville station, although it should be noted that the reported depth of snow on the ground at Schefferville at the end of March, 1981 was not exceptional.

It is to be expected that, with declining winter temperatures, there would a decrease in the amount of snowfall, as was observed at Schefferville in the early 1980s. Since then, however, while temperatures continue to decline regionally, both snowfall and winter rainfall have risen slightly. Such a combination has the potential to increase stress on the caribou on their usual winter range. This might explain an observed shift of the herd westward in the late 1980s (cf. Messier, *et al.*, 1988) and, most recently, the apparent overwintering of significant numbers of caribou along the northeast Labrador coast (Couturier *et al.*, 1996).

Because of the lack of a truly representative observing station in the calving ground and summer range area, any conclusions about climatic conditions there are necessarily tentative. Based on observations made in the 1940s, Rousseau (1968) described the George River Plateau as having cool, windy summers in which scattered snow patches are likely to remain into the next winter. As noted, there seem to have more June days with combined wind and subfreezing temperatures in the mid-1980s than in the previous decade. This period coincides with the caribou population increase, i.e. there is no evidence for increased calf mortality. This would seem to support the conclusion of Miller & Gunn (1986) that caribou neonates generally have a good tolerence for severe weather. Again, climatic impacts on forage conditions seem to be more important. Crête & Payette (1990) noted the effect of residual snow cover in delaying the emergence of green shoots in some years.

Hearn *et al.* (1990) reported a decrease in George River caribou summer survival rates over the 1983-87 period, while winter survival rates remained constant. Huot *et al.* (1994) have attributed the poor body condition of George River caribou in recent years to deteriorating quality of the summer range as a consequence of overgrazing. Crête *et al.* (1996) have described a severely impacted vegetation over extensive areas there, and its recovery may be compounded by a less than optimal summer climate. There have been some recent warm summers with below average precipitation at both Kuujjuaq and Schefferville, though Nain does not share this pattern. Probably as a consequence of cooler, drier, and windier conditions than in the lowlands, insect harassment does not appear to be serious in the George River Plateau area (Messier *et al.*, 1988; Huot *et al.*, 1994). This may in part explain its attractiveness as summer range, despite the poor quality of forage.

Table 4. Years of potentially unfavourable climatic conditions in summer (S) and winter (W) on the range of the George River Herd based on 2σ departures from means of the relevant variables.

YEAR	STATION			
	Inukjuak	Kuujjuaq	Kuujjuarapik	Schefferville
1950-51		W		W
1951-52		W		W
1954-55	W			
1955-56	W		W	
1957-58			W	W
1958-59			W	
1961-62			W	
1962-63			W	
1963-64		W	W	W
1964-65		W		W
1965-66				S
1966-67			W	
1968-69		W	W	W
1969-70	S	W		W
1970-71		S		
1971-72	W			W
1972-73	S			S
1973-74				W
1974-75				W
1975-76		W		
1976-77	W			W
1977-78	W			
1978-79		SW	W	
1979-80	W			
1980-81				W
1981-82				W
1982-83	W	W	W	
1983-84		W		
1984-85		W		
1986-87	W	S		S
1987-88	W			
1989-90	W			
1990-91	W			

The lowland forest-tundra south and west of the George River Plateau is frequented in summer by males and barren females (Crête *et al.*, 1990). Vegetation in these areas exists under different bioclimatic conditions from the upland tundra, is more productive, and will respond differently to regional climatic forcing. Though the cows and calves may pass through these areas after leaving the upland tundra areas in late July or early August, the evidence of their condition in fall would seem to indicate that the nutritional shortfall experienced on the summer range is not being made up in transit (Huot, 1989; Huot *et al*, 1994). It is noteworthy that a small, apparently distinct woodland caribou population, the Caniapiscau Herd, was reported to have a calving area and summer range in the bog and fen areas west of Schefferville and to be feeding primarily on aquatic plants and grasses (Paré & Huot, 1985).

Conclusion

Based on a review of the records for the past 42 year period, there is no clear evidence for a major, long-term shift or trend in climatic conditions over the range of the George River Caribou Herd that might explain changes in the condition of the herd. The most significant trend, that of a decline in winter temperatures, is unlikely to have had a negative impact on the caribou and has been argued as an improvement over conditions in the early part of the century (Crête & Payette, 1990). Our analysis indicates with some confidence an increase since the 1980s in snowfall and winter rainfall in the historic wintering areas. This may have caused increased stress and encouraged movement into areas of lesser winter precipitation.

More problematic is the summer range, which biologists have identified as the critical element in the ecology of the herd and to which current problems of the condition of the animals are attributed. This area is not well-represented by existing climate stations. However, it can be concluded that summer temperatures in the area show no significant trend over the period. With less confidence, there is an indication of reduced summer precipitation and more frequent periods of strong winds and subfreezing temperatures during the neonatal period. The latter may not necessarily have a direct impact on calves, but the combination will negatively affect range productivity.

For the George River Herd, as is the case with caribou in many other areas, it is not possible to demonstrate a simple causal relationship between climate and population dynamics. It seems that climate affects this complex system in a variety of ways. In the most recent period, the weight of evidence points to habitat deterioration on the summer range as the main problem affecting the herd. Similar deterioration does not seem to be occurring in summer range areas of other caribou populations in northern Québec under present climate. This may be a matter of different bioclimatic responses among differing habitat types under the same regional climate, or of a particular range that is deteriorating with overgrazing, irrespective of the climate. Further research should be directed at the mesoscale or subregional differences in climate and vegetation and their interrelationships, as much as to the question of why there continues to be such a strong preference among females of the George River Herd for what appears now to be a marginal summer range.

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Biochemical indicators of condition, nutrition and nitrogen excretion in caribou

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Abstract: Urinary urea nitrogen to creatinine ratios (UUC mg/mg), urinary N^{τ}-methylhistidine to creatinine ratios (UN$^{\tau}$-MHC μmol:μmol), serum urea nitrogen concentrations (SUN mg/dl), and serum N^{τ}-methylhistidine concentrations (N^{τ}-MH nmol/ml) were compared with physical measures of body composition in adult female barren-ground caribou (*Rangifer tarandus groenlandicus*) from the Bathurst and Southampton Island herds during late winter. Body weight and UUC were used to estimate urinary urea nitrogen (urea-N) excretion in free ranging caribou. Only mean UUC reflected differences in fat reserves between populations. None of the biochemical indicators were directly related to body composition. However, elevated UUC were only observed in caribou with depleted fat reserves as demonstrated by low kidney fat index (KFI<40) and/or reduced femur marrow fat (FMF<80). UUC greater than 0.25 were indicative of undernourished animals with depleted fat reserves. SUN and UN$^{\tau}$-MHC showed no clear relationship with fat reserves. The mean estimated daily urea-N excretion for adult female caribou in late winter was extremely low (0.11 ± 0.01SE g urea-N/day, n=76, range=0.011-0.510). The results of my study suggest that UUC can be used to detect nutritionally stressed caribou with depleted fat reserves on lichen winter ranges.

Key words: *Rangifer*, urea, urine, serum

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Introduction

Physical condition and nutritional status are important parameters in assessing the demography of caribou (*Rangifer tarandus*) populations (Messier *et al.*, 1988; Couturier *et al.*, 1990). Body size and the level of fat reserves have been shown to affect productivity and recruitment through effects on fecundity and neonatal calf survival (Dauphiné, 1976; Thomas, 1982; Reimers, 1983; White, 1983; Crête *et al.*, 1993). Historically, indices of condition have been taken from direct carcass measurements. Body measurements, tissue weights, and standard fat measurements were identified as useful indicators of physical condition (Adamczewski *et al.*, 1987a; Huot, 1988; Allaye-Chan, 1991). All of these measurements required either killing or at least handling the animals. The nutritional status of animals has often been inferred from condition analyses given that undernutrition will result in depletion of body reserves. Unfortunately, condition indicies provide little information about current nutritional status.

Recently, several researchers have focused on the use of urinary urea nitrogen to creatinine ratios (UUC) to investigate nutritional status and indirectly assess condition in wild ungulates (DelGiudice & Seal, 1988; DelGiudice *et al.*, 1989; 1991a; 1991b; Cool, 1992). Collection and analysis of urine from snow avoids stress due to capture or harvesting animals, which is of particular importance in the assessment of low density or endangered populations. Elevated UUC have been documented in undernourished white-tailed deer (*Odocoileus virginianus*) (DelGiudice *et al.*, 1987; DelGiudice & Seal, 1988), moose (*Alces alces*) (Cool, 1992), and wapiti (*Cervus elaphus*) (DelGiudice *et al.*, 1991a; DelGiudice *et al.*, 1991b). The management value of UUC was demonstrated by DelGiudice & Seal (1988) who were able to classify white-tailed deer into three categories: early undernutrition, prolonged-reversible undernutrition and prolonged-irreversible undernutrition.

The use of UUC as an indicator of nutritional status depends on the increased excretion of urea nitrogen (urea-N) in response to accelerated catabolism of endogenous proteins. Catabolism of fat and protein reserves is typical of over wintering northern ungulates when energy intake is limited. In most cases of undernutrition, fat reserves are mobilized preferentially and the rate of endogenous protein catabolism increases as fat reserves become depleted (Torbit *et al.*, 1985; DelGiudice *et al.*, 1987). In some situations, particularly with reindeer and caribou consuming low protein lichen diets, nitrogen intake can be limiting despite ample digestible energy (Steen, 1968; Nieminen & Heiskari, 1989). Steen (1968) suggested that reindeer on a lichen diet must catabolize endogenous protein to provide a supply of amino acids for protein synthesis and nitrogen for rumen microbes, even when energy intake allows them to accumulate fat.

Although UUC have been used to classify nutritional status and to indirectly assess body composition, only one study has been conducted to determine if changes in UUC reflect body composition. In black-tailed deer (*O. hemionus sitkensis*), UUC did not consistently reflect individual animal body composition (Parker *et al.*, 1993). The primary objective of my study was to determine if urine and serum nutritional indices reflected body composition in caribou in the spring. Specifically, two urinary indices, UUC and urinary N$^{\tau}$-methylhistidine (N$^{\tau}$-MH) to creatinine ratios (UN$^{\tau}$-MHC), and two serum indices, serum urea-N concentrations (SUN) and serum N$^{\tau}$-MH concentrations (SN$^{\tau}$-MH), were compared to proportions of fat and muscle in harvested caribou. UN$^{\tau}$-MHC and SN$^{\tau}$-MH were included in the analysis because N$^{\tau}$-MH excretion has been shown to be an indicator of endogenous myofibrillar protein degradation in some species (Harris & Milne, 1981; Long *et al.*, 1988). SUN was evaluated because DelGiudice & Seal (1988) found elevated SUN in malnourished deer.

The methodology of my study also permitted an evaluation of nitrogen conservation in over wintering caribou. Caribou consuming a mainly lichen diet with very low (<3%) crude protein (Scotter, 1965; Scotter, 1967; Thomas & Hervieux, 1986) must minimize urinary nitrogen loss to conserve muscle mass. Urinary excretion of urea-N is typically the most significant source of urinary nitrogen loss (Dukes, 1947), therefore, nitrogen conservation was assessed by looking at urinary urea-N excretion.

Methods

Sampling protocol

During late winter and spring in 1990, 1991 and 1992 (February through May), 55 adult, 13 yearling and 6 calf caribou were collected from the Bathurst caribou herd winter range and 48 adult, 23 yearling and 4 calf caribou were collected from Southampton Island. The diet of Southampton Island and mainland caribou consists mainly of lichen during this period (Ouellet, 1992; Thomas & Hervieux, 1986). Animals were shot by native hunters who were instructed on the sex of animals to harvest but to otherwise take animals at random. Immediately after death, a blood sample was taken by slicing through the carotid artery and jugular vein in the lower neck. A urine sample was collected directly as it drained from the animal or from the snow. The animals were then taken to a central location where fresh weights and carcass measurements were made. Maximum depth of backfat was measured along an incision 45° forward from the base of the tail. Kidney fat index (KFI) was determined by dividing the weight of Riney fat by the weight of the kidney and multiplying by 100 (Riney, 1955). The femur and gastrocnemius muscle were collected and frozen. Femur marrow fat (FMF) was determined using the dry weight method corrected for mineral content (Neiland 1970). Animals were classified as being in poor condition if KFI was less than 30 or FMF was less than 50% (Thomas 1982). Gastrocnemius weight was determined after removal of the superficial digital flexor and tendons. Blood samples were centrifuged upon returning to camp and serum was retained. Samples were frozen at -10°C (urine and serum at -20°C) until analyzed in the laboratory.

Indicator muscle, bone, and fat measurements were used to estimate the weight of muscle, bone and fat in each carcass using the equations determined for caribou by Adamczewski *et al.* (1987a). To adjust for differences in frame size between animals of different ages, estimated muscle and fat weights were standardized to bone weights to give muscle to bone ratios (MUSBONE) and fat to bone ratios (FATBONE).

Chemical analyses

Creatinine concentrations (mg/dl and µmol/ml) in serum and urine were determined using a colorimetric method based on the Jaffé reaction (Sigma Diagnostics, St. Louis MO). Urinary and serum concentrations of urea-N (mg/dl) were determined using a colorimetric urea assay kit based on the diacetyl monoxime reaction (Sigma Diagnostics, St. Louis MO). Urine and serum samples were analyzed for N$^{\tau}$-MH (µmol/ml) using high performance liquid chromatography (HPLC) (Scott *et al.*, 1993). Samples were deproteinized with 0.200 ml of 3.0M HClO4, centrifuged at 3000 rpm for 15 minutes, and analyzed using a Varian Model 5500 Liquid Chromatograph with a Varian 2070 spectrofluorometer detector and a Varian 9090 auto analyzer (Varian Canada, Calgary AB). Separations were done on a 15 cm x 4.6 mm 3 micron reverse phase column (Supelco Inc., Bellefonte PA). Standard quality control procedures were run on all analyses.

Urinary creatinine excretion is strongly correlated with muscle weight and is highly consistent within species (Vestergaard & Leverett, 1958; Kertz *et al.*, 1970; Chetal *et al.*, 1975; Forbes & Bruining, 1976). Therefore, creatinine coefficients from reindeer were used to estimate urea-N excretion from caribou based on the ratio of urea to creatinine in urine and body weight using the formula:

$$TTLUREA = ((CREATCO * WT)/UCREAT * UUREA)/1000$$

where TTLUREA= total daily urea-N excretion (g), CREATCO = creatinine coefficient (16.16 mg/kg/day) determined from lean adult female reindeer (Case, unpublished data), WT = body weight (kg), UCREAT = urine creatinine concentration (mg/dl) and UUREA = urine urea-N concentration (mg/dl).

Statistical analyses

Differences between variable means for sex and location were analyzed using least squares analysis of variance (PROC GLM) (SAS, 1988).

Results

None of the animals harvested on Southampton Island were classified as being in poor condition based on KFI or FMF. In contrast, 39% (34 of 87) of the Bathurst caribou harvested had a KFI less than 30 and 6% (4 of 70) had a FMF less than 50%. These differences in fat reserves are reflected in the significant (P<0.0001) differences in FATBONE ratios observed for both males and females (Fig. 1). Bathurst caribou had significantly (P<0.05) larger MUSBONE ratios indicating a larger muscle mass.

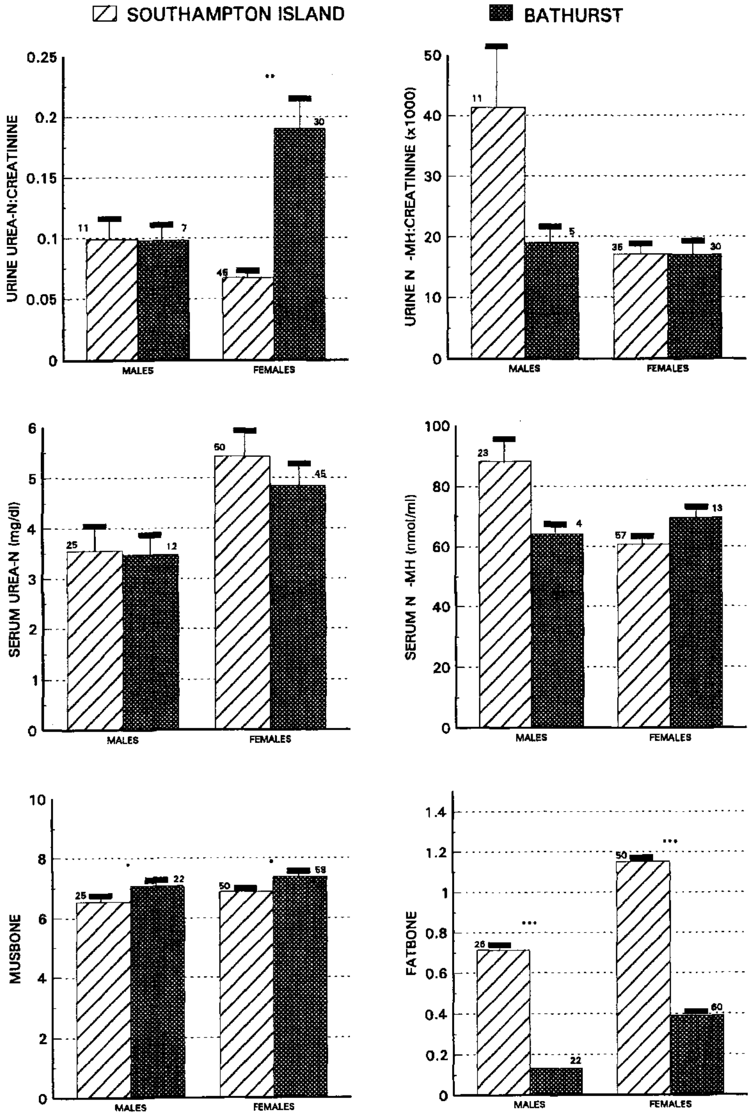

Fig. 1. Herd and sex differences in urine urea-N:creatinine, urine N^{τ}-MH:creatinine, serum urea-N, serum N^{τ}-MH, muscle:bone (MUSBONE) and fat:bone (FATBONE) in caribou harvested during late winter (mean±SE). (*P<0.05, **P<0.001, ***P<0.0001).

Herd differences in fatness were reflected in UUC for female caribou; Bathurst females excreted significantly more urea-N than Southampton Island females (Fig. 1). Although the differences were not significant, SUN showed a trend towards being lower in Bathurst female caribou. UN$^{\tau}$-MHC and SN$^{\tau}$-MH were similar for Bathurst and Southampton Island females and Bathurst males. Southampton Island males had higher UN$^{\tau}$-MHC and serum N$^{\tau}$-MH concentrations although the differences were not significant (*P*>0.05). Six of the males on Southampton Island had serum N$^{\tau}$-MH concentrations in excess of 100 nmol/ml.

UUC, SUN and UN$^{\tau}$-MHC were plotted against KFI and FMF to investigate relationships between the biochemical indicators and body condition (Fig. 2). Elevated UUC were only observed with depleted fat reserves while SUN and UN$^{\tau}$-MHC showed no clear relationship with either KFI or FMF.

The mean estimated daily urea-N excretion for adult caribou from both study areas in late winter/spring was 0.11±0.01 SE g (n=76 range=0.011-0.510). Adult female caribou on the Bathurst range with UUC less than 0.25 excreted slightly more urea-N (0.14±0.02 g/day) than the average estimate; caribou with UUC greater than 0.25 excreted even more (0.38±0.08 g/day).

Discussion

Herd comparisons

The lower fat reserves in Bathurst caribou, as indicated by FATBONE ratios, may reflect a number of ecological differences between the two herds. Southampton Island caribou typically have higher fat reserves in the fall than the mainland herds

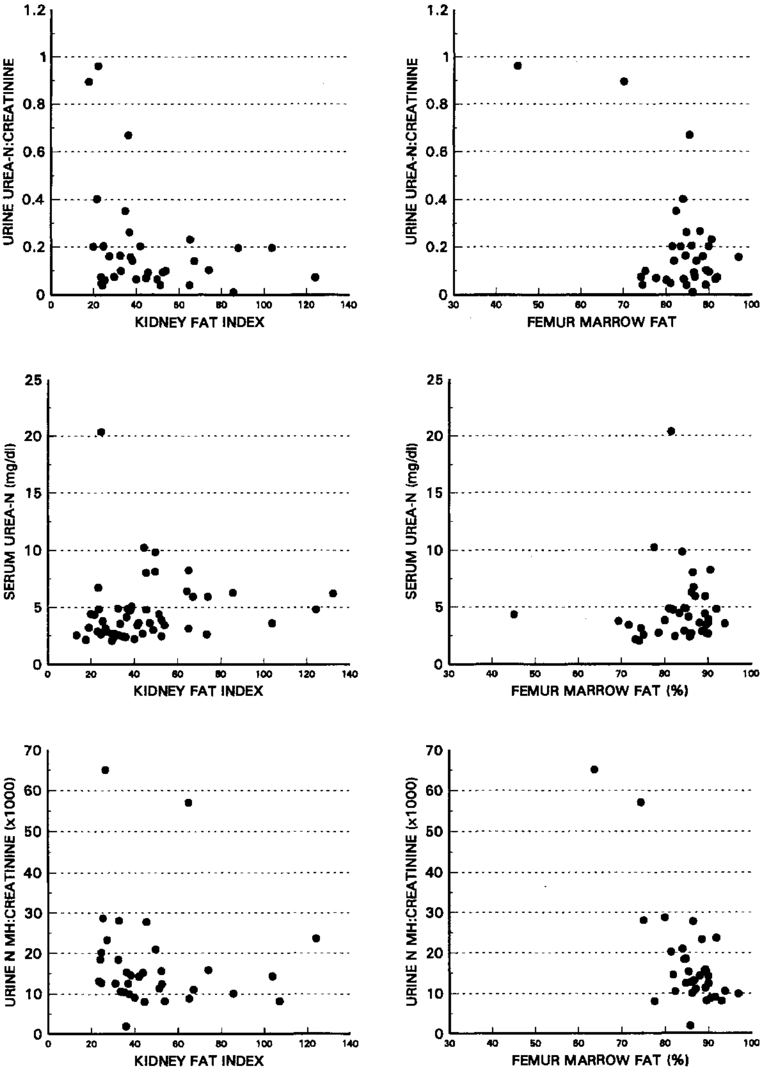

Fig. 2. Urine urea-N:creatinine, serum urea-N and urine N$^{\tau}$-MH:creatinine versus kidney fat index and percent femur marrow fat in adult female Bathurst caribou in late winter.

(Ouellet, 1992). Bathurst caribou could also be expected to have higher over winter nutritional demands resulting from migration to winter ranges and predator avoidance because Southampton Island caribou do not migrate and have no predators. Forage quality and availability could also be important, however, no comparative range or snow pack studies have been conducted.

The elevated UUC observed in female Bathurst caribou are consistent with undernourished animals and suggest that some of the animals were either catabolizing protein or eating a higher protein forage (DelGiudice & Seal, 1988). The first explanation is the more likely one, because the study area was still 100% snow covered and no new high protein vegetation was available. DelGiudice & Seal (1988) also observed elevated SUN in extremely undernourished animals, which were not encountered in this study. The lack of elevated UUC in Bathurst males would suggest that these animals were not experiencing undernutrition; possibly because they have no gestational demands. However, the sample size was small because it was difficult to collect urine from harvested males.

The elevated serum N^{τ}-MH concentrations and UN^{τ}-MHC in Southampton Island males relative to Bathurst males suggests there is a difference between the two herds. Increased excretion of N^{τ}-MH has been associated with either starvation or growth in rats and cattle (Nishizawa *et al.*, 1977; Wassner *et al.*, 1977; Jones *et al.*, 1990). Fat levels would suggest that the animals were not experiencing prolonged undernutrition however, animals could have been experiencing short-term undernutrition at the time of collection. Growth also cannot be ruled out. Ouellet (1992) observed that males on Southampton Island grew through the winter.

Biochemical indicators of body composition

Plotting UUC from adult female Bathurst caribou in the spring versus KFI and FMF indicates that caribou with UUC greater than 0.25 had depleted body reserves (Fig. 2). All of the caribou with UUC greater than 0.25 had KFI less than 40 and all but 2 would have been classified as in poor condition using Thomas' (1982) criteria of KFI less than 30. The two animals with the lowest FMF also had the highest UUC.

DelGiudice & Seal (1988) classified white-tailed deer with UUC below 4.0 as in early undernutrition, UUC between 4 and 23 as in prolonged-reversible undernutrition and UUC over 23 as indicative of prolonged-irreversible undernutrition. As all the UUC values from the harvested caribou in my study were below 1, DelGiudice & Seal's (1988) classification would suggest that no animals were undernourished. This discrepancy highlights the need for caution in extrapolating between species.

It should be noted that although all caribou with UUC greater than 0.25 had depleted fat reserves, not all caribou with low KFI and low FMF had high UUC. A similar pattern was observed in Sitka black-tailed deer where UUC was compared with fat reserves determined using tritiated water (Parker *et al.*, 1993). The reason for this is because KFI and FMF depend on past nutrition while UUC reflects current nutrition (DelGiudice *et al.*, 1990). It is possible that caribou with low fat reserves could still be obtaining sufficient energy in the diet. This would result in low UUC even though they would be classified as being in poor condition based on their fat reserves.

The only other study that compared UUC to fat levels was limited to analysis of winter killed wapiti (DelGiudice *et al.*, 1991a). The animals had UUC in excess of 70 and FMF <10%. None of the Bathurst caribou had reached this state and their undernutrition was likely reversible.

DelGiudice & Seal (1988) also suggested that SUN could be used to classify the phases of undernutrition with SUN <20 mg/dl indicating early undernutrition, SUN from 20 to 40 mg/dl indicating prolonged-reversible undernutrition, and SUN over 40 mg/dl indicating prolonged-irreversible undernutrition. In my study, SUN did not correspond as well as UUC to fat levels, although the only animal with elevated SUN also had a high UUC and a low KFI.

Although UN^{τ}-MHC showed no clear relationship with either KFI or FMF, it remains possible that in later stages of malnutrition excretion of N^{τ}-MH would increase, as has been observed in starving rats (Wassner *et al.*, 1977). However, once animals are severely malnourished monitoring N^{τ}-MH would have no advantages over UUC or visual classification of condition, and would be more expensive.

Nitrogen conservation in over wintering caribou

Urea-N excretion is best evaluated based on dietary nitrogen intake. The late winter diet of Bathurst caribou is primarily terrestrial lichen (Thomas & Hervieux, 1986) with a nitrogen content of approximately 4 g/kg (Scotter, 1965). Assuming an apparent digestibility of 75% (Thomas & Kroeger, 1980) lichens would provide approximately 3 g N/kg. Therefore, the mean daily urinary loss of urea-N observed in animals with UUC greater than 0.25 (0.38 g/day) could be made up by ingesting 125 g of lichen.

The low excretion of urea-N in wild caribou, even in those with elevated UUC, is evident when contrasted with adult female reindeer which excreted an average of 7.9 g urea-N/day (n=3) on a low protein (7.9% Crude Protein [CP]) pelleted diet, and reindeer which excreted an average of 26.6 g urea-N/day on a high protein diet (18.8% CP) (Case, unpublished data). Cattle on a 12% CP diet excreted >28 g urea-N/day but were able to reduce this to less than 2.5 g urea-N/day when fed a 4% CP diet and deprived of water (Livingston *et al.*, 1962). Captive caribou fed a simulated winter diet excreted an average of 18.0 g urea-N/day (Wales *et al.*, 1975).

Hove & Jacobsen (1975) reported reindeer maintained on a lichen diet reabsorbed an average of 93% of urea filtered at the glomerulus. Calculations from their figures indicated that the animals were excreting an average of 0.091 g urea-N/day, which is within the range observed in wild caribou. It is likely, therefore, that the caribou from the Bathurst and Southampton Island herds were also reabsorbing >90% of filtered urea.

The only other large ungulate for which comparable abilities to reduce nitrogen loss in urine has been documented is the camel. Schmidt-Nielsen *et al.* (1957) reported that a camel grazed in the sandy desert for 4 weeks then maintained on a low N diet of dates and hay for an additional 17 days with no access to water reduced urea-N excretion to less than 0.3 g/day. Wapiti and white-tailed deer, which have a well documented ability to recycle a large proportion of urea into the rumen, still excreted in excess of 1.9 g urea-N/day when feed very low protein diets (Robbins *et al.*, 1974; Mould & Robbins, 1981).

Conclusion

The results of my study suggests that UUC can be used to monitor the nutritional status of free ranging caribou on lichen winter ranges and that analysis of urine in snow can be used to conduct physiological assessments caribou, as has been demonstrated in deer (DelGiudice *et al.*, 1989) and wapiti (DelGiudice *et al.*, 1991c). The observation that UUC did not increase above 0.25 until fat reserves were being depleted (KFI<40) suggests that this value could be used to distinguish individual caribou which have both experienced prolonged undernutrition in late winter/spring and remain undernourished. UUC will not detect animals in poor condition which are well nourished, nor will they detect animals in good condition which have only recently experienced undernutrition. This, however, is not a problem as animals in either of these situations are not at immediate risk of starvation or reduced productivity.

Further data are needed from caribou in very poor condition to determine the UUC values for animals with severe or prolonged undernutrition. None of the animals collected during my study would have been expected to die of malnutrition. It would be expected that UUC would continue to increase as the severity and period of undernutrition increased. Data are also needed from caribou populations which are not consuming predominantly lichen diets during winter.

The ability of caribou to reduce urea-N loss in urine may be a function of reduced water flux rate in winter (Cameron & Luick, 1972). The effect is that a larger proportion of urea-N remains available for recycling into the rumen. Further investigation is needed to assess the relative and combined benefit of reduced urea-N loss and increased urea recycling in caribou.

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Brief communication

Modeling energy and reproductive costs in caribou exposed to low flying military jet aircraft

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Abstract: We used simulation modeling to estimate the effect of low-flying military jet aircraft on the productivity of caribou. The base model (CARIBOU, CWS Whitehorse, Yukon Territory) uses daily intake and expenditure of energy to assess the condition of female caribou throughout the annual cycle. The activity budget of the model caribou was adjusted based on field observations of responses to noise disturbance. A subroutine was added that predicted the likelihood of conception based on fall body fat weight. Caribou responses to overflights were evaluated by equipping free-ranging caribou with radio collars and activity sensors that could distinguish between resting and active periods. Collared animals were exposed to 110 overflights by A-10, F-15 and F- 16 jet aircraft during late-winter, post-calving and the insect season. Noise exposure levels for individual animals either were measured directly with collar-mounted dosimeters or were estimated based on the proximity of the caribou to the aircraft during the overflight. A Time-averaged Sound Level (L_T) was calculated from the total daily noise exposure for each animal and linear regression was used to evaluate the influence of daily noise exposure on daily hours spent resting. Results of these analyses then were used to modify the time budgets in the CARIBOU model. That is, if time spent resting declined, then time spent in the two rest classes (lying and standing) were proportionately redistributed into the three active classes (foraging, walking and running). Model simulations indicated that caribou increased forage intake in response to increased noise exposure, but it also predicted that increased noise exposure would cause a reduced accumulation of body fat. Because body fat in fall has successfully been used to predict the probability of pregnancy (see Gerhart *et al.*, 1993), this relationship was used in the model. Preliminary model simulations indicate that increased noise exposure decreases the probability of pregnancy and that unfavorable environmental conditions (e.g., deep snow and severe insect harassment) exacerbate the situation. The threshold at which point the caribou fail to conceive has not been determined at this time, but appears to be well beyond the exposure to aircraft that caribou in the Delta herd are currently experiencing.

Key words: energetics, noise, model, reproduction

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Introduction

This report describes the use of the computer simulation model CARIBOU (Kremsater *et al.,* 1989) to estimate the effects of low flying military jet aircraft on the breeding success of a female caribou (*Rangifer tarandus granti*). Use of lowflying jet aircraft associated with military training has associated concern for the effects of these overflights on wildlife. Northern residents and resourcemanagment agencies have concern for the effects these training exercises may have on productivity of caribou (Wadden, 1989). Some energy expenditures (Fancy & White, 1985; Luick & White, 1986; White & Fancy, 1986) and seasonal energy budgets (Russell *et al.,* 1993) have been documented for caribou and effects of energy and nutrition on fecundity have been estimated (Cameron *et al.,* 1993; Gerhart *et al.,* 1993). The Delta Caribou Herd (DCH) of interior Alaska was selected for the study of short temm effects of noise disturbance on activity budgets because of its proximity to Eielson Air Force Base. Long term effects including fecundity were then predicted using computer simulation. The current version of CARIBOU was developed as part of a contract to the United States Air Force (USAF) in connection with the USAF Noise and Sonic Boom Impact Technology (NSBIT) program.

CARIBOU has both energy and growth modules that work sequentially to simulate growth of a caribou at a daily time step throughout a year. The model begins an execution cycle by calculating daily interpolated values from seasonally corrected tables of activity budgets, forage quality and quantity, and environmental parameters such as snow depth and insect harassment of a free ranging female caribou. For the purposes of modeling, it was assumed that noise disturbance influenced the activity budget. In CARIBOU, forage class intake is determined as a product of time and efficiency of foraging and prevalence of forage class. Likewise, nutrient absorption is determined as a product of forage class intake, digestibility and composition. Considerations of nutrient efficiency of utilization are employed by CARIBOU to calculate a daily energy credit against which daily energy demands are drawn. These demands may include resting metabolic rate, gestation, lactation, and physical activity. An energy credit surplus can result in growth and fattening, a deficit in sacrifice of body fat and protein. Constraints limiting the model include availability of forage and availability of time for foraging, rumen capacity and metabolic demands on energy supplies. The model produces 83 output variables including body, fat, muscle, calf and fetus weights and milk production for each day simulated.

Materials and methods

The simulation model CARIBOU was obtained from the Canadian Wildlife Service, Whitehorse, YT Canada. Initial condition variables such as body weight and seasonal dates were adjusted to resemble animals of the DCH. The program was modified to read a schedule of jet aircraft overflights and associated sound exposure levels (SEL, dB) and then calculate a noise adjusted daily activity budget. The noise adjustment was based on the observed daily hours spent resting in free ranging caribou exposed to varying intensities jet aircraft overflights. Briefly, up to ten DCH caribou were fitted with *Wildlink* Inc. radio collars bearing recording activity monitors (mercury tip switch) and sometimes a noise dosimeter from which an SEL was determined. In cases where a collared animal either did not have a dosimeter or the dosimeter was not triggered, an empiracally derived estimated SEL was provided by the USAF. A ground crew directed jet aircraft to the precise location of the animals under observation and recorded visual observations of the overflown animals. Evaluation of the direct observations of overflown caribou has been summarized elsewhere (Murphy *et al.*, 1993). Since individual activity classes (foraging, lying, standing, walking, running) could not be identified from the activity monitors, the existing emperically determined activty distributions of the control animals were applied to the overflown animals. That is, motion detected in connection with noise disturbance was assumed to have the same relative distribution of foraging, walking and running as motion recorded for undisturbed animals (Kitchens *et al.*, 1993). All SELS from each day for a given animal were combined to estimate a time averaged sound level (L_T, ANSI S 12.40-1990). A regression of daily hours spent resting on L_T was used to make adjustments to the default activity budget of CARIBOU for noise exposure simulations.

Results and discussion

The SELS experienced by caribou as generated by jet aircraft noise were measured or estimated from near zero for animals located a great distance from the jets, to 130 dB. Overflights occurred in three seasons of the year, late winter (early April), post-calving (early June) and insect season (late July/early August). Separate regressions of time averaged sound level (L_T) on hours spent resting were developed for all seasons, but only post-calving had a significant slope (0.03 L_T, n= 50, P= 0.03, S.E.=), therefore modeling was limited to this time of year. The range of L_Ts extended from near zero to 84. The current simulations employed the relatively high L_T of 80 in order to generate a detectable yet realistic response by the model. Consecutive simulation exposure days were set from O (control) to 40 in 5 day increments. The simulations were repeated with the environmental variables set to poor conditions (deep snow, poor forage, heavy insect harassment). A probability of pregnancy prediction was made for each simulation based on fall fat weight (Gerhart *et al.*, 1993) arbitrarily taken as the mid-rut date of October 15 as shown in Table 1. The control runs of CARIBOU indicated that energy demands on a lactating cow were not being

Table 1. A tabulation of body (BW) and fat weights (FW) and probability of pregnancy (PP) as predicted by the computer model CARIBOU when increasing consecutive days of a single event noise disturbance are simulated under both good and poor environmental conditions.

	Good year			Bad year		
Days	BW kg	FW kg	PP %	BW kg	FW kg	PP %
0	76.1	6.52	70.2	65.2	3.59	47.7
5	76.0	6.48	70.0	65.1	3.56	47.5
10	75.9	6.45	69.8	64.9	3.52	47.2
15	75.7	6.41	69.5	64.7	3.46	46.7
20	75.5	6.35	69.0	64.4	3.37	46.0
25	75.3	6.30	68.7	64.1	3.30	45.5
30	75.1	6.25	68.3	63.8	3.21	44.7
35	74.9	6.18	67.9	63.3	3.09	43.8
40	74.6	6.11	67.4	62.8	2.95	42.7

met over the course of the summer. The overflight simulation produced a downward shift in the time course of total body and fat weights which indicated that the "cow" did not completely compensate for the additional energy demands.

The predicted likelihood of conception declined with increasing noise exposure with an accelerated effect as the duration of exposure increased. Plots of body and fat weight (not shown) revealed the same relationship, indicating that the model increasingly drew on body reserves to meet the demands of lactation and increased physical activity. Simulations of a non-pregnant/non-lactating cow predicted that a caribou is capable of increasing body weight and fat over the same period with these levels of noise exposure.

As noise exposure increased, the calculated pregnancy rate under poor environmental conditions fell off more sharply than under good environmental conditions. The model attempted to maintain milk production in the face of a declining energy balance, ultimately resulting in the "cow" attaining a low probability of conceiving. Simulations of a non-pregnant cow predicted a rapid recovery of body condition at the end of lactation and based on predicted fat weight, the animal would be likely to conceive the following year.

The effects of disturbance on caribou varies depending on the type of disturbance, time of year and group composition (nursery bands, bull groups, mixed aggregations) (Gunn *et al.*, 1985; Murphy & Curatolo, 1987; Harrington & Veitch, 1991; 1992). The current implementation of CARIBOU predicts a minimal effect of jet aircraft overflight on caribou fecundity. In the unlikely event of 40 consecutive days of severe noise exposure a caribou is predicted to have a 4 or 5 % decrease in the probability of becoming pregnant under normal or poor environmental conditions, respectively.

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Population demography of Peary caribou and muskox on Banks Island, N.W.T., 1982-1992

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Abstract: The Peary caribou population (excluding calves) on Banks Island declined from 6 970 (± 1133) in 1982 to 897 (± 151) in 1991. The 1992 estimate was 1 005 (± 133). Percent calves in the population varied among years (range 3.2-31.1%). Mean group sizes dropped from 5.0 in 1985 to a low of 2.0 in 1989 and 1991. Median group sizes were significantly larger between 1982 and 1987 than between 1989 and 1992 ($P<0.001$). Large post-calving aggregations prevalent on the NW portion of Banks Island in the early 1980's were absent by the 1990's. The muskox population (excluding calves), increased from 29 168 (± 2104) in 1985 to 52 959 (± 2240) in 1992. Percent calves in the population varied among years, (range 11.8-17.1%). These values may be underestimates, because calves are small and muskox groups sometimes form defensive circles in response to aircraft. Muskoxen were distributed throughout the island during all surveys; however, the greatest increase in density occurred in the southern parts of the island.

Key words: Peary caribou, muskox, Banks Island, population demography

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Introduction

Peary caribou (*Rangifer tarandus pearyii*) and muskox (*Ovibos moschatus*) are an important subsistence food source for the residents of Sachs Harbour, Banks Island. These ungulate populations have been systematically monitored by the Department of Renewable Resources, Government of the Northwest Territories since 1982.

During the past decade, caribou numbers decreased. Severe winter weather is believed to be the major cause of declining caribou numbers (Parker *et al.*, 1975; Gunn, 1992). Annual die-offs of 60-300 caribou were recorded following the winters of 1987-88, 1988-89, and 1990-91 when freezing rains occurred. In response to decreasing caribou numbers, the Sachs Harbour Hunter's and Trapper's Committee established a quota of 150 animals in 1990 and 30 males in 1991. In 1992, the quota was increased to 36 males to allow each family to harvest one caribou.

Over the same period muskox numbers increased. The residents of Sachs Harbour harvest muskoxen to support a local subsistence economy and conduct guided sport hunts for non-resident hunters. In addition, a commercial harvest program has been in place since 1981. During the quota years 1980-81 to 1989-90, the average commercial take was 124 muskoxen/year (range 0 to 260). The first large-scale harvest was conducted during 1990-91 when 494 muskoxen were taken. During the quota year 1991-92, 2 031 muskoxen were taken. The annual quota has been 5 000 muskoxen since 1991.

Scat analysis indicates that both muskox and caribou are taken by wolves (*Canis lupus*); however, data on wolf numbers and predation rates are lacking. Inuvialuit in Sachs Harbour harvest wolves for subsistence use. Fewer than 10 wolves were harvested annually from 1988-89 to 1991-92; however, 50 wolves were harvested in winter 1992-93 (Larter & Clarkson, 1994).

This paper summarizes all Banks Island survey data for caribou and muskox collected during the 10-year period 1982-92. We document changes in population size and distribution of the two arctic ungulate populations and, where methodologies permit, we compare changes in group size and the proportion of calves in each population.

Study Area

Banks Island is the most western island in the Canadian Arctic Archipelago which covers an area of approximately 70 000 km^2 (Fig. 1). The climate is Arctic Maritime along coastal areas tending toward Arctic Desert inland. Winters are long and cold; summers are short and cool. Precipitation is low, with an annual mean of 9 cm (Zoltai *et al.*, 1980).

Sachs Harbour is the only permanent settlement on the Island (71° 59' N., 125° 17' W.). A general overview of the geology and glacial history can be found in Zoltai *et al.* (1980).

Habitat types were adapted from Kevan (1974), Wilkinson *et al.* (1976), and Ferguson (1991). We recognized four major terrestrial habitats: i) Wet Sedge Meadow, ii) Upland Barren, iii) Hummock Tundra, and iv) Stony barren. Wet Sedge Meadows are generally level hydric lowlands dominated by *Carex aquatilis*, *Eriophorum scheuchzeri*, and *Dupontia fisheri*. Upland Barrens are moist well-drained sites found on the upper and middle slopes. Vegetation is dominated by *Dryas integrifolia* and *Salix arctica*. Hummock Tundra is found on moderately steep slopes characterized by individual hummocks vegetated primarily by dwarf shrubs (*D. integrifolia*, *S. arctica*, and *Cassiope tetragona*). Stony Barrens are gravelly areas that are sparsely vegetated; typically these are wind-blown ridges, and sand bars. A more detailed description of the flora of Banks Island can be found in Porsild (1955), Wilkinson *et al.* (1976), and Zoltai *et al.* (1980).

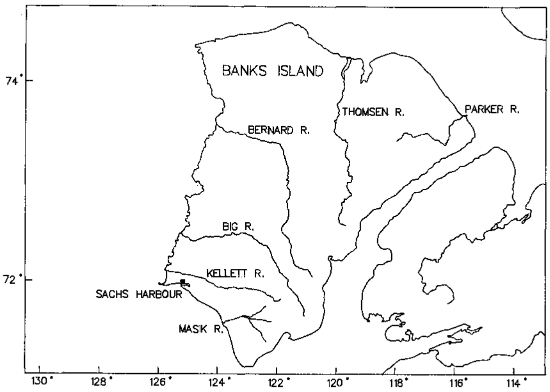

Fig. 1. The study area, Banks Island, Northwest Territories, Canada.

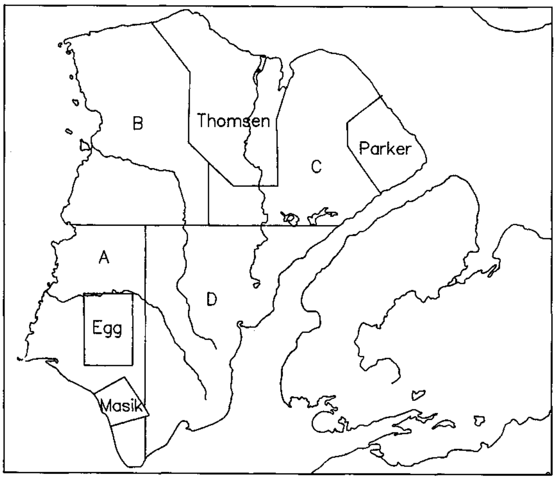

Fig. 2. Banks Island delineated into the 8 strata: A, B, C, D, Egg, Masik, Parker, and Thomsen.

Wolves, arctic foxes (*Alopex lagopus*), and polar bears (*Ursus maritimus*) also inhabit Banks Island.

Methods

Population Estimates

Population surveys were conducted using fixed-wing aircraft in 1982 (Latour, 1985), 1985 (McLean *et al.,* 1986), 1987 (McLean, 1992), 1989 (McLean & Fraser, 1992), 1991 (Fraser *et al.*, 1992), and 1992 (Nagy, J. & Fraser, P., unpubl. data) using strip-transect techniques (Norton-Griffiths, 1978). Coverage varied considerably, lowest being in 1985 when some blocks were surveyed with parallel lines 20 km apart (McLean *et al.*, 1986), and highest in 1992 when some blocks were surveyed with lines 2.5 km apart (Nagy, J. & Fraser, P., unpubl. data).

Surveys were conducted in June and early July, except in 1992 when the survey was in late August. The entire island was surveyed, except in 1982 when an area of high muskox density was omitted. As a result, we believe the 1982 muskox population estimate is likely an underestimate. We estimated caribou and muskox numbers each year, except 1987 when muskoxen were not surveyed. The number of calves (both species) were counted on transect and their percentage in the population was calculated.

Verification of Original Survey Data

We verified the area of each stratum flown by digitizing 1:250,000 scale maps of Banks Island, entering the coordinates of the stratum boundaries, and calculating the resulting areas using a Lambert Azimuthal Equal Area projection in the Spans Geographical Information System (GIS). The accuracy of the Spans GIS was verified by entering the coordinates of an area of known size and then comparing it to the GIS area estimate. These resulting areas were then used to recalculate the survey estimates using the original observations and the Jolly (1969) method for unequal sized sampling units (Norton-Griffiths, 1978). The island-wide estimates of both caribou and muskox are reported. Because we recalculated survey areas, the estimates we report may differ from those found in the original survey reports.

Post-survey Stratification

In order to examine in more detail the changes in muskox density, especially in relation to harvest, we reanalyzed the 1985 and 1991 survey data. We placed the original observations from these surveys into the 8 strata that were used for the 1989 and 1992 surveys (Fig. 2). We recalculated the estimates for each of the 8 strata and the island-wide population, and report both values for 1985, 1989, 1991, and 1992.

Growth Rate

Total estimates for the island population and for each stratum were compared with corresponding data from each subsequent year using two-tailed Student's *t*-tests. For caribou, we compared all estimates derived from 1982 to 1992. For muskoxen, we compared estimates derived for each of the 8 strata from 1985 to 1991. For total island population comparisons we also included the 1992 estimate. We calculated the instantaneous rate of population growth (r) for island and strata populations between surveys following Caughley (1977).

Group Size and Distribution

We used the Kruskal-Wallis (K-W) test (Gibbons, 1985) to assess differences in group size for caribou among years (1982, 1985, 1987, 1989, and 1991). When K-W tests indicated significant ($P<0.05$) results, multiple comparisons (Gibbons, 1985) were conducted on mean class ranks to identify significantly different population subsets. We used an overall significance level of 0.25 for multiple comparisons. Median and mean group sizes are reported.

The post-calving distribution of caribou and muskoxen observed during the 1982 to 1991 surveys was plotted for visual comparisons.

Results

Verification of Original Survey Data

The accuracy of the Spans GIS measurement was ±0.026%. In general, the difference between areas reported in the original surveys and those measured using the Spans GIS ranged between ± 8% for strata flown for caribou and from -7 to ± 6% for strata flown for muskoxen. The most notable differences were found for strata B, C and Thomsen River (Fig. 2). In 1985 the areas for strata B and Thomsen River were underestimated by 10 and 29% respectively, while stratum C was overestimated by 35%. These errors continued through 1992.

A comparison of population estimates presented in the original survey reports and those generated by our analyses indicates that caribou numbers were overestimated by 5.0, 0.3, and 5.6% in 1982, 1985, and 1987, respectively. Contrastingly, numbers were underestimated by 1.8, 1.0, and 1.7% in 1989, 1991, and 1992 respectively. Muskox numbers were underestimated by 11.9, 7.5, 2.1, and 7.4% in 1985, 1989, 1991, and 1992, respectively.

Caribou

The Peary caribou population (excluding calves) decreased from 6 970 (± 1133) in 1982 to 897 (± 151) in 1991 (Fig. 3a). The corresponding densities decreased from 0.11 to 0.01 caribou/km^2 (Table 1). Significant declines occurred during the periods 1982 to 1987 ($P<0.03$), 1985 to 1989 ($P<0.03$), and 1989 to 1991 ($P<0.001$) (Fig. 3a)(Table 1). The 1991 and 1992 estimates were not significantly different ($P>0.05$). The instantaneous rate of growth from 1982-1992 was -0.194. The growth rate declined from -0.099 between 1982 and 1987, to -0.238 between 1987 and 1989, and to -0.540 between 1989 and 1991. The proportion of calves in the total caribou population varied from a low of 3.2% in 1991 to a high of 31.1% in 1992 (Table 1).

Median group size decreased from a high of 2 (mean of 5.0) in 1985 to a low of 1.0 (mean of 2.0) in 1991 (Table 1). Group sizes during 1982, 1985,

Table 1. Population estimates (excluding calves, ±SE), with corresponding density, median and mean group sizes, and the percent calves of Banks Island caribou from 1982-1992.

Year	Area (km^2)	Estimate (+SE)	Density (km^2)	Number of Groups	Median Group Size	Mean Group Size	Percent Calves
1982[1]	61 237	6970±1133	0.11	337	2.0	4.2	18.8
1985[2]	70 266	4931±914	0.07	169	2.0	5.0	14.5
1987[3]	70 266	4251±663	0.06	156	2.0	2.9	20.7
1989[4]	70 266	2641±334	0.04	172	2.0	2.0	23.0
1991[5]	70 266	897±151	0.01	43	1.0	2.0	3.2
1992[6]	70 266	1005±133	0.01	94	2.0	2.1	31.1

[1] Latour (1985), [2] McLean *et al.* (1986), [3] McLean (1992), [4] McLean & Fraser (1992), [5] Fraser *et al.* (1992), [6] Nagy, J. & Fraser, P. (unpubl. data).

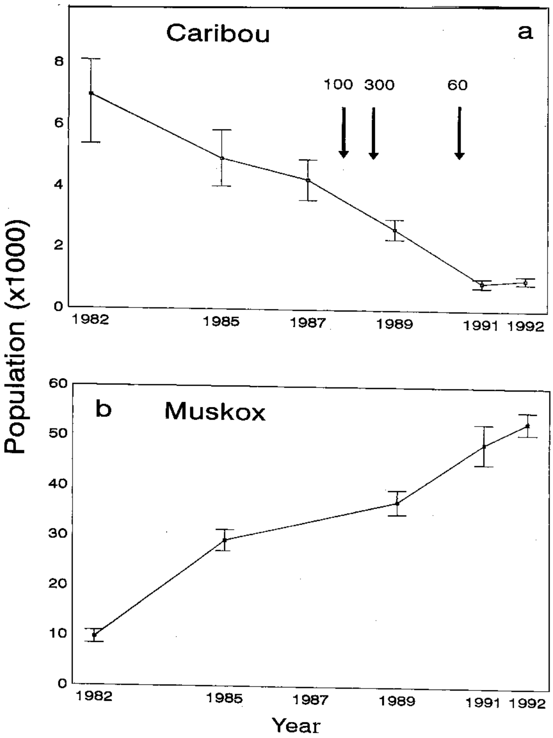

Fig. 3. Estimated population size (± SE) for (a) Peary caribou and (b) muskox from the originally flown surveys. The arrows in (a) point to winters which had freezing rains. The numbers above the arrows correspond to the recorded number of dead caribou. The 1982 value for muskox (b) is likely an underestimate.

and 1987 were significantly ($P<0.001$) larger than those observed during 1989 and 1991. Concomitant with the population decline and decreasing group sizes, was the disappearance of post-calving aggregations that had been prevalent on the northwest portion of Banks Island in the early 1980's (Fig. 4).

Muskoxen

The muskox population (excluding calves) increased from 29 168 (± 2104) to 52 959 (± 2240) between 1985 and 1992 (Fig. 3b) with an overall growth rate of 0.085. Corresponding densities increased from 0.42 to 0.75 muskoxen/km^2 (Table 2). Significant increase in growth occurred between

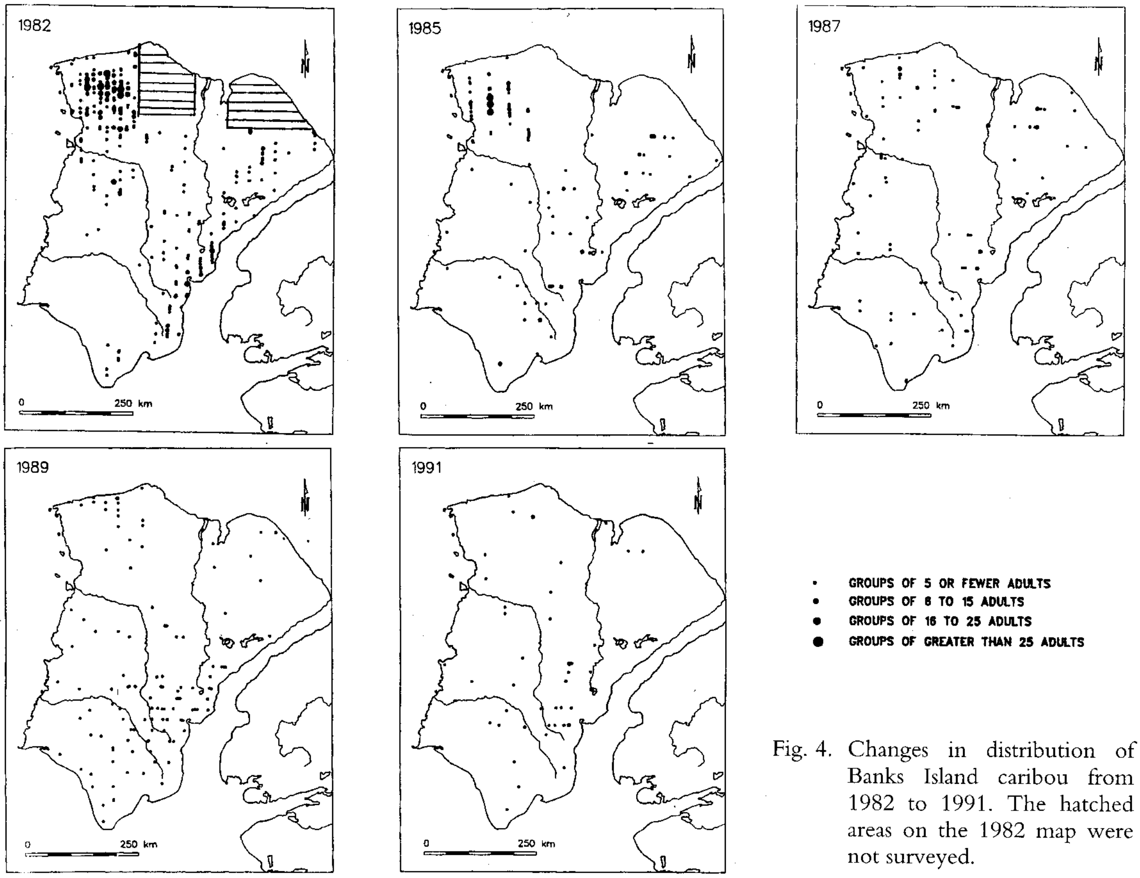

Fig. 4. Changes in distribution of Banks Island caribou from 1982 to 1991. The hatched areas on the 1982 map were not surveyed.

Table 2. Estimates and densities of muskox based upon original transect flight lines and strata, 1985 to 1992.

	1985			1989			1991			1992		
Stratum	Area (km²)	Estimate (±SE)	Density (/km²)	Area (km²)	Estimate (±SE)	Density (/km²)	Area (km²)	Estimate (±SE)	Density (/km²)	Area (km²)	Estimate (±SE)	Density (/km²)
A	57 550	12 524±1839	0.22	10 319	4353±1287	0.42	14 331	17 495±2818	1.22	10 319	7517±1082	0.73
B	n/a	n/a	0.27	14 396	5191±1300	0.36	16 266	8474±1565	0.52	14 396	6637±549	0.46
C	n/a	n/a	0.32	11 584	4282±652	0.37	21 237	18 471±2187	0.87	11 584	5560±726	0.48
D	n/a	n/a	0.09	18 409	4835±651	0.26	18 432	4263±809	0.23	18 409	7546±755	0.41
Egg	n/a	n/a	n/a	2662	2411±439	0.91	n/a	n/a	n/a	2262	4354±332	1.64
Masik	766	766±185	1.00	1372	2524±965	1.84	n/a	n/a	n/a	1372	2684±261	1.96
Parker	3 437	2995±585	0.87	3011	2193±271	0.73	n/a	n/a	n/a	3011	2929±416	0.97
Thomsen	8 513	12 883±818	1.51	8513	11 257±712	1.32	n/a	n/a	n/a	8513	15 733±1448	1.85
TOTAL	70 266	29 168±2104	0.42	70 266	37 046±2429	0.53	70 266	48 704±3979	0.69	70 266	52 959±2240	0.75

Table 3. Estimates (±SE) and densities of muskoxen (excluding calves) based upon restratified data from 1985, 1989, 1991, and 1992 population surveys.

		1985		1989		1991		1992	
Stratum	Area (km²)	Estimate (±SE)	Density (/km²)	Estimate (±SE)	Density (/km²)	Estimate (±SE)	Density (/km²)	Estimate (±SE)	Density (/km²)
A	10 319	2288±1081	0.21	4353±1287	0.42	9128±1675	0.88	7517±1082	0.73
B	14 396	3957±2117	0.27	5191±1300	0.36	6136±848	0.43	6637±549	0.46
C	11 584	3613±1678	0.31	4282±652	0.37	2837±431	0.24	5560±726	0.48
D	18 409	1727±910	0.09	4835±651	0.26	4258±606	0.23	7546±755	0.41
Egg	2 662	1342±924	0.50	2411±439	0.91	4120±616	1.55	4354±332	1.64
Masik	1 372	933±366	0.68	2524±965	1.84	3923±476	2.86	2684±261	1.96
Parker	3 011	2650±1184	0.88	2193±271	0.73	3940±639	1.31	2929±416	0.97
Thomsen	8 513	12 883±2322	1.51	11 257±712	1.32	13 030±1070	1.53	15 737±1448	1.85
TOTAL	70 266	29 294±4132	0.42	37 046±2429	0.53	47 374±2497	0.67	52 959±2240	0.75

1985 and 1989 (r=0.059, $P<0.05$), 1989 and 1991 (r=0.123, $P<0.003$), but not between 1991 and 1992 (r=0.111, $P>0.05$).

The rate of growth of the island-wide population increased during this time period (1985-92), but growth rates were dissimilar across strata (Table 3). Consistent positive growth occurred in strata A, B, Egg and Masik, whereas strata C, D, Parker and Thomsen showed both positive and negative growth during periods between surveys. All strata except for C however, showed an overall trend for positive growth during the period 1985 to 1991 (Table 3).

The proportion of calves in the total muskox population was less variable than in caribou: 11.8% in 1985, 14.5% in 1989, 14.0% in 1991, and 17.1% in 1992. Because calves are small and muskox groups tend to form defensive circles in response to the aircraft, the number of calves and therefore their proportion in the population are likely underestimated.

Muskoxen were distributed throughout the island during all surveys during 1982-1991 (Fig. 5); however the greatest increases in density occurred in strata A, D, Egg and Masik (Table 3). High, but stable, densities of muskoxen were observed in the Thomsen River strata during the period 1985 to 1991 (Table 3). Densities were variable, but generally low, in the remaining strata.

Discussion

Caribou

Based on current and historical data, we cannot attribute the decline of the Peary caribou population on Banks Island to any one cause. Our review indicates that some of the apparent decline in cari-

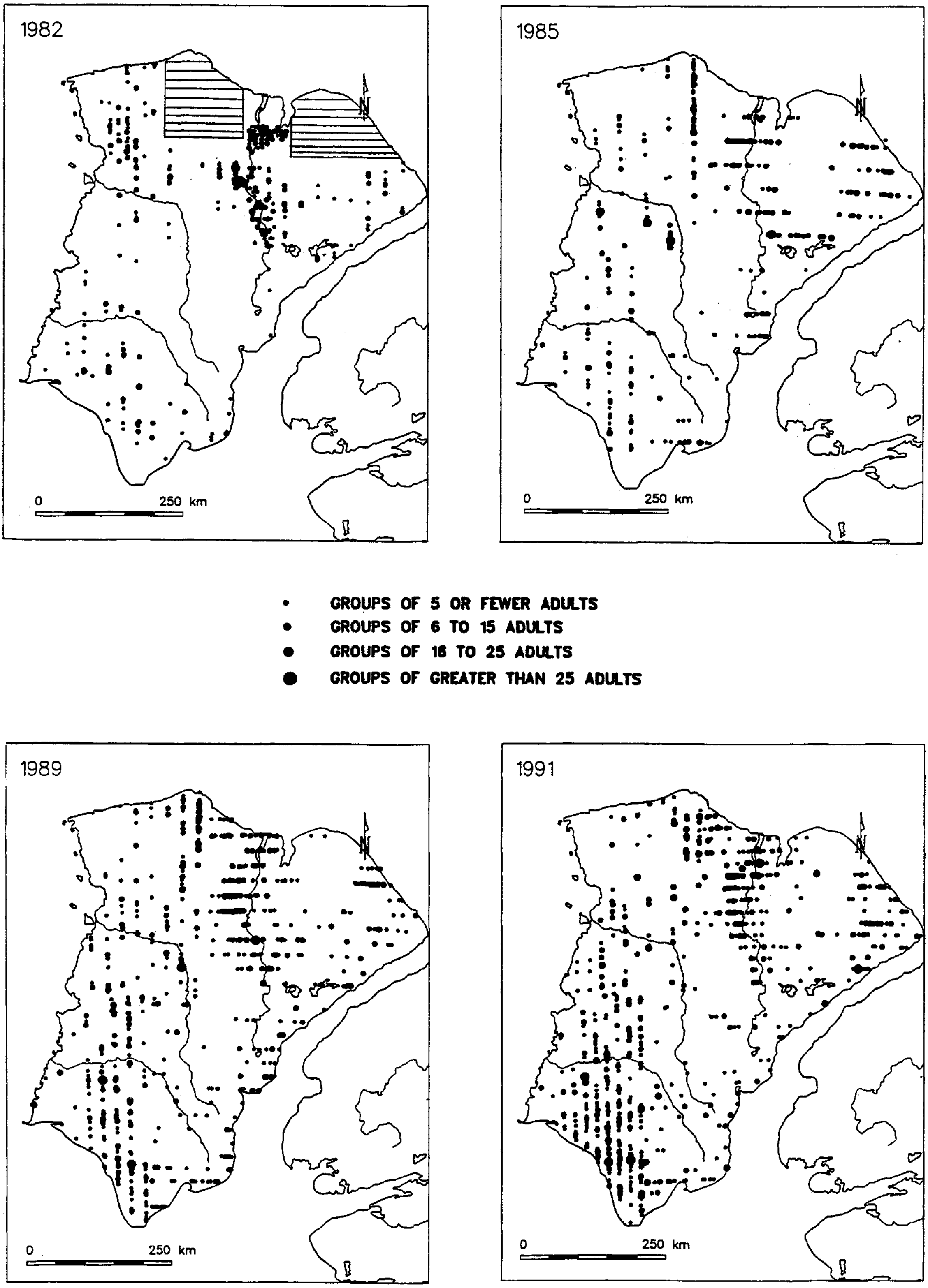

Fig. 5. Changes in distribution of Banks Island muskoxen from 1985 to 1991. The hatched areas on the 1982 map were not surveyed. See fig. 2 for strata boundaries.

bou numbers was due to errors in calculating population estimates. Human harvest and weather caused mortality do not fully account for the decline.

A comparison of the July 1987 and June 1989 population estimates indicates that non-calf caribou declined by 1610 animals. A total harvest of 615 non-calf caribou was reported during that period (Fabijan, unpubl. data), accounting for 38% of decline in numbers. The average annual harvest between 1987 and 1989 was 7.2% of the 1987 population estimate. A loss of 400 caribou due to weather caused winter morality was documented during that period (McLean & Fraser, 1992; McLean, B., unpubl. data), accounting for an additional 25% of animals lost. The loss of 595 non-calf caribou (37%) cannot be explained.

Similarly between June 1989 and June 1991 the population estimate for non-calf caribou declined by 1744 animals. A total harvest of 361 non-calf caribou was reported during that period (Fabijan, unpubl. data), accounting for 21% of the decline in numbers. The average annual harvest between 1989 and 1991 was 6.8% of the 1989 population estimate. A loss of 60 animals due to weather caused winter mortality was documented (Fraser *et al.*, 1992), accounting for an additional 3% of the animals lost. However, the loss of 1342 non-calf caribou (76%) cannot be explained.

During both periods it is unlikely that the unexplained losses were a result of unreported harvest or winter mortality. The annual subsistence harvest by residents of Sachs Harbour ranged from 211-354 adult caribou during the late 1980's (Fabijan, unpubl. data), and was similar to that reported during 1962-72 (Urquhart, 1973). The traditional winter range is located in southwest Banks Island (Urquhart, 1973). Therefore, substantial die-offs on the winter range would have been detected by residents or others travelling in the area.

The current impact of wolf predation is unknown. The vulnerability of the primary prey relative to an alternate prey determines the impact of predation (Messier, 1994). In some areas of western North America, moose populations are the main prey for wolf populations which can remain at levels high enough to deplete caribou populations (*Rangifer tarandus*) populations. This scenario has been used to explain declines in the hunted Nelchina caribou population (Bergerud & Ballard, 1988), and various woodland caribou populations (Bergerud & Elliot, 1986; Edmonds, 1988). Seip (1992) documented that a woodland caribou population that lived apart from wolves and moose during summer, was therefore less vulnerable to wolf predation, had a lower adult mortality rate and higher calf survival than a similar woodland caribou population that lived with wolves and moose. Whether or not one or both populations were hunted was not indicated. Larter *et al.* (1994) documented increasing wolf predation on moose caused by an increasing wood bison population which provided a substantial alternate prey source that maintained high wolf populations capable of depleting the more vulnerable prey population. Wolf predation has a greater impact on moose populations when the moose population is declining (Gasaway *et al.*, 1983).

Peary caribou on Banks Island may be in a situation similar to that described for some hunted moose and caribou populations, where a high biomass of muskoxen supports an increasing wolf population. Wolf numbers were reduced on Banks Island during poisoning programs conducted during the 1950's (Zoltai *et al.*, 1980). Local residents believe wolf numbers on Banks Island have increased during the 1990's. The annual number of wolves harvested increased dramatically from an average of approximately 4/winter during 1988-89 to 1991-92 to 50 during the winter of 1992-93 (Larter & Clarkson, 1994). Although available diet data are limited, they indicate that caribou and muskox are consumed by wolves (Zoltai *et al.*, 1980; Larter, N. & Nagy, J., unpubl. data). Hunters travelling on the land have found caribou killed by wolves (Esau, E. & Lucas, J., pers. comm.). Even if predation rates on caribou are low, the impact may be significant especially given their recent low numbers. Assuming that there were only 50 wolves and 1005 adult caribou on Banks Island during the winter of 1992-93, a predation rate of 1 adult caribou per wolf per year represents an approximate annual adult caribou mortality due to predation of 5%. All wolves on Banks Island were not harvested during the winter of 1992-93, thus adult caribou mortality due to predation may be higher.

The impact of disease in unknown. There have been no reported incidences of harvested animals appearing diseased, but studies have not been conducted to directly address the issue.

Inter-island movement of Peary caribou may have contributed to declining numbers. Miller & Gunn (1978, 1980) documented movements between islands in the Prince of Wales-Somerset Island complex. Residents of Holman (Victoria Island) and Sachs Harbour (Banks Island) and observations from wildlife surveys suggest that caribou cross in small groups between Banks Island and Victoria Island in fall and winter (Jingfors, K., pers. comm.). Residents of Sachs Harbour reported large numbers of caribou travelling past Sachs Harbour and out onto the sea ice south of Banks Island in 1951

(Manning & Macpherson, 1958). This movement appears to have occurred when available forage was scarce (Urquhart, 1973). They noted that some of the animals returned later in the winter only to starve along with caribou that remained on the island. During this time period Peary caribou were observed on the mainland coast near Baillie Island approximately 160 km south of Banks Island (Carpenter, A. & Wolki, F., pers. comm.). The caribou were weak and covered in ice.

These observations suggest that Peary caribou may normally move between Banks and Victoria Island as part of an inter-island population as suggested by Miller (1985, cited in McLean, 1992). However, large scale movements from Banks Island may be driven by reduced forage availability during episodes of severe winter weather. This would have a net negative effect on the island population if these were one way movements.

Whether or not range conditions have deteriorated during 1982-1992 is unknown. Lichen has never been abundant (Wilkinson & Shank, 1974; Zoltai *et al.*, 1980). Current research is examining range conditions in areas of high and low muskox density on and adjacent to the core caribou winter range. Preliminary indications are that lichen biomass is low throughout the range.

Although, competition between muskox and caribou has been considered unlikely in the past (Kevan, 1974; Wilkinson *et al.*, 1976; Parker, 1978; Vincent & Gunn, 1981; Biddlecomb, 1992), reconsideration of caribou and muskox ecology and recent research indicates they may in fact compete for forage resources especially during winter or when muskox densities are high (McKendrick, 1981, White *et al.*, 1981; Klein & Staaland, 1984). It is generally agreed that lichen is an important winter food for caribou, but in areas supporting low lichen biomass caribou switch to other forages, either willow or monocots (Reimers *et al.*, 1980; Klein, 1992; Staaland & Olesen, 1992). Muskox can clearly make use of high protein foods (White *et al.*, 1984), and even though they show many attributes of a classic grazer can be quite selective in their feeding (Oakes *et al.*, 1992). Thing *et al.* (1987) showed willow as a major component of the summer diet of muskox in Greenland.

Because of low lichen biomass on Banks Island, it is not surprising that willows, sedges, and forbs make up most of the caribou diet. The muskox diet is dominated by sedge, but in high density areas willow becomes an important dietary component in late winter (Larter, N. & Nagy, J., unpubl. data).

The area between the Kellet and Big rivers and centered around the Egg River was identified as the core of the caribou winter range on Banks Island (Urquhart, 1973). From July 1985 to July 1991 muskox densities on the southern half of Banks Island increased from 0.19/km^2 to 0.65/km^2. In the Egg River strata, which overlaps in excess of 60% of the core caribou winter range, muskox densities increased from 0.5/km^2 to 1.55/km^2 during that period (Table 4). Because muskoxen are non-migratory, and seasonally utilize to a various extent forage consumed by caribou, there exists the potential for food competition in the core caribou winter range. If this is the case, some caribou may be displaced to less preferred winter ranges or may move to other areas on or off Banks Island in search of more adequate winter ranges. Competition for food cannot be ruled out as a factor contributing to the caribou population decline.

Table 4. The instantaneous rates of growth (r) for each stratum, and the total island for the periods 1985-1989, 1989-1991, and 1985-1991. Rates followed by * indicate a significant ($P<0.05$) difference between population estimates from which the growth rate was calculated.

Stratum	1985-89	1989-91	1985-91
A	0.1608	0.3702 *	0.2306 *
B	0.0679	0.0836	0.0731
C	0.0425	-0.2058	-0.0403
D	0.2574 *	-0.0635	0.1504 *
Egg	0.1465	0.2679	0.1869
Masik	0.2488	0.2205	0.2394 *
Parker	-0.0473	0.2930 *	0.0661
Thomsen	-0.0337	0.0731	0.0019
Overall	0.0587 *	0.1230 *	0.0801 *

The decline was likely caused by the cumulative effects of a combination of factors including human harvest, severe winters, wolf predation, inter-island movement and possibly competition from the expanding muskox population.

Muskoxen

The island muskox population increased during the period 1985 to 1992. Recent data indicate that reproduction has been delayed from 2-year old to 3-year old females (Nagy, J., *et al.*, unpubl. data) possibly indicating some density dependent feedback mechanism. However, these data are limited to animals inhabiting the Egg and Masik strata. These two strata had continuous positive population growth, had the highest or among the highest densities of muskoxen since 1985 (Table 3), and are the two areas where commercial muskox harvests have been conducted. Age of first reproduction may not be increasing in other strata where muskoxen densities are lower.

Population increase and consistent calf proportions continued in both the Egg and Masik strata even though 2 525 muskoxen were harvested from these areas between 1990 and prior to the 1992 survey. Approximately half of the muskoxen were harvested from each strata. Because age of first reproduction has increased, harvesting has not created an increased numerical response of muskoxen in these areas.

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Woodland caribou population decline in Alberta: fact or fiction?

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Abstract: We re-assessed the view of a major woodland caribou (*Rangifer tarandus caribou*) population decline in Alberta. Several historical publications and provincial documents refer to this drastic decline as the major premise for the designation of Alberta's woodland caribou an endangered species. In the past, wildlife management and inventory techniques were speculative and limited by a lack of technology, access and funding. The accepted trend of the decline is based on many speculations, opinions and misinterpretation of data and is unsubstantiated. Many aerial surveys failed to reduce variance and did not estimate sightability. Most surveys have underestimated numbers and contributed unreliable data to support a decline. Through forest fire protection and the presence of extensive wetlands, the majority of potential caribou habitat still exists. Recreational and aboriginal subsistence hunting does not appear to have contributed greatly to mortality, although data are insufficient for reliable conclusions. Wolf (*Canis lupus*), population fluctuations are inconclusive and do not provide adequate information on which to base prey population trends. The incidence of documented infection by parasites in Alberta is low and likely unimportant as a cause of the proposed decline.

Key words: history, surveys, population trend, hunting, predation, habitat loss, pathology

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Introduction

In this paper we analyse the view that a major woodland caribou (*Rangifer tarandus caribou*) population decline has recently occurred in Alberta (Edmonds, 1986), and we offer a re-assessment of the limiting factors supporting this speculation. Many provincial documents refer to this decline as the premise for the designation of Alberta's woodland caribou as an endangered species (Alberta Department of Environmental Protection, 1994), and Edmonds (1986) states, "*Caribou in Alberta have severely declined since the early decades of this century and presently the viability of the remaining herds is either threatened or unknown.*" Fig. 1 shows the Alberta caribou population trend as outlined in the 1986 draft Woodland Caribou Provincial Restoration Plan for Alberta (Edmonds, 1986). The form of the decline is derived from many province-wide estimates that are analysed in this review. Brown *et al.* (1991) re-iterate Edmonds' (1986) views: "*Numbers of woodland caribou in Alberta are estimated to have declined from approximately 9 000 in the mid-1960s to currently less than 2 000.*". Others have reported declines in woodland caribou populations in Canada (Anderson, 1938; Edwards, 1954; Bergerud, 1971; Bloomfield, 1980b; Miller, 1982; Bergerud & Elliot, 1986; Williams & Herd, 1986; Edmonds, 1991; Rock, 1992).

The management of any species requires at least 2 levels of assessment: change in population size and the factors causing the change. The former can often be determined semi-quantitatively within broad limits, while the latter are considerably more difficult to assess. Speculation often serves as the basis for management regulations, so it is important to continually re-assess data and re-interpret trends.

We examined all known historical estimates of woodland caribou abundance in Alberta. We also re-assessed aerial surveys for woodland caribou to examine the validity of provincial population estimates and the rate of decline suggested by Fig. 1. We examined changes in several potential limiting factors that could have caused fluctuations in caribou abundance. Have one or more limiting factors varied enough to cause and maintain a woodland caribou population decline? Human recreational and subsistence hunting and the potential role that natural predators, namely wolves (*Canis lupus*), have played in altering caribou abundance in Alberta were examined. We also discuss the effects of fire, fire suppression, timber harvest and parasites on woodland caribou abundance.

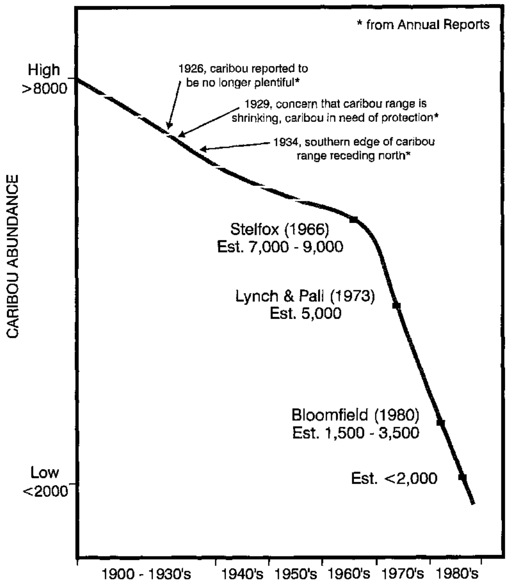

Fig. 1. Proposed woodland caribou population decline for Alberta from 1900-1986 as originally presented in Edmonds (1986).

Two, relatively distinct varieties of woodland caribou (Banfield, 1961) are found in Alberta: (1) a mountain variety in the Rocky Mountains of west central Alberta and foothills near the town of Grande Cache and (2) a woodland, or forest-dwelling, variety found throughout northern Alberta as well as near Grande Cache (Edmonds & Bloomfield, 1984; Edmonds, 1986).

Re-evaluating the Supposed Decline

In the past, wildlife inventory techniques were often speculative. Limited by technology, access and funding, provincial wildlife management decisions often were based on "guesstimates" (Webb, 1959) of a species' status. This is especially true of woodland caribou due to their relatively elusive behaviour, low densities and use of inaccessible habitat. The trend and magnitude of the proposed decline of woodland caribou in Alberta is based on many speculations and is unsubstantiated. The decline (Fig. 1) is also based on the better understanding of caribou in west central Alberta, and the extrapolation of habitat use and population density data from this region to the boreal forest populations.

Early History

Preble (1908) reported that woodland caribou occurred sparingly across northern Alberta in 1900-1901. Although the present distribution of caribou in northeastern Alberta does not extend much further south of the 55th Parallel, some 170 km north of Edmonton, Preble (1908) reported unconfirmed observations of caribou along the North Saskatchewan River near Edmonton. This suggests a change in distribution since this time, at least along the southern range of the boreal forest. Others have described woodland caribou distribution in Alberta as scattered or sparse (McCaig, 1919; Hewitt, 1921), and despite the observation that caribou distribution was limited compared to other native ungulates, they were not considered to be in any immediate danger of extirpation (Lawton, 1923; 1926; 1927; 1928; 1929). Soper (1942) stated that woodland caribou were not a common sight in Wood Buffalo National Park in 1931 (northeastern Alberta), but suggested that they were formerly much more abundant in the park. Others such as Clark (1934) and Anderson (1938) concurred that caribou density was low and their distribution limited.

Banfield (1949) and Cahalane (1947) described the mountain variety of woodland caribou as numerous, and Stelfox (1955; 1956a; 1956b) suggested that 200 - 300 caribou were in the foothills east of northern Jasper National Park in the mid-1950s. Cringan (1957), Webb (1959) and Soper (1964) suggested that Alberta had a stable population of 500 - 1 000 woodland caribou.

In 1965 a crude survey of the north-east region of Alberta was done to determine whether caribou abundance warranted a hunting season. Kerr (1966) concluded that despite low numbers, a hunting season would not be detrimental because hunters would find the area difficult to access.

None of these early estimates are based on conclusive data. In fact, many estimated the provincial population much lower than the 7 000 - >8 000 suggested by Fig. 1.

Early Estimates

The first provincial population estimate was 6 860 - 9 060 (Stelfox, 1966), evaluated from data compiled by aerial and ground surveys, and from reports of Forest officers, Fish and Wildlife officers, hunters, guides and outfitters. Without reliable inventory techniques, this estimate is questionable. Burgess (1970) believed the 1966 estimate was "subject to error", and that 4 000 - 5 000 caribou was a more realistic estimate. Lynch and Pall (1973) also re-evaluated the 1966 estimate and suggested that 4 800 - 5 200 was more realistic.

Most publications or reports on woodland caribou in Alberta refer to the 1973 estimate as a significant decline from the 1966 estimate (Bloomfield, 1980a; Edmonds & Bloomfield, 1984; Edmonds, 1986; Holroyd & Van Tighem, 1983), even though it was a re-evaluation. However, Edmonds (1988) mentions that the Lynch & Pall (1973) estimate of 600 - 700 caribou in the mountains and foothills of Alberta was an adjustment to the Stelfox (1966) estimate of 1 200 - 1 600.

In the late 1960s, a noticeable decline in caribou numbers was reported for Jasper National Park (Stelfox & Bindernagel, 1978), although abundance estimates from 1915 - 1973 were based largely on incidental sightings by park wardens. Soper (1970) upheld the view that a decline had occurred in the Alberta Rockies since sometime in the 1800s.

Bloomfield (1980) recommended a closure of recreational hunting on Alberta's woodland caribou based on the population estimates quoted above and on the apparent decline. His new estimate of the provincial population was 1 500 - 3 500, although he did not support this with data.

Consequently, the proposed decline (Fig. 1) is established from uncertain population estimates and some misinterpretation. Despite the lack of confidence in the estimates, no other data exist to refute the general perception of a decline. Speculative estimates should not be strung together to set up trends.

Recent Estimates

Edmonds (1986) estimated the provincial population at 1 324 - 1 868 based on aerial surveys of certain areas of the province, woodland caribou sighting card returns and regional biologists' opinions. To assess the validity of these numbers, we re-analysed each regional estimate and the surveys on which they were based (Table 1). Most of the aerial surveys from which the Edmonds (1986) estimate was evaluated do not lend themselves to a calculation of density. Many areas of the province capable of supporting caribou were not surveyed, and some estimates of population size were approximated from sighting card returns or radio-telemetry data on two or three individuals (e.g., Arbuckle, 1983; 1984a; 1984b; 1985). Moreover, none of the surveys included estimates of sightability (i.e., the probability that an animal within an observer's field of search will be seen by that observer - Caughley, 1974). Edmonds (1986) arbitrarily provided a sightability estimate of 70% for Keillor (1982a) and 50% for other estimates, but no sightability calculations were provided for the other surveys in Table 1. Under counting animals in relatively dense vegetation is common; for example, a woodland caribou survey in northeastern Alberta in late 1993 provided a sightability estimate of 40% based on the probability of sighting radio-collared individuals (Stuart-Smith *et al.*, in press). As well, the variance associated with the estimates was typically high (Table 1), making many of the estimates meaningless.

Subsequently, Edmonds (1991) put the provincial population at 3 350 animals, with 650 residing in west central Alberta and Jasper National Park. The west central population appeared to be stable and the remainder was of unknown status. Ferguson and Gauthier (1992) placed the provincial population at 3 000 - 3 500, and the 1992 provincial estimate was 4 100 (McFetridge, pers. comm.), which is a re-evaluation of past estimates and is based on potential habitat availability and population density. The most recent estimate, also based on potential woodland caribou habitat availability and estimates of population density, is 3 300-6 200 (Alberta Woodland Caribou Conservation Strategy, in prep).

The Human Predator

Although Bergerud (1974) claims that caribou are more vulnerable to hunting than any other cervid in North America, this may not apply to woodland caribou. Caribou in Alberta live in small groups in forested habitats (Fuller & Keith, 1981; Edmonds, 1988) and, with the exception of the mountain variety (Edmonds & Bloomfield, 1984), they rarely show traditional movements (Fuller & Keith, 1984; Stuart-Smith *et al.*, in press). These behaviours and the use of largely inaccessible habitat reduce the human predation risk.

Fig. 2 shows the estimated recreational harvest of male caribou in Alberta from 1909-1981. No data are available from 1925-1947. The yearly kill is small (Smith, 1962; Lynch, 1973; Bloomfield, 1980), even though it is likely that the numbers from the early half of the century are underestimated since many hunters were without a licence and failed to report to provincial authorities (Edmonds, 1986). Moreover, woodland caribou comprise a modest portion of the Alberta Chipewyan, Cree, Déné Tha and Métis diets; moose (*Alces alces*) are a more important food source (Wein *et al.,* 1992; Desjarlais *et al.*, 1993; Janvier *et al.,* 1993; Poelstra *et al.,* 1993).

Natural Predation

Historically, most ungulate population declines supposedly resulted primarily from habitat degeneration (Leopold & Darling, 1953; Edwards, 1954; Scotter, 1967; 1970; 1971), but the effects of a variety of other factors on woodland caribou populations have been debated for several decades (Edwards, 1954; Bergerud, 1983). Recent research tends to support wolf predation as a leading mortality factor for many woodland caribou populations in North America (Bergerud, 1974; 1978; 1980; 1983; Doerr, 1980; Fuller & Keith, 1980; Fuller & Keith, 1981; Gasaway *et al.*, 1983; Bergerud & Elliot, 1986; Gauthier & Theberge, 1986; Seip,

Table 1. Overview and re-assessment of population estimates originally compiled in Edmonds (1986).

Region	1986 Est.	Source	Recalc. density	Pop. range[a]
Bistcho Lake (north-west)	620 - 800	Hall *et al.* (1974a)	0.0202	0 - 948
		Keillor (1982a)	NCP[b]	NCP
Caribou Mtns. (north central)	200 - 400	Hall *et al.* (1975a)	0.0383	0 - 737
		Brebber & Hall (1979)	0.3306	1312 - 4235
		Keillor (1980a)	0.1905	261 - 789
		Keillor (1981a)	0.1115	0 - 398
		Holton (1985)	0.2574	291 - 891
Chinchaga River (north-west central)	19 - 28	Arbuckle (1984a)	NCP	NCP
Dixonville (north-west central)	48 - 72	Keillor (1980b)	0	0
		Moller (1982)	0	0
		Arbuckle (1983)	NCP	NCP
		Arbuckle (1985)	NCP	NCP
Red Earth (north central)	41	sighting card returns	NCP	NCP
Birch Mtns. (north-east)	44 - 88	Bibaud (1972)	0.0196	180 - 1530
		Hall *et al.* (1974b)	0	0
		Hall *et al.* (1975b)	0.0858	0 - 1328
		Smith (1979)	0.0151	NCP
		Dielman *et al.* (1979)	0.0593	15 - 242
		Fuller & Keith (1981)	0.0313	239 - 346
Lesser Slave Lake (central)	49 - 149	Hall *et al.* (1975b)	0	0
		Keillor (1981b)	NCP	NCP
		Keillor (1982b)	0	0
		Arbuckle (1984b)	NCP	NCP
		Holton (1986)	0.0552	150 - 282
Cold Lake (east central)	114	sighting card returns	NCP	NCP
Swan Hills (central)	0	no recent sightings	NCP	NCP
Grande Cache (west central)	214 - 290	Edmonds & Bloomfield (1984)	NCP	NCP
Jasper & Banff National Parks (south-west)	89 - 115	Kemp (1967)	NCP	NCP
		Hall & Bibaud (1975)	NCP	NCP
		Bibaud (1979)	NCP	NCP
		Bibaud & Hall (1981)	NCP	NCP
		Goski *et al.* (1982)	NCP	NCP
		Rhude (1982)	NCP	NCP
		Holroyd & Van Tighem (1983)	NCP	NCP

[a] 95% confidence interval of population estimate calculated using equations from Krebs (1989); population figures are calculated using the total area covered in each survey.

[b] NCP = No Calculation Possible.

1989), although other mortality sources may be more important for certain populations (Shideler *et al.*, 1986; Van Ballenberghe, 1986). Wolves have been identified as the principal predator, but grizzly bear (*Ursus arctos*), black bear (*U. americanus*), cougar (*Felis concolor*), lynx (*F. lynx*) and coyote (*Canis latrans*) have also been implicated (Miller, 1982). Seip (1991) further suggested that forest-dwelling caribou populations are more vulnerable to predation because wolf populations are maintained by a

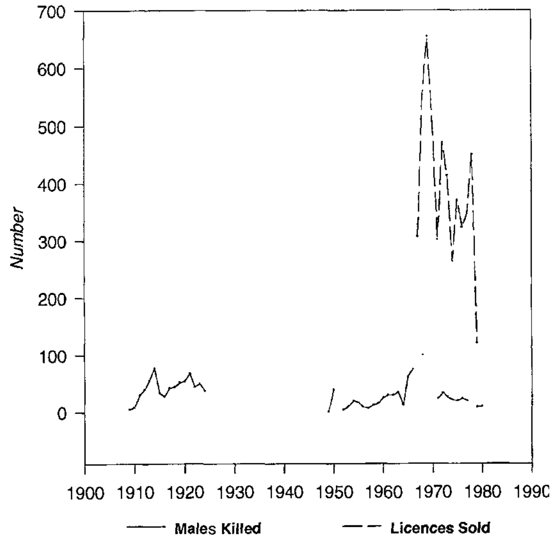

Fig. 2. Yearly human kill of male woodland caribou in Alberta from 1909-1981 and woodland caribou hunting licences sold from 1967-1979. No kill data are available from 1924-1948. Only big game licences required prior to 1967 (Edmonds, 1986).

variety of prey species. As well, many woodland caribou populations do not have long-distance migrations to space themselves from wolves, an important behaviour for reducing predation (Bergerud *et al.*, 1984).

Because Alberta wolf population data are even more speculative than those of woodland caribou, it is impossible to estimate caribou population trends based on these data. One must assume that wolves significantly limit caribou and that the wolf trend data itself is reasonably accurate. Although some have attempted to describe this century's wolf population trend (Stelfox, 1969; Gunson, 1991), no reasonable conclusion concerning the overall effect of wolves on Alberta's caribou abundance can be made.

Habitat Loss

Habitat loss has been postulated as a major limiting factor on caribou (Edwards, 1954; Cringan, 1957; Bloomfield, 1980; Seip, 1990), but Bergerud (1983) stated that there was little evidence to support a cause and effect relationship between habitat loss and population decline. The majority of Alberta's caribou depend on wetlands that have undergone little human-caused disturbance until recently (Edmonds, 1991), although habitat alteration may have influenced the mountain variety of woodland caribou (Bjorge, 1984; Edmonds & Bloomfield, 1984; Edmonds, 1988).

Fire plays a crucial role in the regeneration of certain plant communities and is the primary cause of the complex mosaic structure of the boreal forest (Rowe & Scotter, 1973; Johnson & Rowe, 1975; Schaefer & Pruitt, 1991). Some believe that fire can destroy lichen availability to the point of reducing caribou range (Scotter, 1967), although many have renounced this view (Bergerud, 1971; 1974; Johnson & Rowe, 1975). Schaefer & Pruitt (1991) found a woodland caribou population to decrease by 50% following a fire, but they also suggested that long-term range conditions may actually improve due to fire. Those who support the fire-influence hypothesis also suggest that as a result of increased settlement of the forested zone during the last 200 years, fire frequency and the resulting habitat loss have increased.

Fig. 3 shows that the total area burned in Alberta has decreased since the onset of effective fire suppression in the 1950s (Murphy, 1985), although the total area burned per year in Alberta from 1918-1979 has never exceeded 1.2% of the total forested area (Goff, 1979; Murphy, 1985). In addition, fire suppression is thought to have shifted the coniferous age class structure to older stands (Fig. 4), suggesting that more potential caribou habitat has become available within the last 40 years.

Pathology

Disease may have caused declines or extirpation of small woodland caribou populations (Miller, 1982;

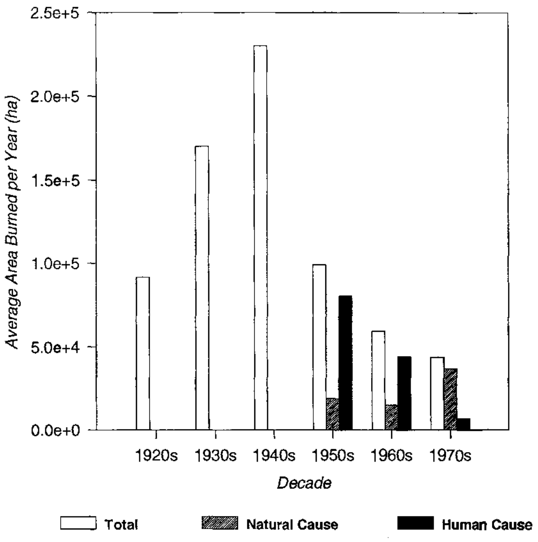

Fig. 3. Total forested area burned annually in Alberta from 1919-1979. Data represents 10-year running averages.

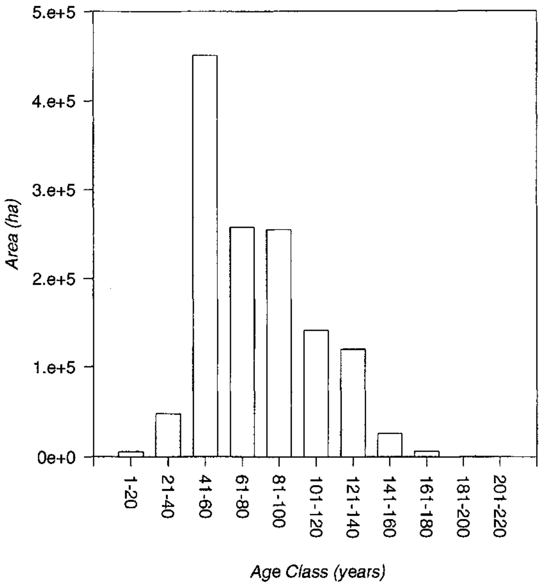

Fig. 4. Age class distribution of coniferous stands in northeastern Alberta (Alberta-Pacific Forest Industries, Inc. 1992).

Bergerud, 1983; Bergerud & Mercer, 1989). *Parelaphostrongylus tenuis*, fatal in caribou (Anderson, 1971; Trainer, 1973; Dauphiné, 1975), has not been reported west of the Manitoba-Saskatchewan border (Lankester & Fong, 1989; Samuel, pers. comm.) and there is no evidence that *P. tenuis* occurs in Alberta.

Larvae of a related nematode, mule deer muscleworm (*Parelaphostrongylus odocoilei*), were found in 28% of caribou faeces collected in west central Alberta (Gray & Samuel, 1986). Severe debilitation and perhaps death occurs in some hosts such as mountain goat (*Oreamnos americanus*) (Pybus *et al.*, 1984), but few larvae were found in caribou faeces suggesting that few adult worms of *P. odocoilei* were established in muscle tissue. Therefore, the potential severe pathology is remote (Gray & Samuel, 1986). The apparently benign muscleworm, (*Parelaphostrongylus andersoni*), occurs in caribou elsewhere (Lankester & Hauta, 1989), but there are no reports of this parasite in Alberta.

The tissue worm (*Elaphostrongylus rangiferi*), is generally found in the Old World, but there is recent evidence that it is established in Newfoundland caribou, the probable result of reindeer from Norway introduced there in 1908 (Lankester & Fong, 1989). Gray & Samuel (1986) found a few large larvae similar to those of the genus *Elaphostrongylus* in the faeces of woodland caribou in northeastern Alberta, perhaps the result of captive Newfoundland caribou escaping in northeastern Alberta in 1908 (Lankester & Fong, 1989).

The infestation of the winter tick (*Dermacentor albipictus*), a common ectoparasite of moose (Samuel, 1989), found on captive reindeer from the Edmonton Valley Zoo prompted the search for this parasite in Alberta's wild woodland caribou. Welch *et al.* (1990) examined caribou hides from 2 locations in Alberta and found an extremely low prevalence of *D. albipictus*. Their presence on caribou is likely a new phenomenon and therefore, not a source of past mortality (Anderson & Lankester, 1974).

The epizootic, besnoitiosis, was reported as morbid in captive caribou and reindeer at the Assiniboine Park Zoo in Winnipeg, Manitoba in 1985 (Glover *et al.*, 1990). This lead to studies by Lewis (1989; 1992) to determine its distribution and pathology in wild woodland caribou in British Columbia. He found a high incidence of infection by *Besnoitia* sp. (23%) with minimal or no detrimental effects. Only two cases of woodland caribou with besnoitiosis have been reported in Alberta (Pybus, pers. comm.).

Discussion and Conclusions

We agree with Seip (1991) that woodland caribou, in Alberta and elsewhere in similar ecoregions, have evolved to exist at relatively low densities. We also concur with the hypothesis of Bergerud & Page (1987) that this cervid has co-evolved with its predators by forming small groups and existing at low densities possibly to reduce predation risk. Because low densities appear to be the norm for woodland caribou across the boreal range (Seip, 1991), the major environmental variable permitting caribou to co-exist with predators is space (Bergerud *et al.*, 1984).

Woodland caribou may not have suffered a decline in Alberta because the estimates supporting the presumed decline originated primarily from anecdotal information and misinterpretation. As well, much of Alberta has not been surveyed effectively to estimate total caribou abundance (Fig. 2). There is not enough evidence to claim that Alberta's woodland caribou population has either decreased or increased significantly during the last century. We suggest that the difference in population estimates during the last decade is evidence of refined knowledge rather than true fluctuations in abundance.

It is doubtful that a single-factor hypothesis could explain a caribou population trend, although it is important to analyse the trend of individual limiting factors. Recreational hunting of woodland caribou in Alberta appears low, but insufficient data regarding poaching and aboriginal harvests preclude any reliable conclusion. Without the necessary data to corroborate the hypothesis that hunting could have caused a decline, it is impossible to weight this source of mortality in terms of its effects on abundance. Nonetheless, woodland caribou are found largely in relatively inaccessible habitat, the exception being the populations of west central Alberta (Edmonds & Bloomfield, 1984; Edmonds, 1986). Woodland caribou there represent a small proportion of the total provincial population and are prone to higher hunting pressures and collisions with highway vehicles given their use of more accessible range (Edmonds, 1986). These factors are not well-documented for the remainder of Alberta's woodland caribou populations.

Data on wolf abundance in Alberta during the past century are inconclusive and cannot be used to predict trends in prey abundance. Further research is required to demonstrate the true relationship between woodland caribou and wolves, especially in the boreal forest region.

The abundance of potential woodland caribou range and the typical burning rate of Alberta's boreal forests suggest that although caribou may be limited ultimately by forage availability, the low densities at which they exist in a seemingly habitat-abundant range suggests that other factors may be responsible for their low numbers. However, the recent expansion of the forest industry into the northern boreal forest (Edmonds, 1991) may indirectly contribute to future population declines. Land-use authorities must therefore maintain contiguous regions of woodland caribou habitat such as black spruce (*Picea mariana*) stands, bogs and fens and certain uplands (Fuller & Keith, 1981; Darby & Pruitt, 1984; Bradshaw *et al.*, 1995).

Habitat alteration resulting in increased moose, or deer, productivity and subsequent wolf population increases (Bergerud, 1974) may have the most detrimental effects on the survival and distribution of northern Alberta's caribou. Canopy closure and tree density are high and understorey shrub growth is low in forests dominated by mature tree stands, a result of intensive fire suppression during the last few decades (Hebert, 1993). Moose population density and distribution may respond to timber harvesting practices in the near future, so land-use managers should attempt to reduce the predicted changes in moose and wolf densities in order to maintain caribou numbers.

The low incidence of infection of caribou parasites precludes this reason as one which could explain a major population decline. We should not, however, be quick to renounce parasite-induced mortality as an important future limiting factor. The increasing range expansion of parasite vectors, such as white-tailed deer (*Odocoileus virginianus*), into caribou range highlights a need for further research in this area.

Management Implications

Imprecise survey data from different years should not be used to establish historical trends. If our ultimate objective is to ensure the healthy continuance of a given species in spite of increasing development in the northern forests, we must have reliable information (Romesburg, 1981) on which to base our management decisions. As is the case for much in wildlife science, opinion often creeps into scientific thought and becomes established as paradigm. Ideas and hypotheses that have the power to sway management decisions must be identified and tested appropriately before being accepted. We strongly suggest that all "documented" declines of any furtive species be scrutinized thoroughly before assuming the worst.

Regardless of the true historical woodland caribou trend in Alberta, we acknowledge the concern for this sub-species and believe that a better understanding of their population dynamics is warranted. Maintaining healthy populations in spite of proposed timber allocations is a challenge for provincial authorities in the future.

Finally, we offer our opinion on the role of provincial authorities in maintaining reliable census data. Admittedly, many of the older survey projects operated on inadequate budgets, although the designs of many of these projects were faulty. In most cases, modification of the survey designs, such as density stratification or sightability estimates, would have answered many more questions. Due to the nature of woodland caribou research, the use of expensive aircraft is currently the only effective means of collecting data. Therefore, it is essential that surveys are designed to maximize quality data returns. We suggest that the focus of woodland caribou management should be switched from enumeration to understanding the dynamics of local populations.

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Brief communication

Winter foraging dynamics of woodland caribou in an artificial landscape

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Key words: Arboreal lichen, bite size, bite rate, intake rate

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Introduction

Woodland caribou (*Rangifer tarandus caribou*) subsist on a nearly monophagous diet of alectorioid arboreal lichens during winter in the high snowpack ecosystems of western North America. This phenomenon provided an opportunity to mimic an entire seasonal diet in a laboratory situation using bottle-raised woodland caribou. Arboreal lichen biomass is reported to vary significantly among tree species (i.e. more lichen on subalpine fir (*Abies lasiocarpa*), than Engelmann spruce (*Picea engelmanii*), among topographical sites (i.e. more lichen on valley bottom trees than on mid-slope trees) and along the vertical axis of trees (i.e. more lichen on branches between 4-5 m than between 2-3 m; Detrick, 1984). The objective of this experiment was to quantify arboreal lichen intake rates of woodland caribou foraging on natural branches collected from 2 land types, and 2 foraging heights within trees. We report the results ofi foraging trials using 8 woodland caribou (3, 2.5-year-old steers; 1, 1.5-year-old female; and 4 steer calves) conducted in an artificial forest during the autumn of 1992.

Methods

A 225 m^2 enclosure was constructed with 9 equally-spaced telephone poles. This "tree" density mimicked that measured in old-growth subalpine fir/Engelmann spruce forests in woodland caribou late-winter habitat (Rominger & Oldemeyer, 1991). Holes were drilled into poles to enable insertion of lichen bearing branches collected from historical woodland caribou habitat in northeastern Washington. Branches were collected from randomly sampled subalpine fir, Engelmann spruce, and snags of both species at a ratio of 5:2:2. Branches were collected from 2 topographical sites (valley bottom and mid-slope) and from 2 foraging heights within trees (2-3 m and 4-5 m). These branches were then bundled by tree and reconstructed on randomly assigned telephone poles prior to foraging trials. Branches generally had both *Alectoria sarmentosa* and *Bryoria* spp. attached.

Trials were conducted by introducing caribou, paired on the basis of behavioral compatibility, into the enclosure to forage upon "trees" reconstructed with branches from a single topographic site and a single foraging height. Each caribou was followed by an experienced observer and bite sizes and bite rate, recorded into microcassettes during a 3 minute trial. The trial was then permuted with the alternate height within the same topographical site. A minimum of 10 bites during the 3 minutes was required for inclusion as a foraging trial.

Mean bite size (grams), bite rate (bites/minute), and intake rate (grams/minute) were analyzed with ANOVA (PROC GLM; SAS Inst., 1987) in a split plot design with caribou/topography as whole plot experimental units and caribou/topography/height as subplot experimental units. Bite size was estimable to 0.1 g and therefore bite sizes <0.05 g were recorded as traces but have been excluded from these analyses (see discussion regarding minimal effect of this protocol). Trials were conducted twice per week and caribou had access to an *ad-libitum* pelleted diet and therefore did not enter trials in a fasted state.

Results and discussion

Foraging data were collected from 194 trials. Mean intake rate varied significantly ($P<0.001$) due to topography and foraging height without a significant interaction ($P>0.4$) and therefore main effects may be assessed independently. Intake rate varied as a function of both topography and foraging height with the lowest biomass combination (mid-slope/2-3 m) having the lowest intake rate (0.85 g

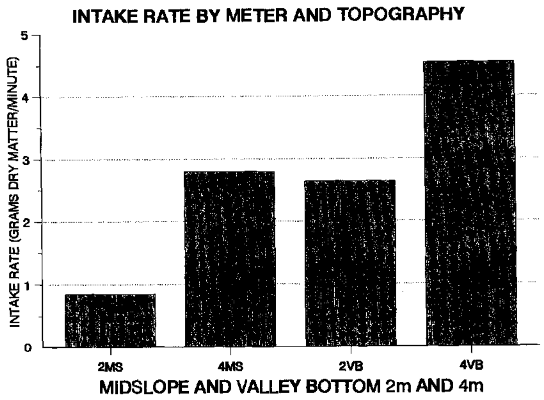

Fig. 1. Arboreal lichen intake rate of woodland caribou (n = 8) at 2 foraging heights within trees and 2 topographical sites.

DM/minute) and the highest biomass combination (valley bottom/4-5 m) having the highest intake rate (4.54 g DM/minute, Fig. 1). Bite size and bite rate also have similar relationships with topography and height therefore having a multiplier effect on intake rate (sensu White, 1983). A nearly 3-fold increase in bite size between the lowest and highest biomass becomes a 5-fold increase in intake rate (Fig. 1). Bite size, bite rate, and intake rate were similar between valley bottom/2-3 m and mid-slope/4-5 m. Biomass estimates for these locations are also similar (Detrick, 1984).

Substitution of the hypothetical values 0.01 g or 0.025 g for trace values increased total intake <1% and <2.2% respectively at topographical and foraging height groupings other than mid-slope 2-3 m. At mid-slope 2-3 m trace-size bites comprised 56.8% of all bites, however substitution of the above values only increased intake by 4.9% and 12.2% respectively.

These data suggest that arboreal lichen biomass and/or bite size are primary factors influencing intake rate. Caribou did not increase bite rate to compensate for smaller bite sizes or decreased biomass. Forest management should enhance lichen production to maximize intake rates for woodland caribou.

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Brief communication

Winter forage selection by barren-ground caribou: Effects of fire and snow.

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Key words: fire, lichens, *Rangifer*, snow, tundra

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Debate over the role of wildfire in the ecology of barren-ground caribou (*Rangifer tarandus*) has generated both questions and controversy. In summer 1988, a wildfire burned 84615 ha of the Selawik National Wildlife Refuge in northwestern Alaska. Portions of the burned area have been used historically as a migratory corridor by the Western Arctic Caribou Herd. The objective of this study was to address the effects of fire on caribou on a tundra range in late winter (March through April) by comparing vegetative cover, production, and snow characteristics at feeding and control sites in burned and unburned habitat. I also compared the protein content and digestibility of a sedge species collected in burned and unburned habitat.

Replicate plots (30 x 30 m), each containing feeding craters and undisturbed snow, were established in burned and adjacent unburned tussock tundra in late March through April 1990 (n=20 burned, 20 unburned) and 1991 (n=16 burned, 16 unburned). Craters were located from the air when possible or by following caribou trails. Plots were randomly oriented with respect to direction and distance from edges of craters. Within each plot, I measured snow depth and hardness at 10 points along the least disturbed edges of feeding craters and at 10 randomly located points in undisturbed snow. Randomization of undisturbed points was achieved by randomly selecting intersections of x,y coordinates spaced at 0.1 m intervals along two edges of the plot; coordinates intersecting in craters were discarded. I collected vegetation from craters in both burned and unburned plots in 1991 for analysis of crude protein content and *in vitro* digestibility. Caribou fecal pellets were collected and microhistologically analyzed to estimate winter diet in the general area.

In late July-August, I revisited plots and established up to 10 0.25 m^2 quadrats within former craters and centred quadrats on the 10 randomly located points sampled in late winter. Species lists were compiled for each quadrat and I calculated the relative frequency of occurrence for each plant species in a plot. Percent relative frequency was defined as follows:

$$\text{Relative frequency species A} = \left(\frac{\text{No. quadrats containing species A}}{\text{Sum of frequency values of all species}}\right) \text{x}100$$

I also clipped above-ground vegetation in 5 of the randomly located quadrats to estimate biomass. Years were analyzed separately, and stepwise discriminant function analysis (DFA) was used to select key variables prior to making statistical comparisons. Based on the results of DFA, snow depth and hardness and the relative frequencies of occurrence of lichens and bryophytes were selected as important variables in both 1990 and 1991. In addition, relative frequency of *Eriophorum vaginatum* was selected as a variable in 1991.

Multiple analysis of variance (MANOVA) indicated that there were significant differences in snow depth and hardness and in plant relative frequency data between burned and unburned plots and between craters and unused areas within plots in both years. I performed ANOVAs to determine which variables contributed to these differences.

Snow depth and hardness were the most influential factors determining selection of feeding areas by caribou in both burned and unburned plots. Snow was shallower and softer at edges of caribou feeding craters than at adjacent undisturbed points in both years. There was little difference in snow depth or hardness between burned and unburned plots.

Frequencies of particular plant taxa were only significant in influencing selection of crater sites in unburned plots in 1990, when caribou craters had higher relative frequencies of lichens and lower frequencies of bryophytes than unused areas. Lichens were primarily in the genera *Cladina, Cetraria*, and *Cladonia*.

Relative frequency and biomass of most vascular plants were reduced in burned plots, with the exception of post-disturbance species. Biomass and relative frequency of *Eriophorum vaginatum* were greater in burned plots than in unburned plots in 1991. Also, protein and *in vitro* digestibility levels were significantly enhanced in samples of this species collected from burned plots in 1991. Bryophytes had greater relative frequencies in burned plots than in unburned plots, but species composition differed between the two areas. Bryophytes in unburned plots consisted mostly of *Sphagnum* spp. and feather mosses; in burned plots, post-disturbance species in the genera *Ceratodon, Polytrichum,* and *Marchantia* dominated. Although lichen biomass was significantly reduced in burned plots in both years, lichens composed 74% and 59% of caribou diet in 1990 and 1991, respectively.

Both long- and short-term consequences should be considered when examining the effects of fire on the foraging behavior of caribou. Post-fire increases in protein content, digestibility, and availability of *E. vaginatum* make burned tussock tundra an attractive feeding area for caribou in late winter. These benefits are likely short-lived, however. Lowered availability of lichens and increased relative frequency of bryophytes will persist for a much longer period.

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Canopy, snow, and lichens on woodland caribou range in southeastern Manitoba

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Abstract: I examined the relationships among snow cover (api), lichen abundance, and canopy composition on the range of the Aikens Lake population of woodland caribou (*Rangifer tarandus caribou*) in southeastern Manitoba. Percent cover of forage lichens (*Cladina* spp.) was positively correlated with maximum total thickness and with maximum vertical hardness of api. Mixed communities of trembling aspen (*Populus tremuloides*), spruce (*Picea* spp.), and balsam fir (*Abies balsamea*) showed the most favourable nival conditions for caribou but had low lichen abundance; those dominated by jack pine (*Pinus banksiana*) were the converse. The results suggest an energetic compromise for woodland caribou when foraging for terrestrial lichens. During winter, caribou exhibited significant selection for jack pine communities whereas mixed communities were avoided.

Key words: habitat selection, foraging, *Rangifer tarandus caribou*, taiga

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Introduction

Api (snow on the ground) and lichens are perhaps the most salient habitat features that influence the behaviour of caribou (*Rangifer tarandus*) in winter. Caribou are well-adapted to both. Their broad hooves, low foot loading, and single-file mode of travel are characteristics that qualify them as chionophiles (Russell & Martell, 1984). During winter, lichens provide a unique, highly-digestible energy source and are often exploited as a principal forage (Luick, 1977; Russell & Martell, 1984).

For *Rangifer*, api and lichens are opposing entries on the energetic balance sheet: travelling on and cratering through snow cover are often energetic investments for obtaining terrestrial lichens. Recent studies have begun to explore these energetic costs (Boertje, 1985; Fancy & White, 1985, 1987) and nutritional benefits (Person *et al.*, 1980; Thomas *et al.*, 1984) but, as yet, we know little of the association between these 2 important range features. Such knowledge seems fundamental for managing habitat and modelling caribou foraging behaviour. Here, I examine the relationships between api characteristics, lichen abundance, and canopy composition on the taiga range of the Aikens Lake population of woodland caribou (*R. t. caribou*) in Manitoba.

Materials and methods

Field investigations were conducted in the vicinity of Taiga Biological Station, Wallace Lake, in southeastern Manitoba (51°01'N, 95°40'W). The study area, part of the Northern Coniferous Section of the Boreal Forest Region (Rowe, 1972), was dominated by Precambrian outcrops with numerous intervening bogs and small lakes. Sampling was based on a map recognising 5 vegetation communities (Schaefer & Pruitt, 1991): mature spruce bog, jack pine forest, mixed coniferous forest, jack pine outcrop with intervening black spruce bog, and mixed deciduous forest.

Overstorey and Lichen Abundance

Tree density and lichen coverage of 5 vegetation communities, 90 - 160 years of age, were sampled 12 June to 31 July 1985. Discrete areas of habitat within an accessible area were selected randomly. Within each discrete area, 2 sampling sites were picked randomly with a 1:15840 aerial photo and a grid overlay of points 50 m apart. At each site a 50-m transect was established. Its exact origin was determined by the toss of a stone, its orientation (north or south) by the toss of a coin. At 3 random points along the transect, a 50-m branch transect was established with a random east or west direction. The abundance of lichens of the genus *Cladina* was estimated from 6 quadrats, 20 cm x 50 cm, placed longitudinally at random 1-m intervals along the branch transect; 6 discrete cover classes, i.e., <5%, 5-25%, 25-50%, 50-75%, 75-95%, >95% (Daubenmire, 1968) were used. The mid-point of each cover class was used in the statistical analyses. The density of trees was determined at each quadrat by tallying individuals (> 2.5 m high) within a plot of radius 2.0 m. For analysis, each site was treated as an individual sampling unit and was represented by the average tree density and lichen coverage from 18 plots.

To display relationships between canopy composition and other habitat features, principal components analysis (PCA) was performed using SPSS/PC+ (Norušis, 1986) on the density of tree species. The effectiveness of PCA lies in its ability to reduce the number of dimensions to display such multidimensional data while retaining much of the original information (Pielou, 1984). Using PCA, therefore, density data of each of 5 tree species (*Pinus banksiana, Picea* spp., *Populus tremuloides, Betula papyrifera*, and *Abies balsamea*) were reduced to one axis, the largest principal component (i.e., PCA axis 1).

Api Conditions

I restricted the analysis to the time when api thickness and hardness were maximal (early March) in 1985 and 1986. I selected a 6 x 50 m site, representative of each community type (Schaefer & Pruitt, 1991), where api profiles were placed haphazardly. In each profile, vertical hardness ($g \cdot cm^{-2}$) of the surface layer, using spring penetrometers, and total thickness (cm) were recorded (Pruitt, 1959). During 1985, 5 profiles were taken per site; during 1986, 4 profiles were taken. For each community type, the 2-year averages of maximum total thickness and maximum vertical hardness were extrapolated to all sites of the same habitat type. The lack of independence of api observations means that such sampling is pseudoreplicated (Hurlbert, 1984). Hence, although I used a Bonferonni-corrected α of 0.005 as an indication of significant linear correlations between variables (Norušis, 1986), these statistical inferences should be treated cautiously.

Table 1. Correlations between density of tree species, api characteristics, and lichen abundance in the Wallace-Aikens lakes study area in southeastern Manitoba, 1984-86. All correlations were significant (Bonferonni-corrected $P < 0.005$).

	Jack pine density	Balsam fir density	Api total thickness	Api vertical hardness
Lichen coverage[a]	0.69	- 0.57	0.51	0.84
Jack pine density		- 0.47	0.44	0.63
Balsam fir density			- 0.44	- 0.57
Api total thickness				0.76

[a] Lichen coverage is expressed as ln (% cover of *Cladina* spp. + 1).

Results

Api variables, canopy composition, and the abundance of *Cladina* lichens were interrelated in the study area (Table 1). Maximum total thickness and maximum vertical hardness of the api were negatively correlated with the density of balsam fir (*Abies balsamea*) and positively correlated with that of jack pine (*Pinus banksiana*). Coverage of forage lichens (*Cladina* spp.) was similarly related; more lichen was associated with increased density of jack pine, less lichen with with increased density of fir.

Correspondingly, greater lichen abundance was positively correlated with both harder and thicker api (Table 1). We can compare the extremes in upland communities: on jack pine outcrops, where coverage of *Cladina* spp. averaged 17%, api was 80 $g \cdot cm^{-2}$ (more than 100%) harder and almost 10 cm (32%) thicker than in mixed coniferous forests where lichen coverage was only 1.5%.

The first principal component from the ordination of overstorey species - tending to separate sites dominated by jack pine from mixed stands of balsam fir, spruce (*Picea* spp.), and trembling aspen (*Populus tremuloides*) - accounted for 34% of the total variation. When plotted against *Cladina* spp. abundance, the above interrelationships can be visualised (Fig. 1). The ordination axis, with mixed communities (types 1, 3, and 5) tending to the negative (left) end of the axis and jack pine habitats (types 2 and 4) to the positive (right) end, was positively correlated with lichen coverage ($r = 0.69$). The superimposed api parameters, hardness and thickness, show relationships to both overstorey and *Cladina* abundance (Fig. 1). Vertical api hardness was better correlated to the canopy ordination axis ($r = 0.67$), however, than was total thickness ($r = 0.38$).

Discussion

Snow cover is influenced by the type and density of the trees above it, a relationship which has been widely documented (e.g., Bunnell *et al.*, 1985). In

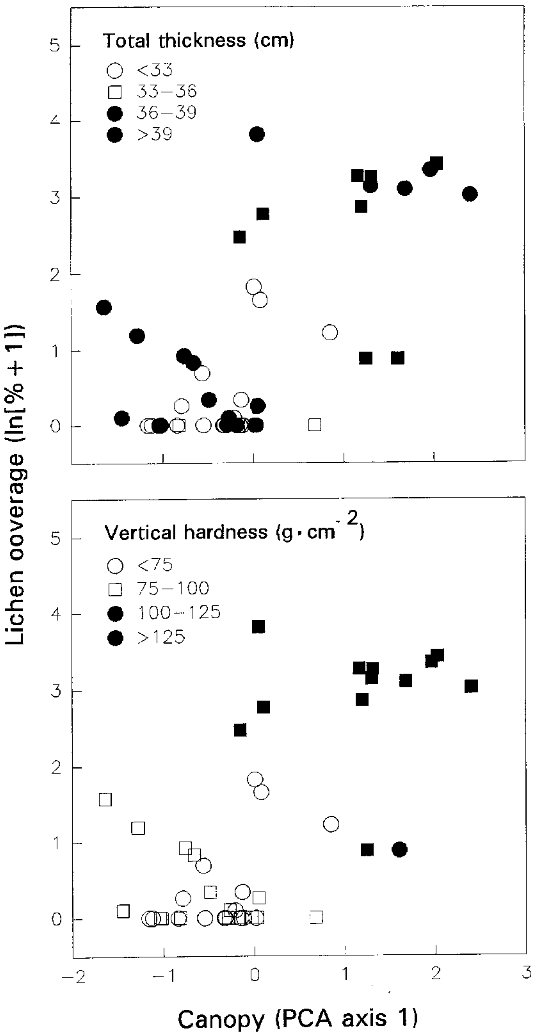

Fig. 1. Maximum total thickness and vertical hardness of api superimposed on a scattergram of lichen (*Cladina* spp.) abundance and the first principal component of canopy species. Jack pine communities tend to the right, mixed spruce/fir/aspen communities to the left.

general, greater coniferous cover reduces api thickness by providing greater snow interception and qali (Pruitt, 1957) formation. It reduces the surface hardness through wind interference and shading of the forest floor (Bunnell *et al.,* 1985).

In this study, the relation between maximum thickness of snow cover and jack pine abundance was counter to this general trend and, initially, appears counter-intuitive. The result may stem from the low sample size, but I offer 2 further, tentative explanations. First, the form of the jack pine - api relationship may not be strictly linear across the full range of jack pine densities. The extent of densities studied here (approx. 0.5 - 1.0 x 10^3 stems·ha^{-1}) was well below that in younger (37-year-old) stands in the study area (approx. 2.5 - 3.5 x 10^3 stems·ha^{-1} [Schaefer, unpubl. data]). Such dense, intermediate-aged stands, although not used by woodland caribou, appeared on cursory inspection to have thinner snow cover than old-growth communities. Coverage of *Cladina* spp., however, was similar (Schaefer & Pruitt, 1991).

Second, and perhaps more fundamental to our understanding, is that the relationships outlined here are probably scale-dependent. Results from many ecological studies (reviewed by Wiens, 1989) suggest that such correlations may depend on scale, i.e., the size of the sampling unit and the extent of sampling chosen by the investigator. Schaefer & Messier (1995), for example, found that correlations between arctic vegetation and snow cover (upsik) appeared stronger when larger sampling units were used in analysis. In this light, the positive association of jack pine and api may be counter to expectations only at the finer, microsite level. The extent of sampling for vegetation in this study was at the 'stand' level; i.e., I used a potential sampling area of 50 x 100 m at each site. At this scale, the increasing amount of jack pine at the expense of other species may be indicative of a relatively more open canopy.

LaPerriere & Lent (1977) have noted a hierarchical nature of habitat selection by caribou: animals first choose regional areas (such as a watershed), feeding areas (such as an outcrop), and finally a crater site (such as a lichen patch). This suggests that the present study of range relations has implications for the feeding area level of habitat selection, but may not validly be extrapolated to higher or lower scales. In general, there is a need for studies of how scale affects the interpretation of ecological phenomena. See Wiens (1989) for an excellent discussion on spatial scaling in ecology.

Nonetheless, the present results are in agreement with previous reports that tree species differ in their efficacy at altering snow cover (Bunnell *et al.*, 1985). In the study area, balsam fir appears to be the most effective species at providing favourable api for *Rangifer.* This accords with the findings of Lull & Rushmore (1961, in Bunnell *et al.*, 1985: 323) who found that balsam fir intercepted a relatively high proportion in snow.

Yet, interestingly, those habitats dominated by fir also contain a paucity of *Cladina* lichens as well as other winter forages for woodland caribou (Schaefer, 1988; Schaefer & Pruitt, 1991). Jack pine communities in old-growth condition had abundant lichen (*Cladina* spp.) but more severe api conditions. This is consistent with Stevenson & Hatler's (1985) generalisation that, for caribou, a trade-off exists between snow cover and forage abundance.

How do woodland caribou deal with such a energetic compromise? Previous investigations (Pruitt, 1959; Bergerud, 1974) have indicated that caribou select feeding sites primarily for abundance of forage, secondarily for suitability of nival conditions. During 1984-86, Aikens caribou exhibited similar behaviour. Winter activity as measured by travel, feeding sites, and pellet groups was significantly skewed towards jack pine habitats while mixed communities were avoided (Schaefer & Pruitt, 1991). These results imply that added investment of cratering and travelling on harder, thicker api (Fancy & White, 1985; 1987) was adequately compensated by the richer lichen mat. Conversely, Ouellet et al. (1993) suggested that caribou (*R. t. groenlandicus*) on Southampton Island failed to exploit the most lichen-rich habitats because of higher snow accumulation, although they reported only weak correlations of lichen biomass and hardness of upsik.

The results may carry implications for the management of woodland caribou habitat. In particular, because of the influence of trees on snow cover, alteration of the canopy by fire or logging may indirectly affect the winter foraging behaviour of caribou. Logging operations, for instance, may have only negligible effects on the biomass of *Cladina* lichens (Harris, 1992), but removal of the canopy by logging can result in thicker and denser api (Kirchoff & Schoen, 1987; Schwab *et al.*, 1987) and, inferentially, greater energy costs for foraging caribou. In the study area, Schaefer & Pruitt (1991) found that api hardness and thickness were substantially greater in burned (i.e., 5-year-old) than in old-growth stands, even though much *Cladina* lichen remained intact within the burn.

The results here suggest an energetic compromise for caribou while foraging for *Cladina* lichens during winter. Further documentation of the relationship between forages and snow may improve our understanding of caribou foraging behaviour and management of their habitat.

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Structures for caribou management and their status in the circumpolar north

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Abstract: Large herds of caribou (*Ranaifer tarandus*) in Canada, Alaska, and Russia that winter in northern coniferous forests and summer in tundra of the Arctic have provided a sustainable source of meat and other products for indigenous peoples for thousands of years. Several different administrative structures for management of large caribou herds have emerged throughout the circumpolar North. In Russia under the previous Soviet government, the herd of the Taimyr Region, numbering around 500 000 caribou, was managed under a harvest quota system for both subsistence use by indigenous people and commercial sale of meat and skins. In North America, as indigenous peoples have gained increasing political empowerment, systems for caribou management have been undergoing change. Establishment of the Beverly and Qamanirjuaq Caribou Management Board in Canada, with majority representation from users of the resource, provides a model and a test of the effectiveness of a comanagement system. The Western Arctic Herd in northwestern Alaska, numbering close to 500 000 caribou, has been managed under the traditional American system of game management, with user advisory groups, but with management decisions resting with a statewide Board of Game, whose major representation is from sport-hunting interests. The Porcupine Caribou Herd, which is shared by the United States and Canada, is the focus of an international agreement, in principle designed to assure its continued productivity and well-being. The diversity of systems for caribou management in the circumpolar North provides an opportunity for comparing their effectiveness.

Key words: reindeer, *Rangifer tarandus*, Russia, Scandinavia, Greenland, Canada, Alaska, subsistence, co-management

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Introduction

Caribou, or wild reindeer as they are known in northern Europe and Siberia (both are *Rangifer tarandus*), are an important subsistence resource for indigenous cultures throughout the circumpolar North. For many of these northern cultures, caribou have been the primary source of food and clothing, and the seasonal patterns of life of these indigenous peoples have followed the movements and availability of caribou. This dependency of many northern peoples on caribou remains as important today as it has been in the past. Although their cultures have evolved, incorporating or taking advantage of the technology, medical advances, educational opportunities, and other social services and material products of western society, the productivity of their northern homelands remains largely unchanged. Caribou and other fish and wildlife resources continue to be the primary support for the economy of northern peoples, whether it be directly for subsistence or through contribution to a cash economy.

Management of the fish and wildlife resources of these northern lands is the legal responsibility of the countries within which they lie. Strategies for management of caribou have varied considerably. It has only been in the last 15-20 years that these large northern herds of caribou have been the focus of substantial increases in attention by the responsible governments.

Russia

In the Soviet Union, prior to its dissolution, intensive management, designed to achieve maximum exploitation of their largest caribou population, was practiced (Klein & Kuzyakin, 1982). This occurred in the Taimyr region of north-central Siberia, where the caribou population had increased to occupy wintering areas formerly used by domestic reindeer. Under the communist government, indigenous reindeer herders abandoned their traditional lands for reindeer grazing where they had lived a subsistence life-style. They were encouraged by the government to move to centralized communities where they were formed into reindeer herding cooperatives, and where medical and educational services could be provided.

When the Taimyr Caribou Herd had increased to several hundred thousand in the early 1970s, the Soviet government began a program of intensive management. Aerial censusing of the herd was begun, and organized hunts using indigenous hunters were conducted at river crossings during autumn migration (Klein & Kuzyakin, 1982). Facilities for dressing slaughtered animals were constructed, including cooling cellars dug into the permafrost. Carcasses were transported to the larger communities and cities of the region, where the meat was processed for distribution throughout the country or sold in local markets. Skins were prepared for processing as leather. Indigenous people, who had traditionally hunted caribou, were allowed to hunt for their subsistence needs. The Taimyr Herd in the past 2 decades has increased from about 350 000 in 1970 to over 600 000 by the early 1990s (B. Pavlov, L. Kolpaschikov & V. Zyryanov, pers. comm.). Aerial censusing with several aircraft and using photography has yielded population estimates and these, along with ground counts of sex and age composition, have provided the basis for setting harvest quotas.

Problems with management of this herd included overharvest of adult females; these females compose most of the early autumn migration when the harvest takes place. Recent attempts to increase the harvest of adult males, including conducting winter hunts, have restored herd sex ratios to prior levels and increased productivity; however, the dispersed nature of the caribou in winter when this effort is concentrated results in high transportation and processing costs. In the late 1960s and early 1970s, natural gas pipelines were constructed across a portion of the migration route of the Taimyr Herd, which obstructed their movements and deflected them away from traditional wintering areas (Klein & Kuzyakin, 1982). Year-round ship traffic on the lower Yenisei River, which maintains open ice-choked channels, has also obstructed movement of caribou to winter ranges on the west side of the river (L. Kolpaschikov, pers. comm.). Although traditional winter ranges were abandoned, the caribou were deflected into new wintering areas that had previously been used by domestic reindeer. Air pollution from the large metallurgical mining and smelting complex around Norilsk has destroyed or caused the reduction of lichens on extensive areas of caribou and reindeer winter range (Klein & Vlasova, 1992).

Although problems were confronted in the management of the Taimyr Herd, the relative success of intensive management brought about a change in official Soviet policy toward caribou and reindeer management. In the early years following World War II, the Soviet policy was to expand reindeer husbandry through gradual replacement of the caribou (Andreev, 1975). Concurrent attempts to collectivize reindeer husbandry and force its expansion into the remote tundra areas occupied by caribou were not successful. By the 1980s the demonstrated success of intensive management of the Taimyr Caribou Herd convinced authorities that the remote areas supporting caribou populations were best left for production of caribou (Syroechkovski, 1986). Attempts to manage the only other large herd of migratory caribou in northern Siberia in a similar fashion through organized commercial harvest have met with limited success. This is a herd of about 200 000 caribou in northern Yakutia. The terrain that it occupies does not include major rivers that bisect its migration routes, as is the case with the Taimyr Herd; thus, appropriate harvest sites are not available.

Under the restructured government in Russia, caribou management is administered by regional governments (L. Kolpaschikov, pers. comm.). Management policy and practice have apparently not changed much, although the currently precarious economy has curtailed funding for aerial surveys and other management activities. Management of the caribou is now expected to be financially self-supporting.

Nordic countries

Northern Finland, Sweden, and Norway in prehistoric times supported large populations of caribou (wild reindeer) that were hunted by the earliest humans that arrived there at least 6 000 years ago (Skogland & Molmen, 1980). When the Sami (Lapp) people learned to capture and herd the caribou, the resulting herds of reindeer gradually displaced the wild caribou, which were deliberately killed in the reindeer herding areas. Today caribou are completely absent from areas occupied by domestic reindeer. The only wild reindeer or caribou occur in forest areas close to the Russian border of Finland and in alpine habitats in southern Norway.

The Norwegian caribou number about 35 000 in several herds. Management, whether on private or government lands, is based upon annual population estimates, composition counts to determine recruitment rates, and periodic assessment of range conditions. Large predators (wolves and bears) were extirpated from these range areas early in this century. Harvest quotas are set by regional governments. In Norway, caribou are the legal property of the landowner; therefore, caribou may be hunted by the landowner within the seasons and harvest quotas established by the central or regional governments. Alternatively, hunting permits can be sold to individuals or groups of hunters by the landowners (private or government) authorizing killing of a designated portion of the total quota for each herd. Annually, about 6 500 wild reindeer are killed by hunters in Norway out of a management quota of over 12 000 (E. Reimers, pers. comm.).

Caribou exist on the arctic archipelago of Svalbard at 79-80°N, which is under the administrative jurisdiction of Norway. These caribou are a unique subspecies that existed there for thousands of years in the absence of predators and human hunters, and parasitic flies, and with few harassing insects. Their adaptations to these conditions and life at this high latitude include short legs and the capability of accumulating much greater fat reserves than other caribou (Reimers & Ringberg, 1983). Following discovery of these arctic islands, whalers, sealers, overwintering trappers, and miners hunted the Svalbard caribou to near extinction. They were given legal protection in 1925, and the population has now increased to about 11 000 (E. Reimers, pers. comm.) and in most areas appears to be near the carrying capacity of the habitat although lichens have been depleted locally.

Greenland

Caribou are restricted to western Greenland, primarily in the large ice-free areas of southwestern Greenland. Caribou formerly were present in northeastern Greenland, but they died out around the turn of the last century as a consequence of extreme climatic variation (Meldgaard, 1986). Caribou have been hunted traditionally in western Greenland by the indigenous Inuit for subsistence use, and sale and export of meat and skins. No large predators are present there, but harassment by insects in summer can be severe and parasitism by skin warble (*Oedemagena tarandi*) and nasal bot (*Cephenemyia trompe*) flies, which were brought there in the 1950s with domestic reindeer (Clausen *et al.*, 1980), has apparently had a serious effect on productivity of the population. Historically, the population fluctuated widely, with a peak in the early 1970s reaching 100 000 (Thing, 1984) and a low of 9 000 in 1993 (H. Thing, pers. comm.). Overgrazing of lichens has reduced the carrying capacity of the range. Harvest quotas have been reduced by the Greenland Home Rule Government, but poor range conditions and annual harvests in excess of the designated quota are believed responsible for failure of the herd to increase. Currently, little effort is expended by the Home Rule Government to monitor herd numbers and condition or to control illegal harvest. A higher priority is placed on increasing the extent and numbers of introduced muskoxen. Their expanding populations are viewed as a substitute for the current low density of caribou as a source of meat for subsistence and possible commercial use.

Comparative management of caribou in Canada and Alaska

The large migratory herds of caribou of northern Canada and Alaska are of importance for subsistence use by indigenous people. Hunting of the caribou in these herds occurs during autumn migration when they can be intercepted at water crossings and, more commonly, in winter when transportation by snow scooter or dog sled is possible. Some hunting occurs in summer when caribou may be close to coastal settlements. The herds involved are (1) the George River Herd in the Ungava Peninsula of Labrador and Quebec, estimated at about 700 000 in 1993, and the largest caribou herd existing at that time; (2) the Leaf River Herd in the northwestern Ungava Peninsula of Quebec, numbering about 150 000; (3) the Qamanirjuaq, and (4) Beverly Herds occupying the barren lands of Northwest Territories (NWT) to west of Hudson Bay and extending in winter into northern Manitoba and Saskatchewan, and estimated at 260 000 and 285 000, respectively; (5) the Bathurst Herd, farther to the west, north of Great Siave Lake and east of Great Bear Lake in the NWT with over 500 000 animals; (6) the Bluenose Herd still farther west in NWT, north and west of Great Bear Lake and east of the Mackenzie River with about 65 000 caribou; (7) the Porcupine Herd, estimated at 160 000, that calves and occurs in summer in tundra regions of northern Yukon and northeastern Alaska and in winter is distributed between Alaska, Yukon Territory, and the northern edge of NWT; and (8) the Western Arctic Herd of northwestern Alaska of about 560 000 animals (sources pers. comm.: 1 and 2 S. Courturier; 3-6 M. Williams; 7 D. Russell; 8 P. Valkenburg). Several smaller herds are also resident in the Canadian arctic islands, in the northwestern mainland of the Northwest Territories and the Alaskan central Arctic. There are also smaller and more southern herds that do not migrate into the Arctic and that are associated with alpine and woodland habitats. These generally number in the tens of thousands or less, and their importance for subsistence use by indigenous people is also correspondingly lower than is the case for the larger northern herds.

A variety of management systems exists for the large migratory herds of Canada and Alaska. Because the George River Herd is shared by Quebec and Labrador, responsibility for its management rests with the Quebec Ministry for Outdoor

Recreation, Hunting, and Fishing, and the Division of Wildlife of the Government of Newfoundland and Labrador. No official policy for sharing of responsibility for monitoring the herd's numbers and population status or for establishing harvest quotas exists. Nevertheless, in recent years biologists of both provincial governments have cooperated in the collection and sharing of data on herd population dynamics and general ecology. There is currently growing pressure from indigenous users and others interested in the herd's welfare and its importance to subsistence and monetary economies of northern Quebec and Labrador for the formal establishment of a cooperative management system - a system that would include the governments of the 2 provinces as well as representatives of user groups.

The large size of the George River Herd stimulated interest in commercial harvest of the caribou, and in the mid-1980s the Quebec government proposed herding caribou into large corrals where they would be held while slaughtering took place. To test the feasibility of this procedure, some caribou were captured in 1987 and held in a portable corral, where they were offered supplemental feed (Crête *et al.*, 1993). Although results of this trial were promising, commercial harvest from the herd was not initiated in Quebec, apparently because of indications of deteriorating body condition and lowering recruitment rates, as well as opposition from various interest groups. In Labrador a small commercial harvest from the herd was initiated by an Inuit cooperative using processing facilities at Nain. The total annual human harvest from this herd has remained low in view of the large size of the herd.

The extreme remoteness of the Leaf River Herd has generated little attention in the past toward its management by the Quebec government. Recent surveys, however, by govemment biologists provide population data that, when compared with those from the George River Herd, indicate that the Leaf River Herd is a vigorous population, with favorable range conditions and a high recruitment rate (Crête *et al.*, 1990). Only a few relatively small communities of indigenous people on the periphery of its range have access to the herd, and the annual hunter harvest is low.

The Canadian Wildlife Service assumed major responsibility for collection of biological data and associated management of caribou in NWT in the years following World War II until the early 1970's. At that time the territorial Game Management Division took over these responsibilities later to become the Department of Renewable Resources of NWT. Caribou populations throughout the mainland of NWT increased during the last three decades, alleviating earlier concerns of potential overharvest by subsistence hunters. Under provisions of the NWT Act indigenous people were granted the right to hunt caribou (and other wildlife) for subsistence use without restriction unless the caribou populations were threatened with extinction.

The Bathurst and Bluenose Herds are under the management jurisdiction of the Government of the Northwest Territories (Hall, 1989). The recent Nunavut settlement granting limited self-government to the eastern portion of NWT did not, however, include jurisdiction over wildlife. Nevertheless, user participation in management decisions affecting both the Bathurst and Bluenose Herds will likely increase with the trend toward regional autonomy in northern Canada and in view of the management model provided by the Beverly and Qamanirjuaq Caribou Management Board.

The Beverly and Qamanirjuaq Caribou Management Board was established in 1982. It is a co-management system that establishes management policy and provides guidelines and priorities for research and monitoring of population dynamics and ecology of the 2 herds, approves methods and means of hunting, and can set and allocate harvest quotas if needed (Thomas & Schaefer, 1991). The Board is composed of 8 representatives of the diverse indigenous groups that hunt these caribou, one representative from each of the 2 provinces, and one representative each from the Northwest Territories and the Government of Canada. This 12-member board oversees a comprehensive program to communicate information about the herds and the Board's activities to the users and other interested parties, including hunter-training programs in user communities, school-educational programs, summer youth camps, and a widely distributed periodical. Financial support that enables the Board to meet annually and to conduct its activities is provided by contributions from the 4 government entities represented as well as occasional foundation grants.

Management of the Beverly and Qamanirjuaq herds under the Board's guidance during its 12 years of existence has been considered highly successful by the government entities that are involved. Opinion among the users, however, is more variable. The success that the board has experienced is associated with marked improvement in communication and mutual understanding between users and government administrators, managers, and biologists, and in the building of trust among the diverse representation on the Board. Since the Board was established, there has been no need to recommend hunting quotas for the indigenous users of the herds because the herds have remained productive and at high population levels. Questions have been raised as to whether this co-management system will be able to deal effectively with the difficult process of establishing harvest quotas should the herds decline markedly in the future. Board members and most observers are, however, optimistic that the shared responsibility for caribou management as well as the building of trust among Board members and with user groups and government will enable the Board to deal effectively with crises that may develop.

The Porcupine Caribou Herd that occupies range lands in the United States and Canada in its annual migratory movements is an international resource. Recognition of the need for international oversight in the management of this herd led to the signing of an international agreement on the conservation of the Porcupine Caribou Herd by the United States and Canada in 1987. This agreement provided for the establishment of an International Porcupine Caribou Board with representation from both countries to cooperate in defining and recommending fundamental requirements to conserve the herd. Although development of this agreement has focused attention on this international resource and its importance to both countries, actions of the board may be considered nonbinding by either of the two countries. For example, disapproval by the board of a proposal for development of petroleum or other activities considered detrimental to the caribou and their habitat could be unilaterally overridden.

In Canada, a Canadian Porcupine Caribou Management Board was established in 1985, modeled after the Beverly and Qamanirjuaq Caribou Management Board, including representation by the governments of Canada, the Yukon, and Northwest Territories, and the 3 indigenous groups in Canada who have subsistence dependency on the Porcupine Herd (Peter & Urquhart, 1991). This board, although with jurisdiction only in Canada, has a positive record of building trust and approval among Canadian users of the herd and the involved government administrators, managers, and biologists. Indigenous users of the caribou in Alaska, supported by environmental organizations, are lobbying the state and federal governments for establishment of a companion Alaska Porcupine Caribou Management Board.

In Alaska, management of Porcupine Herd caribou is under the jurisdiction of the State of Alaska. A Board of Game, with appointments made by the Governor, has responsibility for establishing wildlife management policy and hunting regulations and for setting harvest quotas for resident wildlife throughout the state, including caribou. Local wildlife advisory committees include indigenous hunters that make recommendations to the Board. A state law intended to grant priority for hunting of wildlife for subsistence use by rural residents has been held unconstitutional by the State Supreme Court. As a consequence, an overriding federal subsistence hunting law requires that the federal government assume responsibility for management of wildlife on all federal lands in Alaska where hunting may occur, until the state legislature passes a new subsistence law that complies with the federal subsistence law, as well as the state constitution. Alternatively, the state constitution could be amended, or a much less likely option is amendment of the federal law by the U.S. Congress.

During this period of legal challenge to state jurisdiction over wildlife, the state, through the Alaska Department of Fish and Game, and the federal government, through the U.S. Fish and Wildlife Service, have cooperated in the collection of biological data on the Porcupine Herd and its habitat. Monitoring of population dynamics of the herd and research on its ecology were fostered by legislation of the U.S. Congress related to proposals for oil and gas exploration and development in the coastal plain of the Arctic National Wildlife Refuge in northeastern Alaska. The coastal plain includes calving grounds and summering habitat of the Porcupine Herd. The legislation mandated a 5-year period of research on the ecology of caribou and other wildlife using the area and appropriated money for the study during 1981-85, with some supplemental funding in subsequent years. The funds were shared by the Fish and Wildlife Service with the Alaska Department of Fish and Game, the Canadian Wildlife Service, the University of Alaska Fairbanks, and biologists from these organizations often worked together in the field on both sides of the international border. In a similar way, Canadian financial support for research on the ecology of this herd, funneled through the Canadian Wildlife Service, was used to support studies on both sides of the international border. A comprehensive record of the population biology of this herd now exists (Russell *et al.*, 1993) and provides an excellent background to assist future management of the herd. On the basis of this information, a comprehensive computer model of the population ecology of the Porcupine Herd also was developed.

The Porcupine Herd, as is the case with all the other large migratory herds in North America, has increased in the past decade. Its large size and relatively low annual hunter harvest of <5 000 animals have not made it necessary to impose harvest quotas.

The Western Arctic Herd is under similar management jurisdiction as the Porcupine Herd within Alaska. There has been less focus of attention on the collection of biological data on this herd by the state of Alaska and the federal government because of lesser threats of development activities within its range, its remoteness, and its non international status.

The Western Arctic Herd's precipitous decline from an estimated minimum of 242 000 in the early 1970s (Hemming, 1972), to 75 000 in 1976 (Davis *et al.*, 1980) was accompanied by blame for the decline being placed on the state's record of low-management emphasis on this herd. There was also strong resistance by indigenous hunters to the establishment of harvest quotas by the state when the drastic decline of the herd became known. A higher priority for monitoring the population dynamics of the herd was a consequence of the state's experience following the decline, and more comprehensive efforts to assess recruitment and mortality have been made annually since then. Aerial photo-censuses have been conducted approximately every 2-3 years. The current large size of the herd has generated concern that it may have exceeded, or may soon exceed, the carrying capacity of its range.

In recent years, with increasing herd size, caribou from the Western Arctic Herd have moved into areas rarely or not previously used, at least in this century. This has resulted in the annual encroachment of tens of thousands of caribou each winter into traditional grazing areas of domestic reindeer on the eastern Seward Peninsula. Reindeer herders have been forced to herd their animals more closely and to move them to avoid mixing with caribou. Nevertheless, many reindeer have been lost through mixing with caribou or through predation from wolves that have accompanied caribou into the reindeer-grazing areas. Indigenous people in villages in the eastern Seward Peninsula not directly involved in reindeer husbandry, however, have benefited greatly from the availability of caribou for their subsistence use.

The Western Arctic Herd is an important subsistence resource for over 30 communities, including more than 5 000 households. At its present large size there is little need to curtail human harvest. Residents of the area are allowed unlimited annual harvest, although hunting of adult females is prohibited during May 16 - June 30 and a daily bag limit of 5 caribou has been imposed to limit wastage. For nonresidents of the area the annual bag limit is five caribou of either sex.

Although authority for establishment of hunting seasons and bag limits has rested with the Alaska Board of Game, users of the caribou have made recommendations regarding management of the herd through their local game advisory committees. Indigenous hunters, through these advisory committees, have taken a more active role in management of caribou than was the case during the previous peak and decline of the herd in the 1970s. Effectiveness of this system and continued support by users of the caribou remain to be tested should the caribou population undergo a major decline in the future, necessitating imposition of harvest quotas.

Management of wildlife on federal lands in Alaska had been under authority of the state until 1992, when the state law granting priority for hunting to subsistence users was challenged in court and judged unconstitutional. As a consequence, until the state passes new subsistence hunting legislation to meet requirements of federal legislation, the federal government must assume responsibility for management of wildlife on federal lands. An Office of Subsistence Management has been established within the U.S. Fish and Wildlife Service with participation from representatives of the National Park Service and other federal land-managing agencies. Local advisory committees composed of subsistence users have been developed as part of the federal management system with membership often overlapping with the state game advisory committees. Transition to federal control of wildlife management on federal lands is continuing to evolve with a strong dependence on the Alaska Department of Fish and Game as a source of data on population dynamics of wildlife. This is particularly true in the case of the Western Arctic Herd, and the future of management responsibility for this herd remains uncertain pending legal clarification at both the state and federal levels.

All of the large migratory herds of caribou in northern North America appear to have reached peak population levels or may be at peak levels soon. During the past 2 decades, management regimes for these herds have dealt with population surpluses with no need to constrain hunter harvest. Under these most favorable conditions, users have little cause to be critical of management systems. With the likelihood of declines in caribou population occurring again in the future, as they have in the past, management systems will be put to the test. The need for harvest quotas will become a reality, and the difficult task of allocating these quotas among users will confront the managers. Only then can the relative effectiveness of systems for caribou management across North America be evaluated.

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The Sixth North American Caribou Workshop,
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1-4 March, 1994.

Brief communication

Assessing effectiveness of caribou management systems: Alaska's Western Arctic Herd and Canada's Beverly and Qamanirjuaq Herds.

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Key words: caribou management, comanagement, indigenous people

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In 1992, the United States Man and the Biosphere Program (MAB) funded a proposal put forward by its High Latitude Directorate to do a comparative study of caribou management systems employed for the Western Arctic Herd (WAH) in Alaska and for the Beverly and Qamanirjuaq herds (BQH) in Canada. The objective of the research is to assess the effectiveness of these management systems from the viewpoints of both the uses of the resource as well as the managers. These management systems deal with comparable size caribou populations and they include similar numbers of consumptive users and user communities of primarily indigenous people.

Management of the WAH is through the Alaska Board of Game, the statewide system for management of all resident wildlife. The board is comprised of appointed members from throughout the state with minority representation from indigenous people. Local Advisory Committees consisting of users of the wildlife resources can make recommendations directly to the Board of Game. Management of the BQH is through the Beverly and Qamanirjuaq Caribou Management Board. This board has representation from the governments of the Northwest Territories, Saskatchewan, Manitoba, and the federal Canadian government as well as the indigenous users of the caribou, who comprise 8 of 12 members. Although limited formally to an advisory status, there is precedence of compliance with the recommendations of the Management Board by the responsible governments since its inception in 1982. The BQH management system is considered a comanagement system. Comanagement is the agreed upon sharing of management responsibilities between government and resource users. Determining the effectiveness of comanagement systems, however, may be complicated if: 1) there is no record relating management type to the well-being and sustained productivity of the resource populations, 2) formal comanagement arrangements have not been put into practice, 3) informal management arrangements have been implemented that are not unique to comanagement systems, and 4) other management systems are not available for comparisons that differ only with respect to comanagement. Further complicating the comparison is the fact that the WAH and the BQH have been at high population levels during the more than 10 years that their 2 management systems have been in existence, thus recommendations for harvest quotas has not been necessary.

In order to compare functional effectiveness of the 2 systems, we had to agree on criteria for assessing management effectiveness. We chose to focus on the degree to which resource managers and resource users: 1) share attitudes toward specific harvest and herd monitoring practices, 2) understand each others belief systems about how caribou populations change in size and movement patterns, and 3) share expectations that the system will be able to identify and respond to changes in the herds being studied. We theorized that each of these concepts is directly related to voluntary compliance among users to constraints that may be imposed by the management or regulatory boards.

To obtain this information on beliefs and attitudes of managers and users, we carried out structured interviews. This involved face to face interviews, based on a comprehensive questionnaire form, with about 55 biologists, managers, administrators, and enforcement officers in Alaska and Canada. Similar interviews were done with about 400 resource users in 18 communities in Alaska and Canada. Prior to doing interviews of users we obtained consent from the indigenous peoples groups involved through the Beverly and Qamanirjuaq Management Board in Canada and native leaders in each of the sample survey communities in Alaska.

We are comparing the types of biological data collected as a basis for managing the herds, the methods employed and their historical development, frequency of collection, priority for their collection, financial support available, and problems and limitations with the procedures. This was done through interviews and correspondence with biologists and managers who work with the study herds in Alaska and Canada. We have contracted with ethnographers in Canada and Alaska to prepare reviews of the history of indigenous peoples' use of these herds and the corresponding history of development of management systems that have dealt with the 2 caribou study populations. This information will be compared to results from interviews as a basis for assessing opinions expressed about current management in relation to past management.

The final stage of the project will include analysis and interpretation of the detailed and voluminous data collected and its presentation in a format that facilitates comparison of the effectiveness, efficiency, and acceptability of the 2 management systems.

Our hope is that this analysis will highlight the best elements of each management system, which collectively will serve as a model to improve the management of large caribou herds in North America.

The Sixth North American Caribou Workshop,
Prince George, British Columbia, Canada,
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Brief communication

Oil and the Porcupine Caribou Herd – Can we quantify the impacts?

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Introduction

The Porcupine caribou herd (*Rangifer tarandus granti*) is a large international herd of migratory caribou that annually travels from their taiga wintering grounds in Alaska and Yukon to calving and summer grounds adjacent to the Beaufort Sea. Their summer range is east of the range of the smaller Central Arctic Herd, where considerable oil development has occurred.

In 1980 with the passage of the Alaska National Interest Lands Conservation Act in the U. S., a decision on the future protection of much of the concentrated calving and post-calving grounds of the herd was delayed. Studies were initiated to assess the potential for hydrocarbon development and the impacts of that development on the environment. These environmental studies, along with the lessons of Prudhoe Bay and the Central Arctic Herd, form the basis for environmental impact assessment.

Impact Assessment

In the last two decades, impact assessment was approached from two largely separate fronts; effects on the population and effects on animal energetics. Disruptions and displacements caused by development projects must be assessed at the population level. Therefore, as more is learned about specific populations, it is important to combine the two approaches and assess energetic impacts at the population level. The amount of research and monitoring that was devoted to the Porcupine Caribou Herd and the lessons from the Central Arctic Herd facilitate assessment of the potential impacts of development before development.

Key demographic variables such as parturition rate, calf survival and recruitment rate can vary significantly from year to year. For example, in the Porcupine herd, parturition rate varied from 72% to 86% and calf survival to 1 month of age varied from 66% to 91% over the last 6 years (Fancy *et al.,* 1994). Other factors being equal, this range can translate into in an increasing population or a rapidly declining population. This variation in key parameters has occurred in the absence of any significant development within the herd's range. The key, therefore, is the ability to predict these variables based on natural variation in range condition and the added potential impacts of proposed development. In other words, our ability to translate energetic or body condition indices to the population level is directly related to the strength of the functional relationships that can be derived. Thus, in this paper, we report on a number of ongoing studies to derive these relationships and discuss what projects are in place to further refine and test these relationships.

Progress to date

Relation between body fat reserves and pregnancy rate

In early November 1990 - 1993, 125 adult cows were captured, weighed, and an index taken of body fat (body condition score [BCS], Gerhart *et al.*, 1992) taken. The product of body weight and BCS was called the Body Reserve Index (BRI). Blood samples were analyzed and pregnancy determined (van de Wetering *et al.,* 1994). As outlined by Sasser *et al.* (1989) animals with a positive pregnancy test for PSPB and a negative diagnosis for progesterone were considered to have suffered an early intra-uterine mortality.

Significant logistical regressions were determined between BRI and both pregnancy rate (P of β_1=0.003 Fig. 1a) and early intra-uterine mortality (P of β_1=0.008; Fig. 1b).

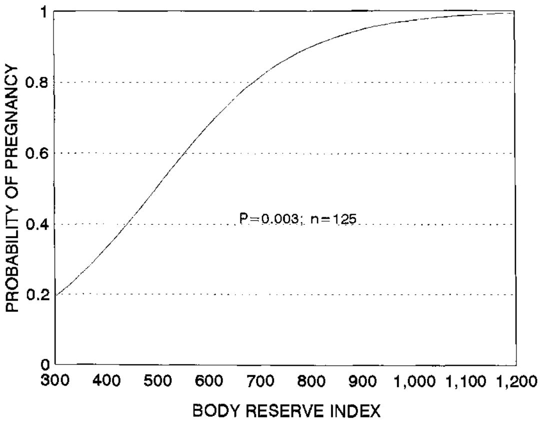

Fig. 1a. Logistic regression relating probability of parturition for adult female caribou to autumn Body Reserve Index, Porcupine Caribou Herd, 1990 - 1993 ($\beta_0 = -3.602$, $\beta_1 = 0.097$, $P<0.001$).

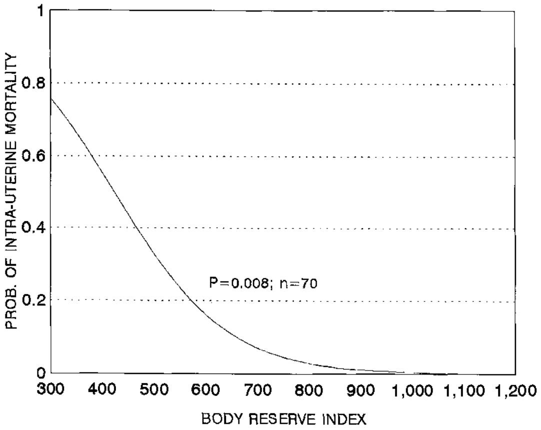

Fig. 1b. Logistic regression relating probability of intrauterine mortality for adult female caribou to autumn Body Reserve Index, Porcupine Caribou Herd, 1990 - 1993 ($\beta_0 = 3.9439$, $\beta_1 = 0.00932$, $P<0.01$).

Table 1. Weather variables within the range of the Porcupine Caribou Herd, 1987 - 1992.

Year	Winter snow[1] (cm)	Spring snow[2] (cm)	Spring Phenology[3]-	Early July temp[4]	Late July temp[5]
1987	68	49	4	12.5	11.5
1988	86	34	3	13.4	10.7
1989	76	0	6	13.0	17.5
1990	95	62	1	14.2	11.7
1991	85	0	5	5.2	9.5
1992	81	63	2	10.5	12.6

[1] - snow depth March 1 at Eagle Plains (Indian and Northern Affairs snow survey bulletins).
[2] - snow depth May 1 at Old Crow (Indian and Northern Affairs snow survey bulletins).
[3] - ranks based on stage of phenology at peak of calving, from satellite AVHRR data.
[4] - mean daily temp. (°C) at Shingle Point July 1-15.
[5] - mean daily temp. (°C) at Shingle Point July 16 - Aug 7.

Table 2. Weather variables as ranks, sum of ranks, fall body weights and parturition rates, 1987-1992.

Variable	1987	1988	1989	1990	1991	1992
Winter snow	6	2	5	1	3	4
Spring snow	3	4	5	2	5	
Phenology	4	3	6	1	5	2
Early July temperature	4	2	3	1	6	5
Late July temperature	4	5	1	3	6	2
Sum of Ranks	21	16	20	8	25	14
Fall Body Weight	95	88	92	88	98	89
Parturition Rate[1]	84	78	82	74	86	81

[1] parturition rate measured in spring of following year i.e. in the 1987 column rate refers to rate in spring 1988.

Relation between weather and parturition rates

For the Porcupine Caribou Herd, Russell *et al.*, (1993a) presented 5 weather-related effects on the energetics of individual caribou. Winter snow depth, spring melt, late spring phenology, early July temperatures and late July/early August temperatures effect activity patterns, feeding rates and movement rates, which in turn alter energy balance to the individual. Fall body weights of adult females in the herd were monitored since 1986 (Allaye-Chan, 1991; Smits *et al.*, 1991; Russell, unpubl. obs.). All these weather factors are integrated by the animal, affecting the body condition during the rut. Table 1 summarizes weather observations taken from key locations within the range of the herd for the period 1986 - 1992. Deep snow, late melt, early phenology and high summer temperatures were ranked among years and totalled annually to provide an index of weather conditions for each year (Table 1). The sum of these ranks was highly correlated to birth rate ($r^2=0.88$, Fig.2).

Porcupine caribou model

The further development of the Porcupine caribou models (combining the Energetics and Population models, Russell *et al.*, 1993b) led to hypothetical

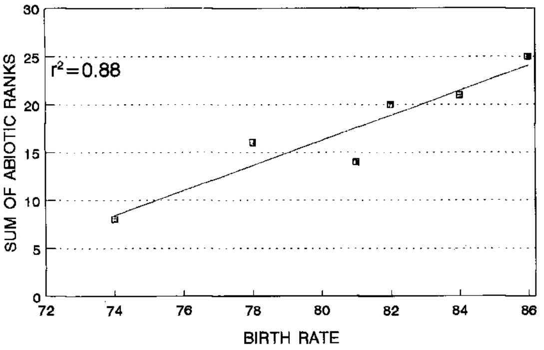

Fig. 2. Relationship between the sum of ranks of abiotic variables to the birth rate of the Porcupine Caribou Herd.

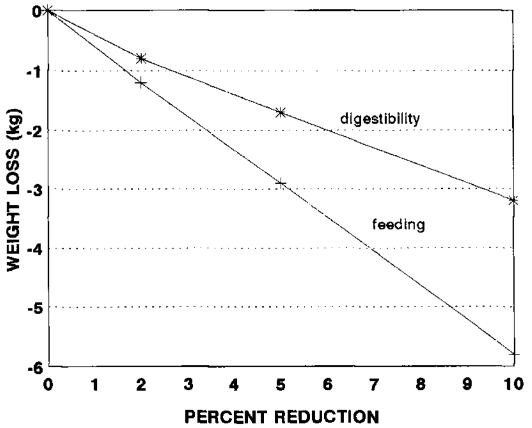

Fig. 3a. Simulated weight loss resulting from a 2%, 5% and 10% reduction in feeding and forage digestibility, June 1 – July 15.

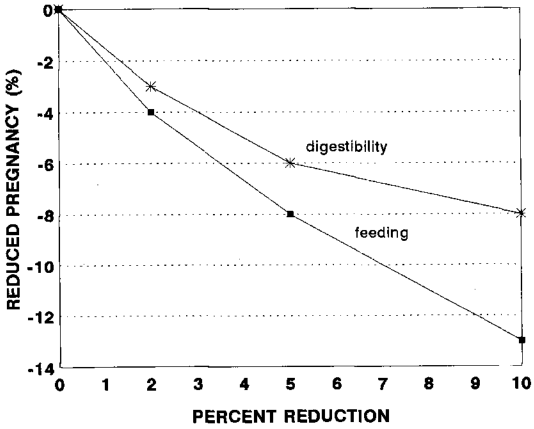

Fig. 3b. Simulated reduced pregnancy rate resulting from a 2%, 5% and 10% reduction in feeding and forage digestibility, June 1 – July 15.

development scenarios. For example, simulated reduced time spent feeding or poorer habitat resulted in lower autumn weights (Fig. 3a) and pregnancy rates (Fig. 3b).

Ongoing Work

Recent research relates birth weight and growth of calves to habitat use as well as condition and growth of mothers. Non-lactating females are also tracked to estimate the energetic investment in raising calves. These data will be used to refine and validate the Porcupine caribou model.

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Ground-breaking Co-management in the Split Lake Resource Management Area of Manitoba, Canada

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Abstract: Settlement in June 1992, of the Northern Flood Agreement between Manitoba, Canada, Manitoba Hydro and the Split Lake Cree First Nation resulted in the establishment of the Split Lake Resource Management Board (SLRMB) which is comprised of community representatives and government appointees. The responsibilities of the SLRMB include: developing annual programs and budgets, conducting wildlife population and habitat assessments, developing land and resource plans, monitoring resource use, and reviewing land use and management proposals. The Board's mandate extends to management of all natural resources including several distinct caribou (*Rangifer tarandus*) populations which frequent the Split Lake Resource Management Area (RMA). After one year of operation, the SLRMB has several accomplishments. Its success is attributable in part, to the Board's effective mix of Split Lake Cree First Nation and government of Manitoba appointees. A good communication strategy has also been crucial for increasing understanding about the board, delivering essential resource management messages, and soliciting input at the community level. Rapport, teamwork, credibility and a resulting "strong voice" have set the framework for the SLRMB to play a significant role in resource management in a large part of northern Manitoba.

Key words: *Rangifer tarandus*, caribou, Aboriginal, Cree, Manitoba Hydro

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Split Lake settlement

Beginning in the 1970s, the regulation of Lake Winnipeg and diversion of the Churchill River in northern Manitoba, has drastically impacted many resources and the communities which depend on those resources (Norway House, Cross Lake, Nelson House, York Land and Split Lake). In 1977 the Northern Flood Agreement (Department of Indian Affairs and Northern Development, 1977) between the governments of Manitoba and Canada, the Manitoba Hydro-electric Board and the Northern Flood Committee Incorporated, set the framework for assessing impacts on natural resources and ensuring impact compensation. Under this agreement, communities were assured of damage compensation and involvement in development decisions within their respective Registered Trapline Zones. Those users with an existing "right as law" (defined by the existence of the Registered Trapline Zones) would be allowed continued use at current levels. In the early 1990s, settlement of outstanding claims under a "global settlement" was attempted by all parties to reduce costs and facilitate development in northern Manitoba. However, negotiations broke down because of disagreements among the communities over settlement priorities.

In June 1992, a separate comprehensive settlement was negotiated between the Split Lake Cree First Nation, the governments of Canada and Manitoba and the Manitoba Hydro-electric Board (Canada *et al.*, 1992). The agreement included settlement terms for: monetary and land compensation, water management, establishment of easements, land-use permits, integrated land-use and resource management, environmental monitoring (approximately $1.5 million), economic and social development (approximately $12 million), resource compensation funding and social development (approximately $11 million), remedial works (approximately $13 million), and implementation (approximately $4 million). In addition, terms and conditions were established for project employment, creation of a Split Lake Cree Distribution Company and operation of a trust account (Tataskweyak Trust). Upon approval, the trust account can be used for natural resources projects, including caribou management.

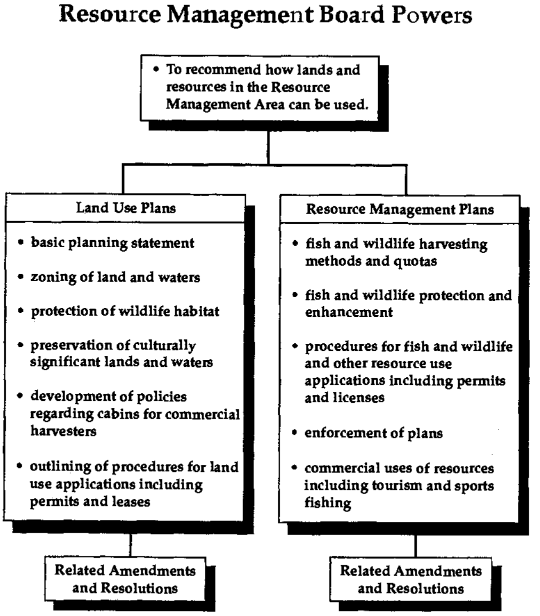

Fig. 1. Responsibilities of the Split Lake Rescource Management Board.

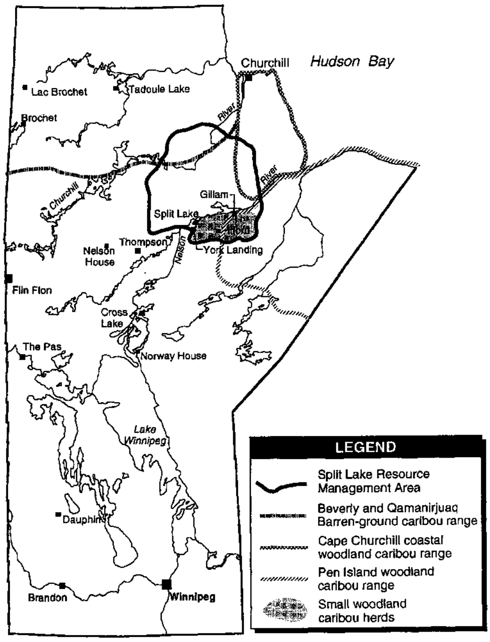

Fig. 2. Approximate distribution of Caribou herds in the Split Lake Resource Management Area.

The Split Lake Resource Management Board

The Split Lake Resource Management Board (SLRMB), formed in December 1992 under Article 5 of the Split Lake Settlement (Canada *et al.*, 1992), comprises five members appointed by the government of Manitoba and five members appointed by the Split Lake Cree First Nation. The government appointees are selected to reflect the interests of the Manitoba government departments of Natural Resources and Northern Affairs, Manitoba Hydro, and the Manitoba Mining Association. The Split Lake Cree appointees are members of the community of Split Lake and include councillors and elders. As defined in the Split Lake Settlement (Canada *et al.*, 1992), the objective of the SLRMB is to ensure that "Integrated Land Use and Resource Management is...achieved" (Article 5.2.1., Canada *et al.*, 1992). The Board's responsibilities are summarized in Figure 1 and include the following specific obligations (Canada *et al.*, 1992): (1) to promote integrated land and resource use (2) to assess consumptive and non-consumptive resource use (3) to monitor resource use (4) to investigate populations and habitats (5) to identify measures to preserve and enhance areas of special significance (through land use plans, zoning, and monitoring) and (6) to review specific plans for forest, land and water management, harvesting of resources, extraction of minerals and commercial interests. The jurisdiction of the SLRMB extends throughout the Split Lake Registered Trapline Zone, which is referred to as the Resource Management Area (RMA) (Fig. 2).

Annual program and budget

The SLRMB is responsible for developing and recommending annual programs and budgets which are to be shared between the government of Manitoba and the Split Lake Cree First Nation. For the fiscal year, 1993-1994 the SLRMB agreed to combine the Board's funding with technical assistance, office support and travel contributions from both parties, totalling approximately $187,000. This budget was used to support a chairperson, a secretariat, a local Project Manager, resource planning experts, and a wide range of resource management activities including biological surveys, collection of traditional land-use knowledge and publication of Board newsletters and an annual report. While much of this work has been done within existing government structures, both parties recognize the work as being specific, and accountable to, the Split Lake Settlement (Canada *et al.*, 1992). At the time of this writing, proposed activities for the fiscal year 1994-1995 include continuance of wildlife monitoring, development of locally-based conservation and education programs, development of a fire-watch program, development of a fish stocking program, land-use mapping, as well as providing technical and travel support for the Board.

Caribou and the Split Lake RMA

The RMA is within the range of several caribou herds (Fig. 2) including the Qamanirjuaq barren-ground (*R. tarandus groenlandicus*) herd, the migratory Cape Churchill woodland caribou (*R. tarandus caribou*) herd, the Pen Island woodland caribou herd (*R. tarandus caribou*) and other small resident woodland caribou (*R. tarandus caribou*) herds. In the winter of 1991-1992 and 1993-1994, the Pen Island caribou ventured further inland than usual (C. Elliott, pers. comm.), bringing them close to the communities of Split Lake, York Landing, Ilford and Gillam. In anticipation of additional harvest by treaty Indians, the government of Manitoba reduced the hunting season and increased their public information efforts in the affected communities. Public information emphasized the role of migration in bringing the Pen Island Caribou Herd into the range of many communities, rendering it an important regional, rather than local, resource. These efforts were effective in eliciting an informed and conservation-based response from the communities, largely because a good working relationship had previously been established between the government and the communities.

The SLRMB has established its monitoring and coordination role, recognizing that a lot of the ground work through cooperative initiatives from field staff has been done effectively and has eased its task considerably. The community liaison aspects are day-to-day business in this region, and not an agreement-based obligation. As part of the SLRMB's efforts to ensure long term management of caribou-human interactions, the Board is planning to develop an information package designed to increase community awareness of management of the Pen Island Caribou Herd. Key concepts to be incorporated into this package include: the significance of migration, the concept of sustainable harvest and its importance in setting harvest levels, and the range of communities dependent on this caribou herd.

The Split Lake Settlement (Canada *et al.*, 1992) stipulates that the SLRMB shall develop and recommend land use plans to guide development policies and decisions by the government of Manitoba and the Split Lake Cree First Nation, including resource management plans for the RMA or any portion of it. Both the Split Lake Cree First Nation and the government of Manitoba have directed the Board to proceed quickly on these initiatives. At present, all requests for resource allocations are referred to the SLRMB until land use and resource management plans are completed and approved. The Board has therefore focused its activities on compiling base line data and traditional information on ecosystem components. Moose (*Alces alces*) was a priority in 1993-1994, because of its consistent and traditional value to the residents, demand from subsistence users, and requests from recreational hunters and outfitters for non-resident use. Caribou are next for concerted management efforts. To date, the Board has recognized sensitivity of caribou to disturbance and access by recommending stringent conditions for mining exploration, to be conditions of the Department of Natural Resources annual work permit.

Conclusions

(1) After just over one year of operation, the Split Lake Resource Management Board has rapidly coalesced into an effective and credible team founded on trust and cooperation among the representatives from the Manitoba government and the Split Lake Cree First Nation.

(2) Innovative budget and program arrangements have maintained momentum, enthusiasm and confidence.

(3) Board effectiveness has been enhanced because appointees: are well respected, are committed to the Board, share a common interest in natural resources, and are effective communicators.

(4) Since its establishment, the SLRMB has been actively involved with various issues of land use and resource planning including economic development proposals, outfitting requests, community consultations and compiling data and local knowledge about resources in the Management Area.

(5) Woodland caribou management, including assessment of populations, distribution, harvest, and development proposals in relation to key habitats, will require priority attention starting with the 1994-1995 program-year. Public information and communication will be key components of the Board's approach.

(6) The mandate of the SLRMB is to bring about cooperative resource management and to manage key wildlife and fisheries species to ensure their sustainability in the face of development, local and Provincial needs, public demand, and habitat changes.

(7) The SLRMB is being assessed and evaluated by other Communities and First Nations across Manitoba and elsewhere, for its effectiveness and value in co-management. It can set the standard and template not only for co-management agreements, but also for a positive, productive and effective working relationship between government and aboriginal people.

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Department of Indian Affairs and Northern Development. 1977. *Agreement between Her Majesty the Queen in right of the Province of Manitoba of the first part and Manitoba Hydro-Electric Board of the second part and the Northern Flood Committee, Inc. of the third part and Her Majesty the Queen in right of Canada as represented by the Minister of Indian Affairs and Northern Development of the fourth part.* Queen's Printer of Manitoba, Winnepeg. 123pp.

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Caribou Co-Management Needs From Research: Simple questions - Tricky answers

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Abstract: Over the past decade, northern Canada has experienced a substantial increase in government reliance on advisory co-management organizations to manage caribou populations. Such groups, which are usually composed of government and local representatives, constantly require information about caribou upon which to base their recommendations. However, the standard 'scientific' approach to obtaining and presenting such information is in many cases no longer appropriate. In order to readjust the scientific focus on caribou research so that it is better attuned to co-management, this paper examines the role that research plays in the Canadian management of the Porcupine Caribou Herd as practiced by the Porcupine Caribou Management Board - a co-management advisory organization with a majority of native representatives.

Key words: *Rangifer tarandus*, Porcupine Caribou Herd, Yukon-Alaska

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The Changing North

Wildlife management in the Canadian north is changing - again. Following the second world war, wildlife research was done by federal biologists and management decisions were made for the Northwest Territories (NWT) and the Yukon by federal administrations. After the administrations were transferred to the territories, the reliance on federal research gradually diminished during the 1970's as territorial departments hired their own research staff. Although this marginally increased consultation with the public, basically the governments continued to operate internally by determining the management issues, designing the research, analyzing the results and making the decisions.

But, eventually, this began to change with the creation of Hunters and Trappers Associations in the NWT and the James Bay Agreement in Quebec (1976), which provided for the first wildlife co-management board - the Hunting, Fishing and Trapping Coordinating Committee. Since then, wildlife co-management organizations have proliferated, either in conjunction with land claims settlements, such as the Inuvialuit Final Agreement (1984) and the Gwich'in Comprehensive Land Claim Agreement (1991), or separately, such as the Beverly and Qamanirjuaq Caribou Management Board (1982) and the Porcupine Caribou Management Board (1985). With respect to barren-ground caribou alone, there could eventually be a separate co-management board for each major herd in Canada.

So Many Questions, So Little Time

Co-management boards were designed to function differendy from governments and so they do. In particular, they are assigned specific species or populations which they are expected to monitor and advise on their management. To do so, such groups require relevant information and, in most cases, the major source is government research agencies. In the past, such agencies dealt with management issues on a scale of priorities that they alone established, but this is becoming no longer possible with the avalanche of requests from all the co-management groups that want information and want it now!

Given the limitations of research agencies to accommodate an ever increasing list of management questions that will not go away, it is necessary to critically reexamine just what kinds of information are needed and how they can reasonably be provided for this new age of co-management.

A Simple Model

A prime example of what types of research are required by co-management is provided by the Porcupine Caribou Management Board (PCMB) because it is a simple system that deals with only one population of one species with the best information available. The only major complicating factor is that the Porcupine Caribou Herd is shared with Alaska which requires additional management coordination.

Nevertheless, how the PCMB uses research information should provide basic clues to understanding other co-management situations where the problems and information needs are less clear cut.

So, How Is The Herd Doing?

Whether it is in the bar, at the grocery store or the gas station, whenever a member of a caribou co-management board appears, the first question is, "So, how is the herd doing?" And, in fact, this deceptively simple enquiry comprises most of what the co-management board needs to know itself, which is basically: How big is the herd?, Is it threatened? and Is it healthy?

Part One: How Big Is The Herd?

The Census Conundrum

Ever since the second world war, caribou managers have operated under the premise that caribou could be accurately counted and, moreover, that they cannot be properly managed until they have been counted. This belief arrived with the modern bush plane because it was so compelling to see caribou from the air spread out across the open tundra and, apparently, so easy to count.

Thus, whenever caribou management was undertaken, the first demand for research has always been, "How big is the population?" And, in response, the biologist's have always strapped on their latest technology and ridden off to battle with caribou statistics.

Beginning in the late 1940's, researchers laboured to perfect the strip census technique which, in its crudest form, consists of visually counting caribou in aerial swaths of known width and extrapolating for total coverage. Some 30 years later, it was clear that the method would never yield satisfactory results for the barren-ground herds. In an effort to overcome the many inherent errors of visual counting, biologists began to experiment with photographic counts and, although they too have evolved in sophistication, the results are often greatly compromised in accuracy and precision.

Considering the time and expense required for such methods, it is necessary to reconsider the assumption that precise population information is feasible and, in fact, necessary for co-management.

A Test Case

The best exception to the general census conundrum is the Porcupine Caribou Herd (PCH) because, under conditions of severe fly harassment, it will form massive aggregations that can be photographed in their entirety which enables a much higher level of accuracy in counting than the standard aerial photo methods afford. Since the herd also has its own co-management board, this provides the only opportunity to observe how co-management actions are related to the nearly ideal condition of knowing the size and trend of the caribou population.

After nearly a decade of tinkering, the photo method for the Porcupine Caribou Herd had been significantly refined so that, throughout the 1980's, biologists were able to quite accurately document an increase in the total population (adults and calves) from 110 000 in 1979 to 178 000 in 1990, which works out to about 5% a year.

In 1987 - two years after the Porcupine Caribou Management Agreement was signed - the herd numbered 165 000 and was still increasing. Given such good population data, what did the Board do? Because the herd was increasing, there was no concern about overharvesting. Although the harvest at the time was not well known, there was obviously no negative impact on the herd. As it continued to increase throughout the decade, the Board did nothing to intervene because, in general, people were pretty happy about the growing population.

In 1983, prior to the Board's inception, the bag limit for non-native hunters in the Yukon was doubled to 2 caribou of either sex. Recently, the Board has been considering an extension of the season for non-native hunters in order to decrease hunting pressure on other woodland herds in the territory. Meanwhile, the NWT increased their bag limit to 5 to be consistent with other barren-ground herds and Alaska has maintained the subsistence bag limit of 25 and export limit of 10. Native hunters in all jurisdictions continued to hunt without restriction and in 1990 the community of Fort McPherson sent 40 caribou to Banks Island in accordance with Trade and Barter provisions of the Porcupine Caribou Management Agreement. It should be noted that all of these actions were taken not to control the PCH per se but to capitalize on its abundance.

By 1989, the population had reached 178 000 and some concerns were being expressed about how big it would get. Would it continue to grow until it exceeded the carrying capacity of its range and crash as the George River Herd was reputed to be doing? The Board considered such fears but recognized that there was nothing that could be done because, with somewhat better harvest data, it was clear that hunting could never be increased enough to check the herd's expansion. Besides nobody, including the scientists, knew how big was too big.

Prediction Up - Population Down

Although it was predicted that the 1991 PCH population would be about 200 000, the 1992 census only counted 160 000 - a drop of 18 000 from 1989 (PCMB 1992, 1993). This was a surprise to everybody, including the biologists who revisited their data and concluded that severe winters could have increased female mortality enough to cause the change.

Since the Board is the focus of the public's scientific knowledge and opinion about the PCH, it's initial concern was whether or not the drop of 18 000 represented a significant decline. Biologists replied that only because the estimates were so accurate could such a small drop be detected and this small a change would never show up with the cruder estimates for other herds. The Board accepted this interpretation and therefore informed the public that the decrease was no cause for alarm.

However, in view of the extreme threat posed by oil development on the herd's calving grounds, the Board strongly urged a repeat census in 1994 to determine whether the decline was definitely a trend or just a hiccup. Otherwise, the Board may have taken the biologists' advice to wait another year before censusing to give more time for a significant change to occur.

Seven Year Summary

Over the past 7 years the co-management response to accurate information on the size and trend of the PCH may be summarized as follows: a) As long as the herd is big and increasing, maintain 'normal' harvests and consider increases. b) If the average harvest is considered to be well below the sustainable level, encourage shifts of hunting pressure from other herds and provide caribou to disadvantaged communities (Note: commercial sales are prohibited by the Porcupine Caribou Management Agreement, 1985). c) When a drop in the population is first recorded do not consider management changes until a downward trend has been confirmed, which may reduce the population below the average sustainable harvest. d) Unless the herd is seriously threatened (eg. by oil development) do not recommend a recount until enough time has passed to make a significant decline obvious.

From the preceding account, it seems that as long as the caribou population is well above the sustainable harvest, the co-management response to population management remains pretty much the same. This is because once the herd grows beyond the ability to control it through harvests, there is nothing else that can be done except capitalize on the situation.

Under this scenario, there are no other basic requirements from research. Even if biologists could - at great expense - determine how big was too big, there is nothing that could be done about it. A classic example is the muskox eruption on Banks Island which has never been resolved scientifically and is beyond management control in any case.

'Lots' And 'Really Lots'

People on the land do not count caribou. Rather, their opinions on the status of a herd are expressed in relative terms. Although these terms vary across the north, some common ones in the Western Arctic are, 'lots', 'not so many' and 'few'. Further refinements to this include 'really lots', 'too many' and 'few few'. Such terms are used, for instance, when hunters are being interviewed at their camps. In conversations about hunting success and caribou numbers, these people do not refer to animals in hundreds of thousands with confidence limits but according to their experience over a lifetime and the memories of their elders.

This approach may seem crude by modern standards but it can serve as a valid management model since, based on the PCMB example and judging from other similar situations, caribou are not managed by number so much as they are managed by categories akin to 'lots', 'not so many' and 'few'.

For the past 7 years there have been 'lots' to 'really lots' of caribou on the Porcupine Caribou Range and this is reflected in liberal harvest controls that will not change significantly until a serious decline becomes indisputable. Thus, whether the herd is 135 000 or 160 000 or 178 000, the actual number and accurate tracking of the increase had little effect on management which lumps all such figures into the 'lots' to 'really lots' categories for which there is one basic management strategy (Fig. 1). And even though the herd has dropped 18 000 in the past 3 years, there are still 'really lots' for management purposes and could remain so despite a further decline until the sustainable harvest level is approached.

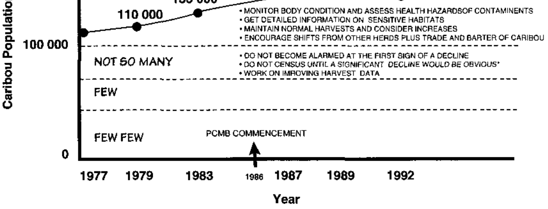

Fig. 1. Mangement response of the Porcupine Caribou Management Board to “Lots” category of Caribou population status.

'Too Many'

In developing this model, it is necessary to consider the other categories as well. What if the PCH had continued to increase as predicted to 200 000 and beyond? Already in 1989, some users were talking about there being 'too many' caribou' - that is, more than they had ever seen before. If the herd continued to grow there would have been more talk about 'too many' caribou and a controversy would undoubtedly have developed, as with the George River Herd, about what is 'too many'. But the bottom line for co-management is that whether there are 'lots', 'really lots' or 'too many' caribou, the response remains the same, i.e. liberal hunting, trade and barter and, where legal, commercial quotas (Fig. 2).

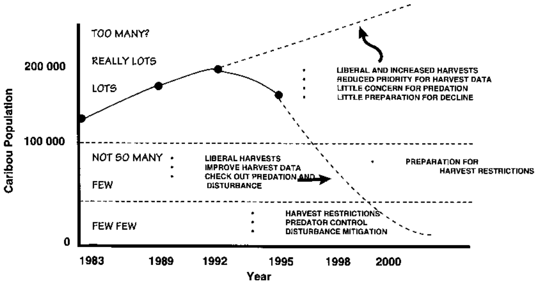

Fig. 2. Possible management responses to various categories of PCH population status in the future.

'Not So Many' And 'Few'

The reverse situation for the PCH is a continued downward trend from 1992. Judging from similar experiences with other barren-ground and woodland herds, if the PCH continues to decline, there will be a prolonged period during which the decline will be monitored and management actions will be debated. Since it is very difficult to restrict harvesting, especially where subsistence needs are paramount, comprehensive harvest restrictions may not be invoked until the population has dropped substantially. This scenario corresponds to the categories of 'Not so many caribou' - when discussions will concentrate on means of controlling the harvest plus the timing and allocation of such controls, and 'few caribou' - when the need for controls will be so apparent that nearly full cooperation can be expected. Hopefully such controls will be undertaken before the herd reaches 'few few', although there is considerable evidence to the contrary (Urquhart and Farnell, 1988, Farnell in press).

So What?

The purpose of considering broad categories for management is to reexamine the preoccupation with caribou numbers, which implies that knowing exactly how many caribou there are is essential to proper management. This can be a pitfall when government departments control management because they tend to become preoccupied with getting a good number without considering how necessary such a number is for decision-making. Co-management, on the other hand, is an opportunity to establish more practical guidelines for population research.

The PCMB example shows that, as long as the abundance of the herd is known in relation to the harvest, having accurate population information is not essential for good management. This does not mean that such information is not greatly appreciated, but it does demonstrate that, for other situations where accurate population data are not available, either due to cost or technique, it is still possible to make appropriate management recommendations as long as some relative measure of abundance can be made that can be related to harvest.

In such cases the basic co-management requirement from research is to determine whether accurate population data are realistically feasible and, if not, to work on providing other means of tracking population status that can be used by co-management. Such means may require some unorthodox 'seat of the pants' approaches that classical scientists resist but nothing is worse than perpetually banking on a method that is expensive, risky, ambiguous and often disappointing.

How Do Population Dynamics Fit In?

'Dynamics' involve energy and activity and every day the PCH is energetically involved in the activities of living and dying. By understanding how such dynamics determine population size and trend, classical researchers have always felt that such knowledge could be used to refine management. But understanding caribou population dynamics has proven to be a Pandora's box of statistics and complexities, whose solutions always seems to move just beyond the capacity of available data to resolve them. This, in turn, sets researchers on an endless quest for more and better information. Ultimately, however, such information may be unobtainable at any reasonable cost.

A good example is the population dynamics monitoring of the PCH which predicted an increase in the population of 178 000 in 1989 to around 200 000 in 1991 (PCMB, 1991). However, during that period, the herd decreased to 160 000 by 1992. In retrospect, biologists believe that harsh winters increased the mortality of adult females (Fancy in press). Also, in determining this, they found from their computer model that as little as a 3% change in

Table 1. Major research and management questions based on the general population status of the caribou herd.

	POPULATION SIZE	HARVEST	HABITAT	PHYSICAL CONDITION
TOO MANY	↑	• CAN HARVESTS BE USED TO REDUCE POPULATION SIZE?	↑	↑
REALLY LOTS		• COULD AND SHOULD HARVESTS BE USED TO TRY AND CONTROL THE POPULATION?		
LOTS	• MEASURE OF ABUNDANCE THAT A) IS AFFORDABLE B) CAN BE RELATED TO HARVESTS ↓	• WHAT IS THE RANGE OF TOTAL ANNUAL HARVESTS? • HOW IS THE HARVEST DISTRIBUTED AMONG COMMUNITIES? • GUIDELINES FOR HARVESTING A HEALTHY POPULATION • HOW MUCH IS WOUNDING LOSS? • HOW MUCH POACHING? • WHAT METHODS ARE HARMFUL?	• WHAT ARE THE HERD'S SEASONAL HABITATS? • WHICH HABITATS ARE MOST IMPORTANT AND SENSITIVE? • WHAT ACTIVITIES CONSTITUTE DISTURBANCE AND WHAT ARE THE PROBABLE IMPACTS? • COULD DISTURBANCE ACTIVITIES BE MITIGATED? ↓	• ARE THE CARIBOU IN REASONABLE PHYSICAL HEALTH? • IS POOR CONDITION DUE TO ANYTHING THAT COULD BE MITIGATED? • ARE CARIBOU CONTAMINATED? • WHAT IS THE CONTAMINATION AND HOW COULD IT AFFECT HUMAN HEALTH? • ARE CONTAMINATION LEVELS DANGEROUS AND IF SO WHAT STEPS SHOULD A USER TAKE? • CAN CONTAMINATION BE MITIGATED?
NOT SO MANY	• IS THE POPULATION DECLINING DUE TO HARVESTS, PREDATION OR DISTURBANCE?	• WHAT IS THE TOTAL ANNUAL HARVEST? • GUIDELINES FOR HARVESTING A DECLINING POPULATION	• IS DISTURBANCE A FACTOR IN THE DECLINE? • CAN DISTURBANCE BE MITIGATED? • IS THERE INTERSPECIFIC COMPETITION?	• IS POOR CONDITION A FACTOR IN THE POPULATION DECLINE?
FEW	• IS A CRISIS IMMINENT? • WILL PREDATOR CONTROL OR DISTURBANCE MITIGATION HELP?	• HOW CAN HARVESTS BE CONTROLLED (QUOTA)?		
FEW FEW	• IS THIS A CRISIS?	• SHOULD HARVEST BE PROHIBITED?	↓	↓ ↓

female mortality could cause the herd to decline but the bad news is that such a change is undetectable with current monitoring methods (D.Russell, Canadian Wildlife Service, Whitehorse, pers. comm.).

One such method is the composition count which is undertaken to determine the percentages of various age and sex classes of caribou. The reliability of such counts is almost always compromised by sample size and accurate identification plus the fact that caribou are never uniformly distributed but grouped in different age and sex classes so that samples are almost always skewed, especially in the spring.

Such information provides many opportunities for fascinating analyses (by researchers) and intense conversations (at management meetings) about what the herd might be doing. But the information is not utilized for making management recommendations since it only applies to a specific year and moreover, is often presented as being inaccurate. Regardless of what such data show or do not show about the dynamics of the population, co-management of a caribou herd does not react on a seasonal or even annual basis but on major trends over periods of years.

Perhaps the greatest lesson from the study of population dynamics is that most of them have little or no management value. No better example exists than the PCH for which there is undoubtedly more population information than for any other barren-ground caribou herd. Yet, the complex analyses of this data have exposed a virtual chaos theory where subtle changes (like female mortality) can have major population repercussions in an unpredictable way. Thus, although all the major barren-ground herds increased during the 1980's no one ever determined why. And, if some of these herds now begin to decline, it is likely that the causes will also be buried so deeply in ecosystem dynamics that they will never be known - meanwhile engendering endless scientific debate and consequent management dithering.

When this view is coupled with the acknowledged difficulty of obtaining accurate data on any of the known factors, the co-management conclusion may be to simply count caribou, wait, and count them again, or where even that is unfeasible, to rely on some measure of abundance without delving deeply into the whys and wherefores.

From the co-management perspective, population studies should be geared toward providing answers that can be acted upon (Table 1). Thus the initial question should not be: 'Why is the herd declining?' but, 'Are there aspects of the herd's decline that can be mitigated?' If factors such as overharvesting, disturbance and predation can be ruled out through appropriate research, then the causes of the herd's decline become more or less academic since nothing can be done to influence it.

Part Two: Is The Herd Threatened?

Overharvesting

a) When there are 'Lots'

The first co-management concern about a caribou herd is whether it is being overharvested. In everybody's mind there is a large (hopefully) population of caribou from which a certain number can be taken each year without causing a decline. Thus, determining how much can be taken depends on 3 factors: population size, recruitment and adult mortality. Theoretically, this will show if the herd is being overharvested or not. In practice, however, such a number is not so obvious.

Throughout the 1980's, and ever since the PCMB was created, the PCH was increasing. The PCMB, therefore, was not preoccupied with harvest data since whatever was being taken was obviously not harming the herd. This does not mean that the Board ignored harvest information and, in fact, a great deal of time and effort has been spent to improve harvest collection methods. But the total annual harvest has not been a prime concern as long as the herd was increasing. Instead, the Board and governments have been content to rely on a general impression of the 'average' annual harvest which is considered to be in the neighbourhood of several thousand (PCMB, 1993; IPCB, 1992).

The underlying concept for this approach is the sustained yield. Although this has never been formally established by the Board, it is thought of as the number of caribou that can be taken each year without reducing the overall population. This is not determined by specific studies however, but on basic population theory as generally accepted by caribou biologists. For many years, the figure often given in this context was 5% of the total population but lately 3% is being quoted more often.

Suffice to say that such figures are largely a matter of opinion rather than hard science and are relevant only to a 'stable' population which is an oxymoron in caribou biology. Furthermore, it is likely that each population has a characteristic combination of parameters that would determine what a 'harvestable surplus' could be depending on the management goals for the herd. If research could shed light on such factors, this would give more relevance to the presently vague concepts of sustained yield and harvestable surplus that co-management has to deal with.

b) When there are 'not so many' or 'few'

There is even less certainty about what the harvest should be for a declining herd, which is what co-management needs to know most. All caribou populations decline at some time and when that happens the hunters in the communities will look to the co-management board to recommend a course of action. Given that it is very difficult to reduce subsistence harvests, both ethically and legally, it is essential that co-management be given the very best advice on what can be taken from a declining herd so that it causes no more hardship than is absolutely necessary on the users while at the same time convinces them that curtailing harvests is indeed the best solution.

But to date research has been relatively silent on strategies for harvesting declining herds. Of course, biologists will offer advice based on their understanding of population dynamics but here opinions differ greatly and what co-management needs is a solid body of research that can be called upon to make and promote their decisions. This then is a field of population research that requires much more attention than it is currently receiving.

c) The harvest data myth

Management on the basis of sustained yield requires accurate monitoring of the total annual harvest. Harvest information is one of the most deceptive components of wildlife management because, in theory, it should be readily obtainable but, in practice, it is rarely satisfactory. Also, for some reason, it is not considered as a valid field of serious research but rather as a nagging administrative problem to be addressed through trial and error. Thus, although many methods have been tried, apparently no one has rigorously examined their effectiveness. There is, in fact, a chronic need for serious harvest data research since, in the co-management world, harvest control is a real tool but a very tricky one to operate.

Disturbance

a) The habitat "bible"

Whether it is a road, a uranium mine, a pipeline or an oil field, every caribou range is subject to development proposals that could have negative impacts on the herd. In such cases, the co-management board is often the focus of coordinating a response to such proposals. To be sure, government also plays a large role, but it is often compromised by conflicting policies whereas co-management is seen as wildlife's foremost friend and champion.

Unless it is a megaproject, there is usually little time for co-management to respond to development proposals and thus it is essential that a backlog of material be available to draw upon for a submission that has to be made within a week. The best backup is information on the range, movements and, especially, habitats of the herd. Without this it is difficult to relate development proposals to the herd and impossible to be convincing about potential impacts. Such information is expensive and time consuming to produce but, unarguably, the most important research of all to equip co-management to do its job.

Ever since the Arctic National Wildlife Refuge was created in 1980, the PCH has been faced with the most devastating of all disturbances - oil development on its core calving grounds. For the past 14 years researchers have been working on this problem and it is largely because of the vast resources and high quality of work that the calving grounds, so far, remain undisturbed. In particular, this research has shown that cows with young calves avoid development facilities and that for the PCH this would force them into the foothills of the British Mountains where calf mortality, due to predation, is so much greater, that a decline would be inevitable.

Such information and a great deal more has been synthesized into a report from the International Porcupine Caribou Board titled "Sensitive Habitats of the Porcupine Caribou Herd" (1994). This is the finest co-management document of its kind because it is designed for use by decision makers who are not biologists. The report is, in fact, an operating manual for the herd's range including straightforward maps, simple explanations and a ranking of importance for each major habitat. Geared as it is for public comprehension and use, this document will undoubtedly become the caribou 'bible' for both co-management and industry in assessing future proposals for the herd's range.

Every co-management group should have such a reference and, because it is such a huge undertaking, research should be dedicated annually to filling in the blanks until the picture is completed. This could take many years but the salvation is that basic habitats do not change much over time and a calving ground or mineral lick or river crossing will be just as important in 10 years as it is now.

b) Impact information

The companion for habitat designation is impact information. This is another major research need for co-management since development proposals must be judged according to their impact on the animals and extrapolated to the population as a whole. Without the knowledge that cows with young calves avoid development, there would be less of a case for saving the '1002' section of the Arctic Refuge.

In Canada, the Dempster Highway was completed in 1979 but there is still no clear perception of how it affects the PCH and whether or not the existing 1 km no-hunting corridor is satisfactory for management.

This is because there is no useful information on how roads and related hunting activities affect caribou movements and energetics.

Impact analyses are probably the most difficult and frustrating of all caribou studies and consequently not too popular for research projects. Still, researchers should be encouraged to undertake such challenges because development pressure will only increase on caribou ranges and there is a critical need for fundamental understanding of impacts from generic forms of disturbance - roads, pipelines, aircraft, heavy equipment etc. Such information could be applied by any co-management organization as, at least, a first step in their assessment of a proposal. By the same token, co-management must relate the need for such information to certain research methods, such as radio-collaring, which may not be popular with all concerned.

Predation

The role of predation on caribou populations has received considerable attention and remains the subject of much debate in a theoretical sense. From the co-management perspective, the role of predation is important when there is competition with hunting or when a population appears to be in trouble. In such cases it is important to thoroughly investigate this factor because there is a potential, albeit politically volatile, opportunity to take some action. Therefore, some basic information on predators should be obtained when a population is high for future comparison when the population may be declining.

Predation should also be a first priority for investigation when a population is in trouble - if only to rule it out and thus spare co-management the endless debates that keep it from taking effective action on the real problem. In most cases, however, where predation is deemed a contributing factor, the management value of each predator study must be ruthlessly evaluated against the time and costs of this notoriously difficult field of research.

Part Three: Is The Herd Healthy?

Body Condition

At meetings of the PCMB, hunters often report on the health of the herd based on their assessments of the condition of animals that they harvest. The health of the caribou is a constant concern in the user communities, although it is also recognized that the physical condition of caribou naturally varies considerably during each year and relatively from year to year.

Originally begun in 1987 as a research project to relate the physical condition of cows in various seasons to annual productivity, the Porcupine Caribou Body Condition Study has been maintained as a monitoring program which involves the collection of about 20 cows 3 times a year. The collections are always made by local hunters in cooperation with the regional biologist who takes the samples and the meat is distributed to the communities. Ultimately, this program will rely on samples from hunter kills rather than collections and, according to the Board's management plan, will be continued indefinitely.

The body condition program is popular with the PCMB because it is a scientific undertaking involving close cooperation between users and biologists. It is also rewarding for both parties to agree on the condition of the animals and the significance to the herd. In addition, the program provides an opportunity to collect samples for related work such as contaminants monitoring.

From a research perspective, gathering data on body condition, when the herd is large and apparently 'normal', could prove invaluable in years to come should a major development occur on the herd's range that affects the condition of the animals or if a natural decline occurs which is related to nutrition. Thus, body condition research and monitoring is a priority as far as co-management is concerned, since it incorporates all of the basic co-management criteria, viz. cooperative, affordable, understandable, and useful.

Contamination

Increasing preoccupation with environmental contamination has had a profound impact on northern communities and the co-management organizations which deal with such issues in relation to wildlife. With respect to caribou, the 2 major contaminants that have caused public alarm are radio-cesium and cadmium.

As far as the Porcupine Caribou Herd is concerned, neither substance is a health hazard but both were initially perceived as such due to a combination of scientific bungling and poor public communication by government agencies. In both cases, the Porcupine Caribou Management Board became the focus for concerns expressed by the users and hence, interpretations of scientific data and health assessments that had some relevance in the real world.

Although contaminants research is continually increasing its sophistication in detecting and tracking contaminants, it is woefully deficient in relating such information to realistic assessments of health risks for users. Such deficiencies include, accurate information on the consumption of various country foods, cumulative effects of contaminants, health implications of using alternative commercial food sources, useful advice on how much can be safely consumed, and explanations of physiological effects of contaminants on the human body.

Parasites And Diseases

In addition to concerns about contaminants, people on the land occasionally find unhealthy animals about which they request information. In most cases, the causes can be attributed to known diseases or parasites but the breakdowns occur in: a) obtaining a good sample for examination and b) explaining the problem in understandable terms to the public. Therefore as far as research is concerned, co-management needs are: a) reliable field techniques for collecting samples by hunters and b) straightforward accounts of parasites and diseases for public education.

Summary

The greatly increasing reliance by governments on co-management organizations for management direction has profound implications for wildlife research both in the way it is approached and the way it is utilized. Researchers who fail to recognize the true requirements of co-management are in real danger of becoming irrelevant unless they fully comprehend just what kind of information co-management groups need (Table 1).

To successfully refocus wildlife research so that it is compatible with co-management approaches to problem solving is more of a challenge than might first appear. Many of the classic approaches must be sacrificed in favour of more down-to-earth methods that are affordable, understandable, useful and acceptable to northern communities. Whereas such methods may be judged as 'unscientific' by the academic, this is of far less importance to co-management groups than having something they can understand and use.

Of course, the bottom line for research is funding, and as one biologist commented at a recent conference," Who pays the piper calls the tune". Hopefully, recent land claim settlements in the North will enable co-management organizations to pay more pipers and, more hopefully, such groups will have the courage to demand research that will be useful to them rather than being persuaded into extravagant programs of little practical value. At the same time, government funding organizations should also recognize co-management needs and not perpetuate highly sophisticated studies which as one PCMB member commented," Tell you everything except how to fix the problem".

In the past, many wildlife populations in the North were largely unmanaged because governments had limited research capabilities which could only focus on a few issues with the standard repertoire of expensive and esoteric research techniques. Under co-management, however, most wildlife populations will get much more attention because that is the sole responsibility of such organizations. But it would be silly to imagine that standard research resources could be expanded to meet escalating demands for information from co-management groups and thus it is imperative that wildlife research be completely restructured to accommodate the new ways of managing wildlife.

Ultimately, co-management approaches to wildlife management and research should benefit all - from the peripheral wildlife populations that were formerly ignored, to the user groups that become intimately involved with both management and research and, finally, to the researchers themselves who have an opportunity both to develop a rapport with the people who rely on wildlife and also to enjoy having their research put into practice rather than collecting dust on a shelf.

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Co-management of the Porcupine Caribou Herd

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The Caribou, the Land and the People

The Porcupine Caribou Herd is a population of 160,000 barren-ground caribou (*Rangifer tarandus granti*) that ranges from the De Cho (Mackenzie) Delta in the Northwest Territories across the northern Yukon and into Alaska almost as far as Prudhoe Bay (Fig. 1). From winter ranges in all three areas, the herd migrates northward in spring to calving grounds mainly on the North Slope of Alaska and extending to the Yukon. Following calving in June, the herd moves to the Beaufort Sea coast and, if the flies are bad, may form dense aggregations in July. Thereafter, various groups of caribou meander back and forth above treeline until fall snow storms encourage them to move southwards. Rutting occurs mainly in October during the fall migration. By November the herd occupies its winter range, although the winter distribution may vary depending on snow conditions (Russell *et al.*, 1993).

Porcupine Caribou are harvested for meat by Gwich'in, Inuvialuit and Inupiat people from 15 communities in Canada and adjacent Alaska. Non-native residents also harvest Porcupine Caribou for meat, and some caribou are taken by non-resident sport hunters. The annual harvest ranges between 3,000 and 4,000 animals. Over the past decade the harvest has remained well below the sustained yield of the population.

The Porcupine Caribou Management Agreement

Interest in the oil potential of the De Cho (Mackenzie) Delta and the Yukon North Slope during the late 1960s and early 1970s focused attention on the Porcupine Caribou Herd because of potential impacts from development. Concerns about the herd and its management were expressed by community representatives at the Mackenzie Valley Pipeline hearings (Berger, 1977) and separately, by the International Arctic Wildlife Range Society. In particular, the user communities were insistent that they become fundamentally involved in the conservation and management of the caribou herd which had always been the basis of their culture and economy. Originally intended for inclusion

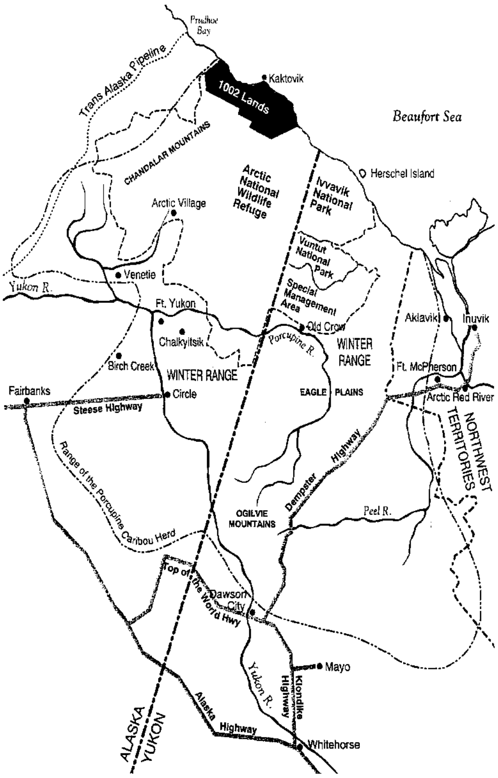

Fig. 1. Range of the Porcupine Caribou Herd.

in the Inuvialuit Final Agreement (Canada, Department of Indian and Northern Affairs, 1984), negotiations on the co-management of the Porcupine Caribou Herd reached an impasse that resulted in its being concluded separately in 1985 (Canada, Department of Indian and Northern Affairs, 1985) - a year after the Inuvialuit Final Agreement was proclaimed. The Porcupine Caribou Management Agreement is however, acknowledged in the Gwich'in Comprehensive Land Claim Agreement (Canada, Department of Indian and Northern Affairs, 1992) and the Council for Yukon Indians Umbrella Final Agreement (Canada, Department of Indian and Northern Affairs, 1993).

The Porcupine Caribou Management Agreement (Canada, Department of Indian and Northern Affairs, 1985) was signed on October 26, 1985 by representatives of the government of Canada, the governments of the Yukon and the Northwest Territories, the Inuvialuit Game Council, the Council for Yukon Indians, the Dene Nation and the Metis Association of the Northwest Territories. The five objectives of the agreement are:

(1) To cooperatively manage, as a herd, the Porcupine Caribou and its habitat within Canada so as to ensure the conservation of the herd with a view to providing for the ongoing subsistence needs of native users;
(2) To provide for participation of native users in Porcupine Caribou Herd management;
(3) To recognize and protect certain priority harvesting rights in the Porcupine Caribou Herd for native users while acknowledging that other users may also share the harvest;
(4) To acknowledge the rights of native users as set out in this Agreement;
(5) To improve communications between Governments native users and others with regards to the management of the Porcupine Caribou Herd within Canada.

The agreement also provides for the formation of an eight member co-management board (the Porcupine Caribou Management Board - PCMB) consisting of two members each from the Yukon Territorial Government and the Council for Yukon Indians plus one each from the Inuvialuit Game Council, the Dene Nation and Metis Association of the Northwest Territories and the governments of Canada and the Northwest Territories. The duties of the PCMB are to facilitate communication among governments and user communities in the course of providing recommendations to governments concerning the management of the Porcupine Caribou Herd.

Co-management and the Porcupine Caribou Management Board

The PCMB held its first meeting in June 1986 and has been operating continually ever since. In the course of the past seven years, the board has established a reputation among both the user communities and governments, as a reliable organization that is fulfilling the terms of the Porcupine Caribou Management Agreement. Cooperative management of wildlife is a complicated process but we believe that the success of the PCMB can best be summarized as the three "C's" of co-management: composition, communications and consensus.

Composition

Wildlife management boards are generally created according to two models. Under the first model, a board is comprised entirely of non-government representatives. In the Yukon and Northwest Territories, such boards include the Yukon Fish and Wildlife Management Board, the Inuvialuit Game Council, and the Mayo Renewable Resources Council. Under the second model, both government and non-government representatives participate on the board. Examples of the latter include the Beverly and Qamanirjuaq Caribou Management Board and the Wildlife Management Advisory Council (in the Yukon Territory).

The PCMB belongs to the second group and its membership represents equally, government and native user groups. We believe that this arrangement has several advantages over models which exclude government representation, the most important of which is that it removes the adversarial relationship between government and the public because the government representatives are seen to be part of the management team. As such they are able to explain how governments work, what governments can and cannot do, and how the board can best approach government to promote its interests. Government representatives also have access to bureaucracies which the board can use to its advantage for information gathering, report preparation and a host of other administrative functions. The relationship between government and non-government board members is enhanced if government representatives remain on the board for a number of years.

By contrast, a board without government representation remains continually suspicious of government and frustrated by perceived government inefficiency. As well, such boards are disadvantaged by having to rely on their own, often meagre resources to undertake many tasks that could otherwise be assigned to a government representative. In the experience of the PCMB and from observations of other co-management organizations, the fear that government members will dominate such boards is a minor risk that is far outweighed by the advantages of government participation. Certainly, it is possible for an aggressive individual to be manipulative but this is rare, especially when government members are involved with the communities in their regular work, and thus can empathize with community perspectives and concerns.

The PCMB adheres to the view that non-government representatives must be well supported by the board to ensure their full participation. Foremost is a respectable honorarium that acknowledges that value and importance of the member and provides adequate compensation for time taken away from work. Secondly, the community member must not feel isolated from the board's operations between meetings. To ensure this, the PCMB provides telephone credit cards to each of the community members so they can easily communicate with the chairman, the secretariat, and with each other. It is also important that the community member not be considered a `volunteer' and therefore, he/she should be compensated for any significant time spent on board work in the communities. Volunteer "burn-out" is a chronic problem in the north and must be strictly avoided to ensure enthusiastic participation of community representatives.

Communication

Communication is at once the most important and the most difficult component of wildlife co-management. The first request from the user communities to the PCMB was to improve communications on Porcupine Caribou issues. To do so the board undertook a study of communications in northern communities (MacPherson, 1987) which recommended the following media in descending order of effectiveness: television, radio, and printed material. Based on this report, the board initiated a communication program that includes television announcements, video documentaries, bi-weekly radio bulletins, monthly newspaper columns and publication of the minutes and summaries of board meetings, annual reports, special reports, pamphlets and posters.

In designing and maintaining its program, the PCMB has found that communication is an endless process and strategies that work best are both passive (radio, newspaper) and persistent. While many people might not read a lengthy newsletter, most people will read newspaper articles or listen to the radio. Radio and newspaper announcements are frequent (every two to four weeks) to ensure maximum exposure to the community. In the past seven years the PCMB has produced over 15 videos, 150 radio bulletins and 75 newspaper columns. Such items also stimulate the mainstream media to follow-up with interviews and subsequent stories so that more communication is generated at no cost to the board. A less orthodox, but very successful form of communication has been the distribution of items carrying the PCMB logo (ball caps, pens, mugs and knives). These serve to remind the public of the importance of the Porcupine Caribou Herd and the role of the board as an organization that works for the communities.

Early in its operation, the Board recognized that education was an essential component of communication and with support from governments and private foundations, the PCMB has initiated a number of projects including a range model for very young students, an elementary school curriculum complemented by a four-part video series, a college scholarship program and a computer package for high schools. All of these materials are designed to increase knowledge and understanding about the caribou herd and its habitat so that the user communities can participate more fully in caribou management.

At the same time, it is crucial for governments to understand and appreciate traditional knowledge and cultural values. This is also a demanding education and communication challenge and one that the PCMB has been promoting through its management plan but which has so far generated few genuine successes. Cross-cultural training and utilizing traditional knowledge are popular topics for reports and conferences but are rarely transmuted into real actions. To counter this, co-management organizations must overcome substantial bureaucratic reluctance to leave the office environment and spend significant time in the communities and the bush.

Communications, if taken seriously, will undoubtedly become the black hole of effort and innovation for any co-management organization. It seems that no matter how much is done and how clever the projects are, it is never enough. Some organizations do not experience these frustrations because they never seriously try to facilitate communications but instead rely on the standard procedures which are barely adequate for any audience.

Consensus

Although the PCMB has equal representation from government and native users, the Yukon Government appoints as one of its representatives, a resident from a user community and hence, there has always been a native majority on the Board. However, since the Board operates by consensus according to native preference, majority representation is not a significant element of decision-making. Consensus has never been formally defined by the

Board but in practice, consensus consists of an understanding that members will work to resolve a problem until all members are satisfied and the resulting motion is passed unanimously. In the 7 years of the Board's operation only one motion has been defeated by a split vote and a subsequent one passed with one abstention.

In conjunction with including government representation on the Board, the consensus principle greatly alleviates the tension of decision-making at the Board level. Not only can each member be confident that particular concerns will ultimately be addressed but consensus eliminates the need for members to form alliances and lobby each other for support on particular issues. This creates a positive atmosphere where each member can think independently about each item and also not worry about trade-offs that might be hard to explain back home.

The PCMB applies the same consensus approach to its consultation with the user communities. The board has found that by providing clearly understood information and a forum for community input, agreements can ultimately be reached on even the most contentious issues. This may entail considerably more time and effort but by building consensus, the recommendations of the Board have greater support and often a process of community self-management can be initiated. This in turn reduces the need for formal regulations being imposed by an outside authority. The best example of a consensus solution to a problem pertains to the sale of caribou antlers for oriental medicine. After considering the economic, conservation, cultural and legal aspects of the issue it was determined that the Gwich'in communities were culturally opposed to such sales while the Inuvialuit had no such constraint. In addition it became clear that no government regulation could be formulated to satisfactorily address these considerations. In the end, the Board was able to achieve a consensus agreement by the communities to voluntarily prohibited antler sales. This agreement has been completely effective without any government intervention.

Consensus management has the additional benefit of strengthening the confidence of the communities in the Board's ability to address their concerns and creates an environment of mutual respect where the Board also recognizes the community's ability to be responsible managers of the caribou.

As Western Arctic MP Ethel Blondin would say, co-management is a "tricky dance" (E. Blondin, pers. comm.) and every co-management organization that is created must be prepared to learn new steps to suit its particular mandate. However, based on the experience of the PCMB and observations of the authors, some approaches appear to be fundamental to successful co-management. We suggest that in designing a co-management system, particular attention should be given to the composition of the management board, methods of communication and approaches to decision-making. Systems which give the greatest independence and freedom to the co-management organization and its members seem to work best because they provide greater dignity to the organization, generate more enthusiasm from the members, and increase confidence and creativity in problem solving.

Ultimately, the success of a co-management organization rests with the user communities. Over the years members of the Porcupine Caribou Management Board have observed that it is the knowledge and concerns held by the people in the communities which are affected by caribou management policies, that provide the greatest inspiration to the Board. In return, the Board must never lose sight of its primary objective which is to manage and conserve the Porcupine Caribou Herd by incorporating native participation at every level of decision-making.

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Brief communication

Human impacts on George River Caribou: An Overview

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Human activities have had, historically, varying degrees of effect on caribou (*Rangifer tarandus*). In northern Europe, caribou have been moulded into the semi-domestic reindeer. In North America, many sedentary woodland populations have been eliminated or severely reduced in number. Migratory, barren-ground populations, on the other hand, have recently experienced population highs reminiscent of levels estimated to have occurred prior to the last century of increased exploitation (Bergerud, 1988). The George River population is no exception and, in fact, may serve as a model of this recent expansion. For much of this century, the population appeared to be of little consequence, compared to its importance in the late 1800s. Beginning in the 1950s, an increase from perhaps less than 10,000 individuals to over 600,000 by the mid-1980s propelled the population into a central position regarding human activities in northern Quebec and Labrador. Although there is of yet no clear evidence that human activity has had much to do with either the population's increase or the initiation of its current decline, the issue of potential impacts by humans is now a major concern. Decisions made now concerning these impacts may determine the ultimate level of the next population low, its duration, and the period to the next population peak.

The nature of human impacts varies along a number of dimensions. Influences can be direct or indirect. Hunting represents the most direct of influences; ultimately, its impact of the population may be either positive or negative. Global warming, on the other hand, may be among the most indirect, acting through effects on vegetation or snow conditions. Impacts may also be permanent or transient. Loss of habitat through development, whether for mining, hydroelectric power, or human habitation, may exert relatively long-term effects. Low-level aircraft flights may cause relatively transient effects that may be easily reversible. Ultimately, it is the cumulative impact of these various influences that is of greatest concern. Below I will focus on three forms of human impact that are of most immediate concern.

Hunting is an activity with the potential for both positive and negative effects (Harrington, 1988, 1991). Over-hunting may send a population into an early decline; under-hunting may allow it to peak relatively early. Judicious hunting, on the other hand, may sustain a population peak. However, a sustained population high may not be beneficial in the long term, if other negative effects (over-grazing, disease) are enhanced during a prolonged period of high density. Three sources of hunting can be identified: a local, subsistence component; a broader, sport component; and a commercial component. Subsistence hunting is generally governed by economic principles; the availability and accessibility of caribou must allow a reasonable expectation of return for effort expended. Low caribou densities do not warrant sustained hunting effort, relaxing hunting pressure under these conditions. Sport hunting, on the other hand, is driven by outside market factors, namely the number of interested clients and the relative cost of hunting in Quebec and Labrador compared to elsewhere. In addition, a sustained level of hunting is required to keep the outfitter solvent. Thus sport hunting may continue at much lower caribou densities than would support a subsistence hunt. Finally, the development of a commercial hunt requires a relatively large initial financial investment, both for materials and marketing. To remain viable, it requires a stable and sustained supply of caribou. Thus exploitation may continue at low population densities. In the management of these hunts, coordination and cooperation is required among each user sector and the various managers with jurisdiction within the population's range.

Hunting pressure is directly linked to accessibility to caribou habitat. Development which makes travel easier (road development, development of interior airstrips, etc.) opens up more country to hunting, thus increasing overall hunting pressure.

The potential impacts of low-level military jet fighter training has been another recent area of concern. Low-level flying does not likely exert a significant direct effect on caribou. Caribou may be startled by low-level overpasses and may run briefly, but these effects are short-lived and unlikely to have important population-wide effects except under rare circumstances (Harrington & Veitch, 1991). On the other hand, low-level jet overpasses may have important although largely indirect negative impacts on caribou population dynamics. Calves overflown more often during the first two weeks postcalving survive for shorter periods of time (Harrington & Veitch, 1992). Females overflow by jets during the post calving period move longer distances during the next 24-hours than they normally do (Murphy *et al.,* 1993), perhaps making their calves more accessible to predators. The vulnerability of caribou to negative impacts from low-level jet activity likely varies dramatically depending on season. In addition, although the high frequency of jet flights makes them an important concern, helicopters on a per flight basis have a greater potential for negative effects than either fixed-wing or jet aircraft.

Hydro-electric development is the third source of potential human impacts of caribou (Harrington, 1991). Habitat alteration and habitat loss are two of the potential effects of such development. Some of these impacts would be permanent, as in winter range flooded under reservoirs; others would be long term, such as return of vegetation following human-caused wildfires, and still others might be short-term, such as changes to river drainage patterns or lake ice conditions caused by lowering of reservoirs for power overwinter. In addition, the opening up of previously inaccessible areas will increase the vulnerability of caribou to hunting activity.

Habitat loss exerts its influence by lowering the carrying capacity of the habitat. Loss of critical habitat, therefore, is of most concern. The fact that calving range is the one "constant" in the caribou's migratory movements, and that summer range appears to be overgrazed at present and may be limiting the population, indicates that protection of habitat in or about calving and summer range is a priority.

No one factor is likely to be the key element. Rather, the effects of various factors will be additive, multiplicative, or compensatory. In the end, it may not be possible to construct a model that adequately characterizes the influence of these factors and the relationship among them. But it is important to monitor human influences of the population, so that changes in the relative magnitudes, at least, of these variables can be detected before their impacts become serious. Until a fuller understanding of the impacts of these various activities is acquired, it may be more appropriate to accept the alternative hypothesis that there is an impact, rather than the null hypothesis that there is none.

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The George River Caribou Workshop,
Labrador City, Labrador, Canada,
27-29 January, 1994.

Brief communication

The Joint Management Concept

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In Canada, public attitudes are evolving toward acceptance and encouragement of shared management of wildlife resources between responsible government departments and user-groups. The co-management approach is given national recognition in the publication, *A Wildlife Policy for Canada* (Wildlife Ministers' Council of Canada, 1990) which is designed to complement existing governmental legislation and policies so that there may be a comprehensive set of policies guiding the management of Canada's flora and fauna throughout the nation. The policy recognizes the necessity of effective participation of aboriginal groups in the management of wildlife in certain regions and urges governments to involve aboriginal peoples in wildlife management either through comprehensive land claim agreements or by other means. The government of Quebec, for its part, has adopted a motion to encourage the negotiation of agreements with aboriginal nations which would include the right to participate in wildlife management.

Several co-management wildlife regimes exist in northern Canada today and others are under negotiation. Certain of these are designed to manage wildlife in general while others are specifically for caribou. The James Bay and Northern Quebec Agreement (JBNQA) was signed in 1975 (Canada, Department of Indian and Northern Affairs, 1975) and the Northeastern Quebec Agreement (NEQA) was signed in 1978 (Canada, Department of Indian and Northern Affairs, 1978). These very comprehensive agreements apply to approximately 1,000,000 km^2 of northern Quebec. Beneficiaries of the agreements are the Inuit of northern Quebec, the James Bay Cree of Quebec and the Naskapi Indians of Quebec. As mandated by the JBNQA, the Hunting, Fishing and Trapping Coordinating Committee was formed in 1977. This committee is composed of an equal number of aboriginal and government representatives. It is primarily a consultative body to the governments of Quebec and Canada and is intended to be the preferential and exclusive forum where the beneficiaries of the JBNQA and the NEQA and the two governments may jointly formulate regulations pertaining to hunting, fishing and trapping of wildlife.

The Coordinating Committee has the authority to establish harvest quotas for moose and caribou for both aboriginal and non-aboriginal hunters, subject to the principle of conservation. In turn, it is the responsibility of the government to draft regulations to ensure that these quotas are met. In the implementation of co-management, government board members see the committee's role as advisory to the responsible governments in the management of wildlife resources, whereas the aboriginal parties perceive the committee as an equal partner with the governments in this task. This fundamental difference in the concept of co-management has, in the past, contributed to mutual frustration and impatience on the part of the Quebec government, and the three aboriginal parties to the JBNQA.

Initial attempts by the Inuit party to direcdy assume part of the responsibility for the managment of caribou together with a portion of the pertinent government budget, were rebuffed by the Quebec government which has maintained its role and responsibility as the sole legal entity for caribou managment in Quebec. The aboriginal parties have frequently criticized the government's management of caribou. Most significantly, the aboriginal parties have criticized on biological and economic grounds, the government policy of encouraging increased exploitation of the George River caribou herd. As well, the government has been criticized for failing to develop a cohesive caribou managment plan. Although draft management plans for caribou have been submitted by the Quebec government, to the Coordinating Committee and although the committee has reviewed those plans, an official caribou management plan for northern Quebec has not yet been adopted by the government of Quebec.

In May 1985 the Inuit members of the Coordinating Committee tabled a proposal for the establishment of a caribou management board for northern Quebec, which would be formulated along the lines of the Beverly and Kaminuriak Caribou Management Board. The Quebec government responded by suggesting that caribou could be managed cooperatively by the Coordinating Committee and three existing government committees. Negotiations continued until the government recommended, as a compromise, the creation of a single caribou management board with representation from the aboriginal parties, the Quebec Government and the "Secrétariat des activités gouvernementales en milieux amérindien et inuit". Finally, after studying and comparing the principles and objectives of the Beverly and Kaminuriak Caribou Management Board with those of the JBNQA and with those of the proposed Quebec Management Board, all parties agreed that, in the light of these comparisons, the Hunting, Fishing and Trapping Coordinating Committee would be best suited to collaborate with the government in managing caribou. Consequently the notion of a caribou management board for Quebec was abandoned. Since this decision, the Coordinating Committee has continued to press the government for a caribou management plan while participating fully in reviewing and commenting upon government initiatives in caribou management.

The commercialization of caribou meat was proposed by the government in 1985 with the support of the Inuit Party. The Cree party was initially reticent to support the project and the Naskapi were opposed. However, intense discussions external to the Coordinating Committee between the Native parties on the subject of commercialization eventually led to negotiations with the Quebec Government and the amending of the James Bay and Northern Quebec Agreement (Canada, Department of Indian and Northern Affairs, 1975) in 1993 to permit commercialization. In 1985 the Quebec party proposed the creation of a winter sport hunt for caribou in the Cree area of primary interest. This area had been closed to sport hunting of caribou since 1973. The Cree expressed concern over the security of Cree families on their traplines at this time of year and for the protection of their hunting and trapping equipment stored in the forest. The aboriginal parties were unanimous in opposing the hunt. However, after three and a half years of consultation with the Coordinating Committee and bilateral discussions between the Cree and the government, the sport hunt in zone 22 was opened in 1989. The hunt has been very popular with sport-hunters. Bilateral consultations have continued between the Cree and the government and certain regulations concerning the hunt have been modified in the light of Cree comments and recommendations. Local Cree have recently expressed the desire to participate in the hunt as guides and outfitters - an approach which the government welcomes.

The responsibility of the Coordinating Committee in the management of wildlife, including caribou, in northern Quebec is self-evident. Since its establishment in 1975 the committee has attempted to fulfil this responsibility. Initially the committee was hampered in its efforts largely due to a different interpretation of this responsibility among the parties. However, a three stage process for reviewing and discussing management initiatives has evolved over the years which has been shown to be effective. Initially the initiative is discussed at the table of the Coordinating Committee. If necessary, the item is referred to a working group. Finally, the government initiates discussions on the item at the community level, if required. Protection is accorded the Coordinating Committee from being shut out of the decision making process by safeguards in the JBNQA which oblige the government to consult with the committee prior to adopting a new regulation or other decision. Through trial and error over the years, the committee has come to fulfil its intended role - that of "coordinating" wildlife management in northern Quebec in conjunction with the responsible governments.

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Section 4.

Papers presented as posters

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Calving photocensus of the Rivière George Caribou Herd and comparison with an independent census

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Abstract: Vertical photographs of the calving grounds have been used since 1984 to estimate the caribou (*Rangifer tarandus*) population of the Rivière George Caribou Herd (RGCH) in Northern Québec and Labrador. In spite of large confidence intervals, the 1984 and 1988 estimates suggested that the herd stabilized at more than 650 000 caribou (fall estimate including calves) making the RGCH the largest caribou herd in the world. Between 1984 and 1990, studies suggested that the former rapid growth of the herd deteriorated the calving and summer habitats. This poor habitat quality affected physical condition, pregnancy rate and calf survival. It was important to have a valid estimate of the herd size and a photocensus was done in June 1993. Contrary to previous censuses, a slightly different sampling design was applied in 1993. Two methods were used to estimate the number of females in the June population. In the first method, the number of females was derived from the estimated number of calves on the photographs and from the June female/calf ratio. The second method was used in the previous census and is based on the number of adults on the photos and on the June female/adult ratio. It is suggested that the first method of estimating female abundance in June is better due to sampling problems associated with a strong adult sex segregation during calving. From the first method, the herd size in October 1993 was estimated at 583 829 adults (±33.79%) and at 749 869 caribou including calves (±33.15%) while the second method provided estimates of 764 221 adults (±23.55%) and 981 565 caribou including calves (±22.64%). It was possible to compare those population estimates with an independent census. In July 1993, an oblique photocensus of the post-calving aggregations was conducted by Russell *et al.* (1996). A new analysis of their raw data provided an estimate of 608 384 adults (±14.35%). Both estimates from the June and July photocensus were combined. From the first and second method respectively, combined herd size estimates were 775 891 (±13.40%) and 823 375 (±12.36%) caribou including calves. The management implications are discussed and it is emphasized that the herd is still underharvested.

Key words: Aerial survey, calving grounds, Labrador, Québec, *Rangifer tarandus*, ratio

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Introduction

Sound management of a large wild ungulate population is based on precise and unbiased population estimates. Confidence intervals around population estimates based on calving grounds census can be high for caribou (*Rangifer tarandus*) due to the clumped distribution of the animals relative to the number and shape of the sample units, the sampling fraction, the accuracy of stratification, a visibility bias, and the precision of the correction factors used to extrapolate the number of caribou estimated in the census area to an estimation of the population size (Crête *et al.*, 1991). Systematic aerial censuses have been done on Northern Québec caribou herds since 1954. A major improvement has been brought with the introduction in 1984 of the vertical photography technique (Goudreault, 1985; Crête *et al.*, 1989; 1991).

The calving grounds traditionally used by parturient females and the surrounding areas were surveyed in 1993. Major elements of the June 1993 census method were used on the same herd in 1984

(Goudreault, 1985), in 1986 (Crête *et al.,* 1987) and in 1988 (Crête *et al.,* 1989; 1991). Previously, the abundance of females outside the calving grounds was estimated from the locations of a radio-collared caribou sample. During the June 1993 census, the photosampling area was enlarged to count females not only on the calving grounds but also in surrounding areas. This photosampling technique was successfully used on the Rivière aux Feuilles Caribou Herd (RAFCH) in June 1991 (Couturier, S., unpubl. data). The reliability of the June 1993 census has been measured using an independent photocensus on the Rivière George Caribou Herd (RGCH) in July 1993. The second census technique performed by Russell *et al.* (1994) relied on the July aggregation behavior demonstrated by caribou almost every year. This technique has been used in the Northwest Territories (McLean & Russell, 1988; Russell, 1990).

Both 1993 censuses of the RGCH were done at a critical time during the herd's history. Recent studies (Couturier *et al.,* 1990; Hearn *et al.,* 1990; Crête *et al.,* 1994) confirmed earlier statements made by Couturier *et al.* (1988a, 1988b) and by Messier *et al.* (1988) on the demographic processes affecting herd growth. After having been extremely rare at the beginning of this century (Messier & Huot, 1985), the RGCH showed a rapid rate of increase until it recently became the world's largest caribou herd (Williams & Heard, 1986). The survival rate of the adults and possibly that of the calves, the pregnancy rate of the females and the physical condition of the caribou have decreased in the past decade, which has accounted for the herd's stabilization in numbers. Crête *et al.* (1996) demonstrated that the survival of females and the pregnancy rate remained relatively low until 1992-1993. Couturier *et al.* (1988a, 1988b) hypothesized that the poor condition of the RGCH females could be explained by overgrazing on the traditional calving grounds during the summer months. Recent studies confirmed the deterioration of the calving grounds and the surrounding areas (Crête & Huot, 1993; Manseau *et al.,* 1996). Dendrochronology was carried out on evergreen root and stem scars left by migratory caribou (Morneau & Payette, 1994). It confirms the intensive use of the calving grounds area from the mid-1970's until the late 1980's. Nevertheless, the foraging quality and the general condition of the herd (birth weight, calf/female ratio, etc.) seem better in 1993-1994 probably due to a change in the migratory pattern of the herd (Couturier, S., Doucet, J.G., unpubl. data).

The purpose of this paper was first, to estimate the abundance of adult females (≥ 1 year old) present in the herd in June and then, to apply the summer survival rate to compute the number of females in October 1993. The abundance of males and calves was later estimated from relative ratios observed during the fall classification. From these calculations, the total RGCH size is estimated and finally combined with an independent estimate (Russell *et al.*, 1996). The combined herd size estimate is used to discuss management implications and harvest strategy for the herd.

Methods

The calving grounds study area has been described by Crête *et al.* (1991). Couturier *et al.* (1990) presented information on the annual distribution of the migrating RGCH and RAFCH, the location of their respective calving and wintering grounds, and the weather and vegetation characteristics of the caribou habitat in Northern Québec and Labrador. Crête & Huot (1993) presented additional information on caribou density with reference to foraging quality and lichen use.

Telemetry survey

From June 4 to 10, 1993, a high altitude (2400-3000 m) aerial telemetry survey was done with a Partenavia twin-engined plane flying at 220 km/hr to determine the locations of radio-collared females. A GPS (Global Positioning System) navigating instrument was used to record locations of radio-collared animals, which were marked on 1:250 000 maps. The observation team covered 444 000 km^2 in 57.6 hours by spacing flight lines at approximately 40 km (Fig. 1). Extra telemetry flights (13.4 hours, 18-19 June 1993) were added over the Péninsule d'Ungava to determine possible herd switching. Ninety-four radio-collars of the RGCH were considered active in June 1993, of which 76 were females. Most of the radio-collars of the RGCH (82 radio-collars) were deployed in different areas of the RGCH annual range more than 8 months before the photocensus. We assumed that the distribution of the sample of radio-collared caribou was representative of the herd's distribution. The 94 radio-collars contained 35 PTT's (Platform Transmitter Terminals) which were located with the Argos satellite-monitoring system. Twenty-three PTT's were carried by females. Most satellite location data were retrieved about every four days (2 to 5 days) from Service Argos inc. (Landover, Maryland). To the 94 active RGCH radio-collars, we must add 5 females and 2 males of the RAFCH and two females of the Monts Torngat Caribou Herd (MTCH) which brings the total number of active radio-collars in Northern Québec and Labrador to 103 in June 1993. Due to budget constraints, it was impossible to do a teleme-

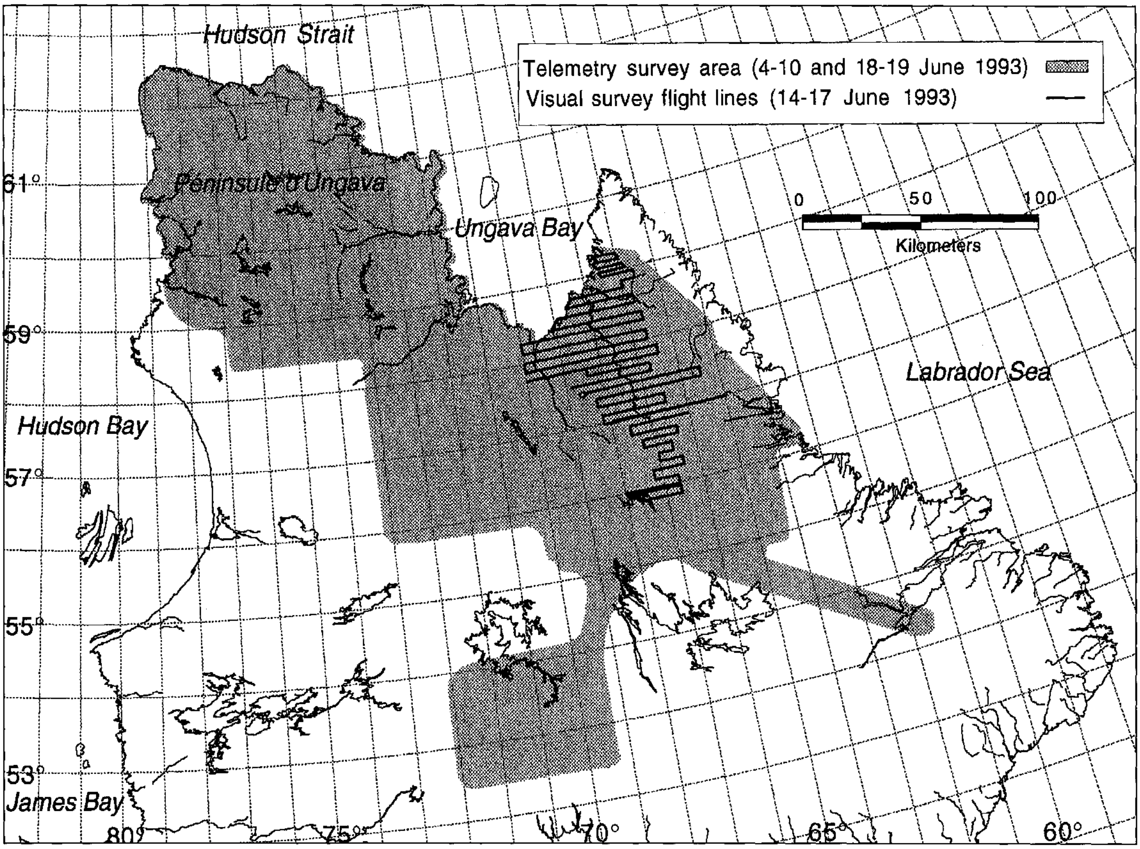

Fig. 1. VHF telemetry (4-10 and 18-19 June, 1993) and visual surveys for the strata delimitation (14 - 17 June, 1993).

try survey of the larger area used by the RGCH in October 1993 to estimate the summer survival of radio-collared females. Therefore, we used the female survival rate from June to October 1992 (Crête *et al.*, 1996).

Low-altitude visual survey

The same twin-engined plane was used from 14 to 17 June 1993 to perform the low-level (40-60 m) and low-speed (180 km/hr) visual survey of the RGCH in the area where most radio-collared females were found (Fig. 1). The goal of this survey was to estimate the abundance of females. Flight lines were spaced 13 km apart and covered 49 000 km^2 during 28.3 hours. Two observers sitting near the side-windows recorded the number of females, males and calves within a 500-meter strip band to each side of the aircraft. During June, adult sexes are distinguishable by their antler status. Data were recorded by a third person on 1:250 000 maps.

Once the visual survey was completed, female density figures were estimated by calculating the number of females observed over each 10 km segment of the flight line (hence, per 10 km^2). This information was used to delineate the sampling area and define three density strata for female caribou: low density (1 to 5 females/10 km^2), medium density (5.01 to 10 females/10 km^2) and high density (> 10 females/10 km^2). Computations of female densities allowed us to estimate the mean and the variance of densities in each stratum to determine the number of sample units using the Neyman's optimal allocation for stratified sampling (Cochran, 1977: p.99).

Helicopter vertical photocensus

Once the density strata were defined, a team of three observers boarded an Astar 350B helicopter from June 20 to 26 to carry out vertical photographic sampling. Aerial photographs were taken with an automatic aperture priority 35 mm Olympus camera equipped with a 50 mm f:1.8 lens and an automatic winder. Vertical photographs were taken at 10 s intervals with an automatic time-delay. Most photographs were taken on 36 exposure Kodachrome 64 ASA film. A Kodachrome Professional 200 ASA film was used under darker conditions. Lens aperture was set at f:4 and shutter speeds varied between 1/500 and 1/1000 s. Under darker conditions, lens aperture was changed to f:2.

One complete roll of film, from 36 to 39 color slides, was used for every sampling site and covered approximately 13 km on the flight line. Sample units were systematically distributed along east-west flight lines. On the photograph lines, the helicopter flew at an average speed of 150 to 180 km/h and tried to maintain a constant altitude of 200 to 240 m above ground level (AGL). The AGL altitude of each photograph was variable because of the topography of the terrain. The altitude of each photograph was recorded from a radar-altimeter with digital display (models TRA-3000 and TRI-40; TERRA inc.). This radar-altimeter has a precision of 6.1 m for altitudes between 122 and 305 m. Most photographs were taken between 180 and 270 m.

Composition counts on the sampling area in June 1993

From 19 to 25 June 1993, a second helicopter team studied the herd composition on the photocensus area to determine the composition of the adults, as distinguishing sexes on aerial photographs is impossible. The sampling design of the composition counts was based on satellite radio-collars locations. Observers landed near a satellite radio-collar and used binoculars to classify a target sample size of 300 caribou per site. Field observations included many different categories of which 3 were kept for analysis: adult male (≥ 12 months old), adult female (≥ 12 months old) and newborn calf.

Composition counts of the RGCH in October 1993

The October 1993 sampling design was determined from Argos satellite telemetry data. Once in the area of the satellite radio-collar, observers used a vantage point on the ground to classify a target sample size of 300 caribou for that particular location. Composition ratios (male/female, calf/female) were used to estimate the relative abundance of males and calves in the fall population.

Analysis of aerial photographs

Counts of adults and calves on each color slide were made by visually scanning a grid, which divided the surface into ten equal parts. Projections were made onto a 56.0 cm by 37.5 cm white surface using a Kodak (Carousel 5600) slide projector. To confirm the observations made by the first observer, 35 sample units (i.e. 35 slide films) were randomly drawn and analyzed independently by a second observer with previous experience in this type of work. Both observers had the choice of keeping or discarding a photograph from the analysis due to technical flaws (out of focus, exposure problems, etc.). When a slide was discarded by one observer, it was also rejected for the other observer. A paired sample analysis of 1212 photographs showed no difference in counts of adult caribou in 1155 slides, representing a 95.3% agreement between observers. A 96.8% agreement (1173 slides) was found for the calf count.

Statistical analysis

The mean number of photographs per sample unit was 33.1 (16 to 38). The AGGREGATE command of the SPSS software package (Norusis, 1990) clustered data (number of caribou (y), photographed area (x), snow cover, etc.) of all 36 slides to create the sample unit. Differences between strata ($\alpha \leq 0.05$) were tested using the ONEWAY command (Norusis, 1990), followed by a Scheffé test (Sokal and Rohlf, 1981). Unless otherwise indicated, estimates in this study are presented with their 90% confidence interval ($\alpha = 0.10$).

The photocensus is based on a two-stage stratified sampling plan with clusters of photos allocated systematically in two dimensions. An estimate of caribou abundance was calculated using the separate ratio estimator. This ratio was the mean number of caribou counted for all sample units ($\bar{y}_h$) in stratum h over the mean photographed area of a sample unit ($\bar{x}_h$) in stratum h. The estimator from the 3 strata is shown in the following equation (Cochran, 1977: 164, equation 6.44):

$$\hat{Y}_{Rs} = \sum_{h=1}^{3} \frac{\bar{y}_h}{\bar{x}_h} X_h$$

where X_h is the total area of stratum h.

The variance of this estimator is found by modifying equation 6.45 in Cochran (1977: 164) as follows:

- the finite population correction factor is neglected. This factor becomes unimportant since the sampling fraction is close to zero in this study;
- the total number of sample units in stratum h (N_h) is unknown and is estimated by $X_h/\bar{x}_h$

Therefore, we can consider the following equation for the variance:

$$V(\hat{Y}_{Rs}) \simeq \sum_{h=1}^{3} \frac{X_h^2}{n_h \bar{x}_h^2} (S_{yh}^2 + R_h^2 S_{xh}^2 - 2R_h \rho_h S_{yh} S_{xh})$$

To obtain an estimator of the above variance, the equation parameters must be substituted by their estimated values from the sample. For example, the expression $S_{yxh} = \rho_h S_{yh} S_{xh}$ is estimated from the sampling covariance between y^ion and x^ion in stratum h:

$$S_{yxh} = \sum_{i=1}^{n_h} \frac{(Y_{hi} - \bar{Y}_h)(X_{hi} - \bar{X}_h)}{n_h - 1}$$

Thereby, for each stratum, we can compute an estimation of the variance using equation 6.13 (Cochran, 1977: 155).

As we know the altitude AGL of the aircraft, the focal length of the camera lens (50 mm) and the film format (24 mm by 36 mm), it is possible to compute the area covered on the ground by each slide:

$$S = 0.3456\ A^2$$

where : S = area in m^2
A = altitude of aircraft above ground level in m
0.3456 = correction factor for focal length (0.50 m) and 35 mm film format

Radio-telemetry data were used to calculate the summer survival rate of adult females (≥ 2 years) with the program MICROMORT (Heisey & Fuller, 1985). Combined estimates for the June and July post-calving photocensus were computed using the procedure described by Gasaway *et al.* (1986). This method weighs each independent estimate by the inverse of the sampling variance of that estimate so that the combined estimate has the smallest variance possible of any weighted unbiased combination of the two independent estimates. The population estimates $\hat{N}_1$ and $\hat{N}_2$ and their respective variances $V(\hat{N}_1)$ and $V(\hat{N}_2)$ can be combined to obtain the combined estimate, $\hat{N}_c$ and its associated variance, $V(\hat{N}_c)$ as shown in the following equations:

$$\hat{N}_c = \frac{(\hat{N}_1 V(\hat{N}_2)) + (\hat{N}_2 V(\hat{N}_1))}{V(\hat{N}_1) + V(\hat{N}_2)}$$

$$V(N_c) = \frac{V(\hat{N}_1) V(\hat{N}_2)}{V(\hat{N}_1) + V(\hat{N}_2)}$$

Results

Delimitation and stratification of the sampling area in June 1993

Ninety-eight VHF radio-collars (98) were located in June 1993. Most (89) belonged to the RGCH, from which 72 were carried by females (Table 1). Of this group of females, 57 (79%) were found within the three density strata of the photocensus sampling area. With RGCH females near the sampling area (< 50 km), the presence of VHF radio-collared females rose to 92%. After the telemetry survey and before the aerial photography, satellite monitoring showed that the females travelled slowly toward the center of the high density stratum located on Rivière George, north of 58°N. Males showed a slight tendency in the opposite direction, moving away from the sampling area occupied by females. Twenty satellite radio-collared females of the RGCH out of 22 (91%) and 2 males out of 12 (17%) were located within the sampling area at the time of the photography (Table 1).

Table 1. Locations of radio-collared caribou during the telemetry survey (n = 103[a]) and from Argos satellite data (n=37).

Herd	Location	Radio-collared caribou, (8-10 June 1993)[a] (including Argos collars)			Argos radio-collared caribou, (22-26 June 1993)		
		Females	Males	Total	Females	Males	Total
RGCH	High density	34	1	35	10	2	12
(94 active collars)[b]	Medium density	12	0	12	2	0	2
	Low density	11	1	12	8	0	8
	< 50 km[c]	9	7	16	2	4	6
	50 - 200 km	2	7	9	0	5	5
	> 200 km[d]	4	1	5	1	1	2
	Total (RGCH)	72	17	89	23	12	35
RAFCH	In the 3 strata[d]	2	1	3	0	0	0
(7 active collars)	>200 km	3	1	4	0	0	0
MTCH	In the 3 strata[d]	1	0	1	1	0	1
(2 active collars)	<50 km	1	0	1	1	0	1
TOTAL		79	19	98	25	12	37

[a] Includes 11 locations that were made between 6 and 7 June and between 15 and 24 June 1993.

[b] Five active radio-collars (4 females and 1 male) of the RGCH were not located during the survey.

[c] Distance from the photocensus sampling area.

[d] Possible herd switching.

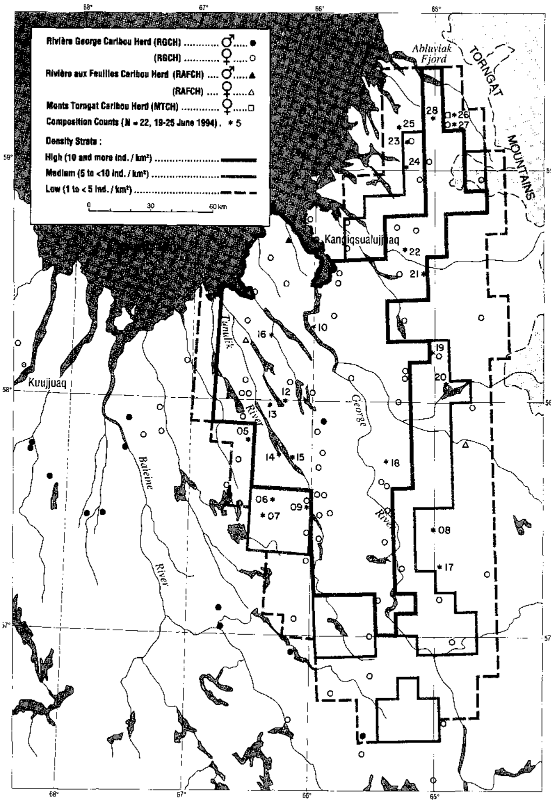

Fig. 2. Stratification pattern, locations of most VHF and satellite radio-collared caribou (8-10 June 1993, includes some locations that were made from 6-7 June and from 15-24 June 1993) and composition sampling locations (19-25 June 1993).

Two females (PTT 8318 and 14230) were within 10 km of the sampling area on June 25 but were visually observed a few days before within the medium density stratum. All satellite radio-collared females were therefore in the sampling area during photography.

Locations of most (82 out of 98) VHF radio-collars were found in the northeastern part of the herd range (Fig. 2). Most radio-collared males in large aggregations were located between Kuujjuaq and Rivière Baleine in June 1993. They were regularly observed during frequent flights to the study area. It became possible to visually follow male group displacements and to notice that they did not approach the photocensus sampling area.

June 1993 photocensus

During aerial photography, 181 sample units were surveyed from 20 to 26 June 1993 with 118, 32 and 31 sample units in the high, medium and low density strata, respectively. The adult and calf numbers were significantly different between the high density stratum and the two lower density strata whereas a non-significant difference was found between the latter (Table 2). Therefore, a third density stratum was not needed and did not increase the precision of the sampling. The mean sample unit size was 0.525 km². The aerial photographic sampling fraction accounted for 0.288% of the sampling area. Snow cover was very low due to an early spring in Northern Québec and Labrador. A total of 652 003 ± 19.45% adult (≥ 1 year old) caribou and 244 674 ± 23.86% calves were estimated in the sampling area.

Composition counts of the RGCH in June and October 1993

In late June 1993, 24 satellite radio-collars were found within the photocensus sampling area. Two of these were carried by males but were mistakenly not included in the composition count. A visual contact was made in 20 out of 22 cases. Of the 20 satellite radio-collared female observed, 11 had calf at heel, 2 had recently lost their progeny (distended udders and no calf at heel) and 7 were not parturi-

Table 2. Some results of the Rivière George Caribou Herd stratified photocensus, June 1993 (standard errors are shown in brackets).

Variables[1]	High density n=118	Medium density n=32	Low density n=31	ALL STRATA n=181
Adults/sample unit	23.77^A (3.18)	4.47^B (1.51)	1.58^B (0.52)	16.56 (2.21)
Calves/sample unit	9.13^A (1.47)	1.47^B (0.55)	0.48^B (0.26)	6.29 (1.00)
Adult density (caribou/km²)	43.95^A (6.23)	9.79^B (3.09)	2.8^B (0.88)	30.88 (4.31)
Calf density (calves/km²)	17.15^A (3.06)	3.35^B (1.18)	0.75^B (0.42)	11.90 (2.07)
Mean sample unit area (km²)	0.538^A (0.011)	0.488^A (0.020)	0.514^A (0.022)	0.525 (0.009)
Altitude (m)	219.6^A (1.91)	211.1^A (3.36)	214.5^A (3.07)	217.3 (1.49)
Snow cover (%)	2.4^A (0.4)	3.0^A (0.8)	8.0^B (1.5)	3.5 (0.4)
Sampling area (km²)	14 255	6 793	12 019	33 067
Sampling fraction (%)	0.446	0.230	0.133	0.288
Adult estimate	563 262^A (74 254)	54 974^B (17 750)	33 767^B (10 791)	652 003 (77 105)
Calf estimate	216 268^A (34 423)	18 069^B (6 724)	10 338^B (5 459)	244 674 (35 496)

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[1] Pairs of numbers followed by a different letter within a row differ at $\alpha \leq 0.05$ (ANOVA and Scheffé test).

ent (Table 3). This gives a pregnancy rate of 65% in the satellite radio-collared female sample. The estimated female/adult ratio was 0.8855 ±3.98% over the sampling area, with no significant differences between density strata. Relative abundance of calves or birth rate can also be found from the June composition data. We assumed that the calving was completed at the time of the classification. The calf/female ratio was 0.5547 ±20.03% and its inverse, the female/calf ratio was 1.8027 ±20.03%.

During the fall composition count of the RGCH, 19 sample units were surveyed from 21 October to 2 November 1993. Male/female and calf/female ratios were 0.4925 ±31.75% and 0.4245 ±5.99%, respectively. For comparison, fall composition data of the RGCH from 1973 to 1993 are shown in Table 4.

Extrapolation for the RGCH size from the June 1993 photocensus

The previous census method requires the application of the female/adult ratio from the June 1993 composition count to the estimated adult number counted on photos. In this case, the adult estimate of 652 003 caribou (Table 2) had to be multiplied by 0.8855, resulting in a female estimate of 577 373 for June 1993. As the female summer survival rate is 0.8869 and the adult sex ratio is 0.4925 male/female, the size of the population in October 1993 would have been 764 221 ±23.55% adult caribou. Adding the calf cohort to the adults resulted in a total herd size estimate of 981 565 ±22.64% caribou (Adult's method, Table 5).

We caution the use of the female/adult ratio in June 1993 since the result of 0.8855 might be slightly biased, being too high in comparison with previous

Table 3. Composition counts of the Rivière George Caribou Herd, 19 - 25 June 1993 (n=22).

Location[a]	PTT[b]	Calf at heel	Males (≥1 an)	Females (≥1 an)	Calves	TOTAL	Calf/ Female	Female/ Adult
5 (L)	4900	No	53	69	3	125	0.043	0.566
6 (M)	8318	No	53	91	1	145	0.011	0.632
7 (M)	14230	No	52	94	3	149	0.032	0.644
8 (L)	15196	Yes	18	176	83	277	0.472	0.907
9 (M)	4921	No	129	424	48	601	0.113	0.767
10 (H)	4924	No	31	269	40	340	0.149	0.897
12 (H)	14225	?[c]	17	216	95	328	0.440	0.927
13 (H)	11123	Yes	21	186	87	294	0.468	0.899
14 (H)	4920	Yes	21	235	154	410	0.655	0.918
16 (H)	15201	?[c]	5	328	272	605	0.829	0.985
17 (L)	15199	Yes	43	202	60	305	0.297	0.824
18 (H)	4918	No	39	211	57	307	0.270	0.844
19 (M)	15200	Lost[d]	31	248	139	418	0.560	0.889
20 (M)	8317	Yes	28	84	37	149	0.440	0.750
21 (H)	15197	Lost[d]	23	276	179	478	0.649	0.923
22 (H)	15193	Yes	29	241	129	399	0.535	0.893
23 (M)	11125	Yes	4	293	265	562	0.904	0.987
24 (M)	3599	Yes	4	252	199	455	0.790	0.984
25 (L)	15194	Yes	22	300	244	566	0.813	0.932
26 (L)	3598	Yes	10	342	282	634	0.825	0.972
27 (L)	4922	No	5	214	180	399	0.841	0.977
28 (H)	11131	Yes	7	239	211	457	0.883	0.972
		13/20[e]	645	4990	2768	8403	0.555	0.886
		7.7 %	59.4 %	32.9 %				

[a] Number refer to Figure 2; H, M and L refer to high, medium and low density strata, respectively.

[b] The platform terminal transmitter (PTT) identification number: all PTT's are carried by female caribou.

[c] This satellite radio-collared female was not observed during the classification.

[d] The calf was assumed to be dead based on distended udder of the female.

[e] Out of 20 satellite radio-collared females that were observed, 13 gave birth or 65%.

Table 4. Composition counts during the rutting period for the Rivière George Caribou Herd, 1973 to 1993[a].

Date	n[b]	Males (≥1)	% Males	Females (≥1)	% Females	Calves	% Calves	Total	Calf/ fem	Male/ fem	Fem/ adult
10-23/10/73			29.8		45.1		25.1	2 092	0.557	0.661	0.602
4-5/1074			29.1		48.4		22.5	1 593	0.465	0.601	0.625
4-19/10/75			27.9		47.8		24.3	24 060	0.508	0.584	0.631
20-31/10/76			24.0		50.9		25.1	7 619	0.493	0.472	0.680
12-22/10/77			23.8		48.8		27.3	2 900	0.559	0.488	0.672
1-8/10/78			36.9		42.6		20.4	27 769	0.479	0.866	0.536
21-24/10/79			31.3		46.6		22.1	13 938	0.474	0.672	0.598
23-25/10/80			30.7		44.8		24.5	9 079	0.547	0.685	0.593
19-20/10/81			29.9		44.6		25.5	6 338	0.572	0.670	0.599
19-25/10/82			29.5		45.8		24.8	4 050	0.541	0.644	0.608
24-26/10/83			35.0		43.0		22.1	7 034	0.514	0.814	0.551
22-24/10/84			28.8		51.6		19.6	5 527	0.380	0.558	0.641
21-29/10/85	12	2 453	29.2	4 275	51.0	1 660	19.8	8 388	0.388	0.574	0.635
30/10-10/11/86	14	1 735	28.7	3 070	50.8	1 244	20.6	6 049	0.405	0.565	0.639
31/10-5/11/87	10	710	24.4	1 570	54.1	624	21.5	2 904	0.397	0.452	0.689
10/88	11	1 904	28.2	3 687	54.6	1 160	17.2	6 751	0.315	0.516	0.660
23/10-2/11/89	14	885	31.8	1 403	50.4	493	17.7	2 781	0.351	0.631	0.613
13-21/10/90	14	1 408	30.0	2 603	55.4	686	14.6	4 697	0.264	0.541	0.649
22-25/10/91	18	2 225	23.7	5 446	58.1	1 698	18.1	9 369	0.312	0.409	0.710
26/10-1/11/92	14	1 184	19.9	3 835	64.4	940	15.8	5 959	0.245	0.309	0.764
21/10-2/11/93	19	1 470	25.7	2 985	52.2	1 267	22.1	5 722	0.4245	0.4925	0.670
Mean 73-93			28.5		50.0		21.5		0.438	0.581	0.636
Mean 73-83			29.8		46.2		24.0		0.519	0.651	0.609
Mean 84-93			27.0		54.3		18.7		0.348	0.505	0.667

[a] Counts from Messier *et al.* (1988): 1973 to 1984, or made by: S. Luttich, LWD: 1985, 1991 and 1992; D. Vandal, MLCP and S. Luttich: 1986; D. Vandal: 1987; D. Le Hénaff, MLCP and S. Luttich: 1988; S. Couturier, MLCP: 1989, 1990 and 1993.

[b] Between 1988 and 1990, sampling sites were selected from VHF radio-collars locations. Since 1991, they are selected from satellite radio-collar locations.

data. As the outlying areas of the calving grounds were included in the June 1993 census and that more adult and yearling males are normally found in these areas, we expected the female/adult ratio to be lower than in previous censuses. The female/adult ratio was 0.86 on average on the calving grounds in the RGCH censuses done from 1984 to 1988 (Crête *et al.,* 1991). The photocensus of the RAFCH in 1991 is the only available data with a similar sampling design. Female/adult ratio was 0.77 and 0.41 for the high (calving grounds) and low (outlying areas) density strata respectively (Couturier, S., unpubl. data).

Another estimating tool was found for the female cohort. Having considered that the calf count on aerial photographs is accurate and that the June 1993 calf/female ratio is reliable, we used the inverse of this ratio (female/calf=1.8027) to estimate the abundance of females in June 1993. This resulted in a decreased precision because of the larger confidence interval for this ratio. This method relies on estimating the number of calves present on the slides and extrapolating for the number of females from the female/calf ratio in the photocensus area. A total of 244 674 ±23.86% calves was estimated in June. By multiplying the female/calf ratio to this number, we obtain an estimate of 441 086 ±31.29% adult females present in June 1993. Using the summer survival rate, we obtained the intermediate result of 391 185 ±32.06% female caribou in October 1993. According to the male/female ratio, the adult population was 583 829 ±33.79%. From the calf/female ratio, we estimated 166 041 ±32.63% calves. The total RGCH population estimate was 749 869 ±33.15% caribou in October 1993 (Calf's method, Table 5).

Discussion

Composition counts in June and October 1993

In spite of a seemingly acceptable sample size (n=22 sample units for 8403 classified caribou), some pro-

Table 5. Herd size calculation for the June 1993 photocensus of the Rivière George Caribou Herd, based on the number of calves (Calfs method) and on the number of adults (Adult's method) followed by the combination of each result with the Post-calving photocensus estimate.

	Estimate	Confidence interval ($\alpha = 0.10$)
• Calfs method (From the number of calves in June)		
Number of calves in the June photocensus	244 674	± 23.86%
Female/calf ratio in June 1993	1.8027	± 20.03%
Number of females in June 1993	441 086	± 31.29%
Summer survival rate of females	0.8869	± 6.98%
Number of surviving females in Oct. 1993	391 185	± 32.06%
Male/female ratio in October 1993	0.4925	± 31.75%
Number of adults in October 1993	583 829	± 33.79%
Calf/female ratio in October 1993	0.4245	± 5.99%
Number of calves in October 1993	166 041	± 32.63%
Total herd size (including calves)	749 869	± 33.15%
• Adult's method (From the number of adults in June)		
Number of adults in the June photocensus	652 003	± 19.45%
Female/adult ratio in June 1993	0.8855	± 3.98%
Number of females in June 1993	577 373	± 19.86%
Summer survival rate of females	0.8869	± 6.98%
Number of surviving females in Oct. 1993	512 054	± 21.05%
Male/female ratio in October 1993	0.4925	± 31.75%
Number of adults in October 1993	764 221	± 23.55%
Calf/female ratio in October 1993	0.4245	± 5.99%
Number of calves in October 1993	217 344	± 21.90%
Total herd size (including calves)	981 565	± 22.64%
• Combined estimates including calves		
Calfs method and Post-calving census[1]	775 891	± 13.40%
Adult's method and Post-calving census[1]	823 375	± 12.36%

[1] Computed from Russell *et al.* (1996).

blems possibly affected the June composition count. Since we not only surveyed the calving grounds but also the outlying areas where many adult and yearling males were normally found, the June 1993 female/adult ratio seems too high. We thereby expected to find a female proportion closer to 0.75 in June considering that many males were not on the photocensus area. Such a proportion would have brought the fall population to 647 000 adults or 831 000 caribou including calves. Due to the different sampling plan used in past censuses, very few comparison data are available to determine the relative abundance of females on our sampling area. An unusually high female proportion in our June 1993 composition count can be due to several reasons. Certain areas were not surveyed as thoroughly as others, namely the southern and eastern portion. Also, two satellite collars carried by adult males were located within the high density stratum of the sampling area and were unfortunately not included in the composition survey. Including these collars to the sampled groups would have decreased the female proportion, bringing the population estimate down.

In October 1993, care was taken to cover the entire rutting distribution of the RGCH (400 000 km^2) and all satellite radio-collars were visited. This effort permitted to determine the male/female ratio at 0.49, which is very similar to the 1984-1993 average. The extrapolation for the total number of caribou in the fall largely relies on the two ratios found during the October 1993 composition count.

Proposed improvements to calving grounds photocensus

Some improvements of the 1993 method could be beneficial to subsequent census efforts. To carry out a better coverage of the herd and to decrease the confidence interval, a minimum of 200 sample units should be obtained during the aerial photography of the sampling area. Also, a minimum of 30 sample units should be inspected during the June and October composition counts. Although large scale movements were not observed during the June 1993 census, this eventuality remains, both within the density strata and in outlying areas. Such movements could invalidate the stratification process and the final estimate. We recommend to eliminate the visual survey and encourage the use of radio-telemetry to determine the density strata. This would shorten the census by 5 days, an important economy of time that eliminates problems associated with caribou movements. This proposed change would require having at least 125 active radio-collars in the herd, of which a third would be satellite radio-collars. Moreover, the telemetry survey is not really weather-dependent while the visual survey is often delayed by flying conditions.

We recommend to use only two density strata. A third stratum in June 1993 was found useless probably due to caribou movements between stratification and photography. The surface area represented by each stratum decreases as the number of strata rises, which in turn, increases the chance that caribou movements, even on a small scale, scramble the initial stratification. Two density strata were successfully used in the 1991 census of the RAFCH (Couturier, S., unpubl. data).

We suggest to give more importance to the calf/female ratio in subsequent censuses. During calving, we believe that it is easier to correctly find an unbiased estimate for the female/calf ratio than for the adult sex ratio. Segregation of sexes among adults is greater at this time and a low sampling effort could result in a biased female/adult ratio, which may have occurred in June 1993. Unfortunately, the confidence interval of the female/calf ratio is larger and suggests that the sample size should be increased to reach a better precision. Since it is possible to find two estimates for female abundance in June: one from the female/adult ratio and the other from the female/calf ratio, we could attempt to combine both estimators. This would hopefully result in smaller variance than their respective variances but care should be taken to correctly evaluate the covariance between both female abundance estimators.

Comparison with an independent census

A second independent photocensus was done on the RGCH in July 1993 by Russell *et al.* (1996). Their results can be compared to those found in our study. The results in the post-calving census are twofold. First, all photographed caribou belonging to selected aggregations are counted. The selection of the counted groups with the use of the telemetry data prevents the possibility of recounting the same caribou twice and provides a minimum count for the caribou population. However, the minimum count is not the total population size since many caribou groups are not tallied (not located during telemetry, not seen during the survey or not fully aggregated). Second, while photographing the caribou aggregations, a telemetry survey was carried out to identify radio-collared caribou. Thereby, the July 1993 census estimated the RGCH size by extrapolating for missing radio-collars from the photographed aggregations.

Russell *et al.* (1996) shown that the minimum adult population size of the RGCH was 358 460 in July 1993. These caribou were associated with 72 of the total of 92 radio-collars considered active in July 1993. Using the Petersen index method (White & Garrot, 1990), Russell *et al.* (1996) estimated the RGCH size at 540 040 ±12.8% (C.I. at α=0.10) adult caribou in July 1993. By attempting to take into account groups less aggregated (with one radio-collar only, poor aggregation conditions), those missed but with a radio-collar and those without radio-collars, we performed a new analysis with the data set collected by Russell *et al.* (1996). A detailed description of the statistical methods is given in Rivest *et al.* (1994). This proposed method relies on a stochastic model to correct small biases caused by missed groups and those that are less aggregated. Rivest *et al.* (1994) calculated a similar estimate for the adult population of 608 384 ±14.35% caribou. The fall herd size including calves became 781 408 ±14.65%. This result, and its confidence interval, was combined to our fall estimates (Table 5). The combined estimates were 775 891 ±13.40% and 823 375 ±12.36% for our two calculation methods, respectively. Both combined results with past censuses of the RGCH are shown in Fig. 3.

RGCH management implications

Survival and productivity monitoring could be more sensitive to detect demographic trends of the RGCH than comparison of successive population estimates derived from aerial censuses. Between 1976 and 1988, the low precision of aerial censuses impeded detecting minor changes in population size. However, the results of the 1993 aerial censuses show that it will now be possible to reach confidence intervals of 20% at a=0.10. This precision raises the question of the optimum interval length between successive censuses. Between 1980 and 1988, a 2-year interval has been used in surveying the RGCH. This has been lengthened to 5 years since 1988. Caribou managers of the Northwest Territories (Williams, M., pers. comm.) and elsewhere in North

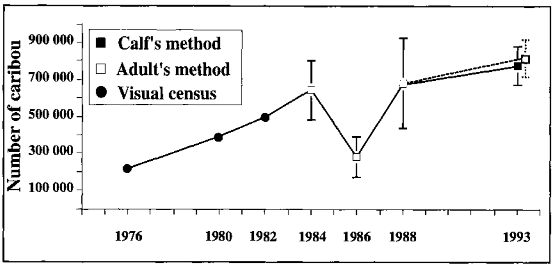

Fig. 3. Fall herd size estimates (including calves) for the Rivière George Caribou Herd, 1976 to 1993 (confidence interval at $\alpha = 0.10$ are shown, both combined estimates are presented for 1993).

America have been surveying large migratory herds at 2 to 4 year intervals. On one hand, it may be useless to shorten the 5-year interval if the annual rate of change of the population is small (≤ 5%). On the other, it may be inappropriate at this time to lengthen the interval because all observers agree that the RGCH is now at a very critical demographic state where a major decline is likely to occur.

If we could predict the rate of change in the size of the RGCH, it would be possible to determine the optimum census interval with the method described by Gerrodette (1987) and used recently in the software TRENDS (Gerrodette, 1993). To stay on the safe side, we suggest that the worst possible scenario for the RGCH is a major decline with a rate of change of 15% per year. In such circumstances and with 20% confidence interval of the estimates, TRENDS shows that the optimum census interval for the RGCH should be 4 years. For a rate of change of 10% annually, the analysis shows that a 5-year interval could detect significant changes within the population. The cost of a mistake would be much higher if a decline goes undetected longer than necessary instead of a reduced census efficiency. We suggest that the 5-year interval between successive censuses should be kept for the RGCH.

Between the censuses, an equal attention should be paid annually to autumn calf/female ratio and to the adult female survival rates because they both contributed significantly to the recent change in the demographic trend of the RGCH (Crête *et al.*, 1994). Both satellite and VHF radio-telemetry of the RGCH will continue to be necessary for estimating survival, and for regular management of the herd: harvest development, determining the habitat use, particularly on the calving grounds; deriving a sampling tool for the determination of the population ratios; etc. Crête and Huot (1993) recommended that radio-telemetry will also be necessary for monitoring the movements of the RGCH near training areas of military aircrafts in Northeastern Québec and Labrador. The energetic and survival consequences of low-level flying on caribou are not known for the RGCH and may represent a threat to the herd, particularly for the calving females. Luick *et al.* (1996) and Kitchens *et al.* (1996) have suggested that increased exposure to low-level flying may increase the energy expenditure while decreasing the probability of pregnancy. The monitoring of caribou movements by radio-telemetry will also continue to be useful in the area of hydro-electrical reservoirs (Doucet *et al.*, 1992).

Although the 1993 census slightly differed from previous ones and according to the differences between the density strata, we consider that the high density stratum closely represents the traditional calving grounds of the RGCH. The high density strata in the 1993 census covered 14 255 km^2, which is lower than the 22 857 km^2 calving grounds area observed in 1988 (Crête *et al.*, 1989) and the 20 250 km^2 area observed in June 1987 (Vandal & Couturier, 1988). No complete calving grounds delimitation has been done for the RGCH between 1989 and 1992. The June 1993 high density stratum should be designated as the calving grounds of the RGCH and be protected under the Québec Wildlife Habitats Act.

Demographic trends and regulation factors

Results of the June 1993 RGCH photocensus and their comparison to a second independent census suggest that the RGCH still remains the largest caribou herd in the world (Williams & Heard, 1986). Although many observers of the RGCH have mentioned that this herd can not increase anymore, it remains important to study the factors that have made 1993 a good year for the herd. The 73% increase in the calf/female ratio in the fall (Table 4) is a good indicator that the herd is in better condition and that a population decline will not occur in the short-term. From scientific monitoring of the commercial harvest in Labrador, physical condition of the caribou, especially fat reserves, were better in April 1993 than in previous years (Luttich, S.N., unpubl. data). Birth weights of both sexes combined increased from 5.08 kg (standard error =0.10, n=49) in 1992 to 6.85 kg (s.e.=0.17, n=45) in June 1993 (Couturier, S., and Luttich, S.N., unpubl. data). Large-scale mortality of newborn calves (49 calf carcasses observed), unrelated to predation, have been fortuitously observed in June 1992 during 8 hours of helicopter flights under poor visibility conditions. By excluding 2 cases of predation, no other calf mortality was found in June 1993 during extensive low-level flights under very good visibility conditions.

Earlier mentions on the deterioration of the general condition of the RGCH were made by

Couturier *et al.*, (1988a, 1988b). During the following years, other observers (Messier *et al.*, 1988; Couturier *et al.*, 1989 and 1990; Huot, 1989; Hearn *et al.*, 1990) have confirmed that many demographic indicators gave insight as to the stabilization or the decrease of the herd's size. Some intrinsic mechanisms have been identified, namely by Messier *et al.* (1988), Hearn *et al.* (1990), Crête *et al.* (1990a), and Crête & Huot (1993). Knowledge and interest on the RGCH-habitat relationship (Huot, 1989; Crête *et al.*, 1990b; Crête *et al.*, 1993; Manseau *et al.*, 1996; Morneau & Payette, 1996) and on the climate's effect on the herd (Crête & Payette, 1990; Maarouf *et al.*, 1994) has increased. The deterioration of the summer habitat has been identified as a key factor in this herd's regulation. Predation by wolves could become an important element in the demography of the RGCH (Heard & Williams, 1992; Heard, 1994) and deserves closer attention in the future management of the herd.

Since the beginning of the 1990's, most observers expected to see a decrease in the herd size without being able to predict when this would begin nor how fast it would proceed. The size of the RGCH observed in 1993 by two independent censuses coincides with a stabilization of certain demographic parameters. We hypothesize that the better condition of the RGCH observed in 1993 can be attributed to the considerable change in the migratory behavior of the adult females of the herd. Most females of the RGCH spent their 1992-1993 and 1993-1994 winters near the Labrador Sea coast. This change in the migratory pattern probably accounted for an economy in their energy budget so that they showed a better physical condition in spring 1993. Low snow cover, a suitable habitat and especially a lower energy expenditure related to a shortened migratory route between the wintering grounds and the calving grounds (based on satellite tracking, Couturier, S. & J. Doucet, unpubl. data) might explain for the better condition in 1992-1993 by comparison to previous years. It will be important to obtain data on physical condition of the females, their pregnancy rate and the birth weight of calves in spring 1994 and later. If our hypothesis is valid, the October 1994 calf/female ratio will again be relatively high due to the repeated use of the eastern wintering grounds used by many females in 1993-1994. Although the use of the Labrador coast seems to be an interesting solution for the females of the herd, we do not believe that this will solve the problems to which the RGCH is faced because of the limited availability of habitat in this region.

Demographic indicators must be monitored very closely in the upcoming years to rapidly adjust the way in which we carry out the analysis of the herd's general condition. New findings will have to be rapidly communicated to the users of the RGCH. Although little chances exist, an increase in the herd's size could be dangerous to the relatively poor summer habitat that remains an important problem. At best, managers and observers should hope that the RGCH stabilizes at its actual level or somewhat lower due to a substantial increase in the annual harvest. In 1992-1993, Québec sport hunters and Natives harvested 12 454 and 4657 caribou, respectively. In the same year, 14 932 caribou were taken in Labrador. If we inflate the above kill figures by 20% for the unreported crippling loss (Miller, 1983; Davis *et al.*, 1980), the total RGCH harvest reached about 38 000 caribou, an amount unprecedented in the monitoring of this herd. The combined 1993 census results confirm that the RGCH is still underharvested and that a harvest increase is still the best strategy in trying to decrease the pressure on the habitat. However, as Couturier *et al.* (1990) have stated, a flexible harvest strategy must be implemented to allow yearly reevaluation of the quotas if the RGCH begins to decline rapidly.

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Stability of Hematological Parameters in Woodland Caribou (*Rangifer tarandus caribou*) Blood Stored at 4°C

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Abstract: Eighteen free-ranging female woodland caribou were captured in northern Alberta in January and February 1993. Blood was collected into ethylenediaminetetraacetate (EDTA) tubes which were packaged in coolers containing ice packs, and transported to the laboratory where they arrived within 48 hrs of collection. Complete blood counts (CBC) were performed on five consecutive days to assess the stability of hematological parameters. Average values of hematocrit (HCT), mean cell hemoglobin (MCH), mean cell volume (MCV), red cell distribution width (PDW), white blood cell count (WBC), and red blood cell count (RBC) remained stable with no statistically significant changes occurring during 5 days of post-collection storage at 4°C. Mean RBC values exhibited significant differences ($p<0.05$) between geographic locations. Mean platelet volume (MPV) increased significantly ($p<0.001$) with storage time, while platelet (PLT) values decreased ($p<0.001$) over time and were significantly different ($p<0.01$) between locations. For optimal hematological results, it is recommended that sample analysis be performed within 24 hours of blood collection; however, if caribou blood samples are properly stored at 4°C, useful information may be obtained from stable parameters up to 5 days following collection.

Key words: hematology, wildlife, temperature, changes, time

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Introduction

Hematological analysis, in conjunction with other screening procedures, provides valuable information when assessing animal health (Jain, 1986). For complete blood counts, it is generally agreed that blood constituents in EDTA remain stable for 24 hours at 4°C (Brittin *et al.,* 1969; Cohle *et al.,* 1981; Lampasso, 1968). However, when blood samples are collected from wild animals living in remote areas, transportation time to analytical laboratories may exceed 24 hours.

Because hematological values are often used for screening purposes, it is critical to determine their stability over time, under field conditions. Although the majority of hematological constituents in human blood remain stable for up to 5 days following collection (Cohle *et al.,* 1981), using these guidelines for wildlife blood could be misleading. The objective of this study was to determine the stability of hematological parameters in woodland caribou blood stored at 4°C.

Materials and method

Study area, blood collection and transportation

A total of eighteen female woodland caribou were captured by aerial net gun technique (Barret et al., 1982) during January and February of 1993 in the following two northern Alberta areas: between 55°30'N and 56°15'N, and 111°15'W and 112°35'W (referred to as location 1); and between 55°10'N and 55°40'N, and 112°42'W and 113°30'W (referred to as location 2). The animals were physically restrained without the use of an anaesthetic. Blood was collected from the superficial digital veins directly into 7-mL tripotassium EDTA Vacutainer tubes (0.081 mL of a 15% solution of tripotassium EDTA, Becton Dickinson & Co., Rutherford, NJ, USA) using 18-gauge needles (Becton Dickinson & Co., Rutherford, NJ, USA) After collection, blood tubes were wrapped in paper towels (to insulate from freezing), packed in a styrofoam cooler containing ice packs, and transported by courier to the Animal Pathology

Laboratory at the Alberta Environmental Centre. The blood samples were received and analyzed within 24 to 48 hours of collection.

Hematological analysis

Prior to analysis, all samples were mixed at room temperature (22°C) for 10 to 15 minutes on a rocker (AMES Aliquot Mixer. Ames Division, Miles Laboratories Inc., Elkhart, IN, USA) which tilts back and forth at 18 cycles per minute. Hematological determinations including white blood cell count (WBC), red blood cell count (RBC), hemoglobin (HGB), hematocrit (HCT), mean cell hemoglobin (MCH), mean cell volume (MCV), mean cell hemoglobin concentration (MCHC), platelets (PLT), red cell distribution width (RDW), and mean platelet volume (MPV) were performed on a Coulter Counter S-Plus IV (Coulter Electronics, Inc. Hialeah, FL, USA) within 24 hours of collection (day 1). The samples were kept refrigerated at 4°C, and were reanalyzed every 24 hours for four consecutive days (days 2 to 5). All samples were analyzed in duplicate.

Statistical analysis

Least square mean estimates of location, time, and location-by-time were obtained by fitting blood data using a repeated measures analysis of variance model coded in SAS version 6.08 software (SAS Institute Inc., Cary, NC, USA). Time (days=1, 2, 3, 4 and 5) was the repeated factor in the model. "Animals within locations" was used as the error term to calculate F-values to test for location effect. The overall mean square error was used for testing time and location-by-time effects.

Results

The average values for WBC, HCT, MCH, MCV and RDW did not change significantly ($p<0.05$) with storage time or between collection locations 1 and 2 (Table 1). The values for MPV did not differ between the two locations, but increased signifi-

Table 1. Mean ± standard error of hematology parameters of female woodland caribou from two locations in northern Alberta, on day 1 through day 5 of blood storage at 4°C. (Values having no mean differences between locations).

Parameter	Storage time (days) following collection					Combined Means (day 1 through 5)
	1	2	3	4	5	
n	13	18	18	18	18	
HCT	0.57±0.002 Range 0.52-0.63	0.57±0.002	0.58±0.002	0.58±0.002	0.58±0.002	0.58±0.001
HGB g/L	202.8±0.44 Range 183-219	203.5±0.36	204.3±0.36	204.4±0.36	204.7*±0.36	204.0±0.20
MCH pg	16.65±0.081 Range 15-18	16.64±0.067	16.80±0.067	16.70±0.067	16.80±0.067	16.67±0.037
MCV fL	47.47±0.103 Range 43-52	47.40±0.085	47.55±0.085	47.49±0.085	47.66±0.085	47.51±0.025
MPV fL	6.34±0.115 Range 43-52	7.16*±0.095	7.36*±0.095	7.53*±0.095	7.65*±0.100	7.31±0.053
RDW	9.50±0.435 Range 7.5-18.7	8.74±0.338	9.23±0.338	9.95±0.338	9.18±0.338	9.34±0.187
WBC 10^9/L	5.32±0.049 Range 2.8-7.2	5.35±0.040	5.39±0.040	5.34±0.040	5.41±0.040	5.36±0.022

Values with a superscript * are significantly different ($p<0.05$) from the mean on day 1. Hematological determinations on day 1 were performed within 24 hours of blood collection.

candy ($p<0.001$) with storage time. Values for HGB on day 5 showed a small but statistically significant change ($p<0.001$). The RBC values showed differences between locations ($p<0.05$), but did not change with storage (Table 2). The PLT values differed between locations ($p<0.01$), and with storage time ($p<0.001$). Platelet values from location 1 decreased 26% between day 1 and day 5; those in location 2 decreased 11%. The values of MCHC on days 3 and 4 were significantly greater than on day 1 ($p<0.05$) for location 1. However, values on day 2 through day 5 were not different from day 1 for location 2.

Discussion and conclusion

This study found that HCT, RBC, WBC, MCV, MCH and RDW values remain stable in female woodland caribou blood stored ar 4°C, for 5 days following collection; hemoglobin values remain stable for 4 days. Platelet numbers decreased and platelet size increased, suggesting that platelet aggregation occurred with storage. Cohle *et al.* (1981) found that platelet numbers in blood from healthy human donors were stable for 5 days following collection. The differences in RBC and PLT values between locations suggest that there may be a location effect for some hematological parameters.

Results from this study indicate that caribou blood samples, when handled under our specified conditions of collection and storage, provide useful information for most hematological parameters up to 5 days following blood collection.

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Table 2. Mean ± standard error of hematology parameters of female woodland caribou from two locations in northern Alberta, on days 1 through 5 of blood storage at 4°C. (Values having mean differences between locations)

Parameter	Location	n	Storage Time (days) following collection					Combined Means (day 1 through 5)
			1	2	3	4	5	
PLT 10^9/L	1	6	214.4±10.37 Range 132-269	154.1*±8.71	147.1*±8.71	162.0*±8.71	157.3*±9.45	167.0±15.89
	2	7	253.9±9.65 Range 197-317	239.6±7.79	211.6*±7.79	221.5*±7.79	225.9±7.79	230.5±14.08
RBC 10^{12}/L	1	6	11.67±0.065 Range 11.05-12.41	11.65±0.055	11.68±0.055	11.71±0.055	11.75±0.055	11.69±0.214
	2	7	12.48±0.061 Range 11.60-13.09	12.51±0.049	12.63±0.049	12.59±0.049	12.60±0.049	12.56±0.192
MCHC g/L	1	6	352.1±1.72 Range 344-357	353.4±1.44	357.5*±1.44	358.1*±1.44	352.9±1.44	354.8±1.40
	2	7	350.1±1.60 Range 346-359	351.0±1.29	351.0±1.29	347.5±1.29	350.5±1.29	350.1±1.26

Values with a superscript * are significantly different ($p<0.05$) from the mean on day 1. Hematological determinations on day 1 were performed within 24 hours of blood collection.

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Population growth and status of the Nushagak Peninsula caribou herd in southwest Alaska following reintroduction, 1988 - 1993

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Abstract: Caribou were reintroduced to the Nushagak Peninsula, Alaska in February 1988, after an absence of over 100 years. The purpose was to reestablish caribou in the area and once again provide hunting to local residents. The Nushagak Peninsula caribou herd (NPCH) has grown rapidly from 146 reintroduced caribou to over 1 000 in 6 years at an exponential rate of increase of $r = 0.317$ or about 38%. The dramatic growth of the herd was attributed to the initial high percentage of females in the herd, high calf production and survival, pristine range, few predators and no hunting. Abundant high quality forage on the Nushagak Peninsula is the probable reason for the enhanced body condition and high natality even among 2-year-olds, and it has most likely contributed to the high calf survival and recruitment. Lack of predators and hunting has allowed calf and adult mortality to remain low. Although the size of the NPCH has grown steadily over the past 6 years, no significant dispersal from the peninsula has occurred. The population density of the NPCH was estimated to be 1.0/km^2 in 1993. We believe the herd will continue to grow, and could reach a density of 2.3/km^2 by 1998, even with a 10% harvest beginning in 1995. While the current growth of the NPCH makes the reintroduction a success, the increasing density, lack of dispersal and potential for over-grazing, presents managers with hard decisions.

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Introduction

Historically, a large caribou population roamed the coast ofi the Bering Sea from Bristol Bay to Norton Sound. Archaeological excavations near the village of Togiak in 1960 suggested that caribou were important to the native population (Kowta, 1963). Presumably, caribou once concentrated in the mountains up river from Togiak Bay and in the rocky headland towards Cape Newenham. Large caribou herds were also observed "roaming over the mountains of the Nushagak Peninsula" (Petrov, 1900). Petrov (1884) noted that caribou were virtually absent from the lower Yukon-Kuskokwim River area by 1880. While still numerous in the upper Kuskokwim drainage (Capps, 1929), caribou were absent in the Togiak and Goodnews drainages as early as 1900. Alaska Game Commission (1925-1935) noted only small scattered herds in the Kilbuck Mountains by the mid 1930s. Caribou disappeared during a period of human population growth, including an influx of caucasians and intense commercial trade.

Reindeer were introduced into the Bristol Bay area in the early 1900's to provide the native community an economic base and a reliable source of red meat. Herds flourished from Togiak to the Nushagak River, north to the Seward Peninsula. The Togiak and Kulukuk River drainages had several active herders and the Nushagak Peninsula was reportedly an important grazing area. By the 1930s, the reindeer industry faltered and by the 1940s, reindeer were gone from the area.

The concept of reintroducing caribou to the Togiak area was first addressed in "Alaska Wildlife Management Plans, Southwestern Alaska" (Alaska Department of Fish and Game, 1976). The Togiak National Wildlife Refuge was established in 1980 by the Alaska National Interest Lands Conservation Act. One of its purposes was to allow restoration of populations to their historic levels. The nearest caribou herds to the Togiak Refuge are the Mulchatna caribou herd (MCH), Kilbuck caribou herd (KCH), and the North Alaska Peninsula herd (NAPH). Hunting pressure, natural barriers, and human settlements appeared sufficient to prevent any of these herds from expanding onto the Togiak Refuge in the near future.

Caribou were reintroduced to the Nushagak Peninsula in February 1988 under a cooperative

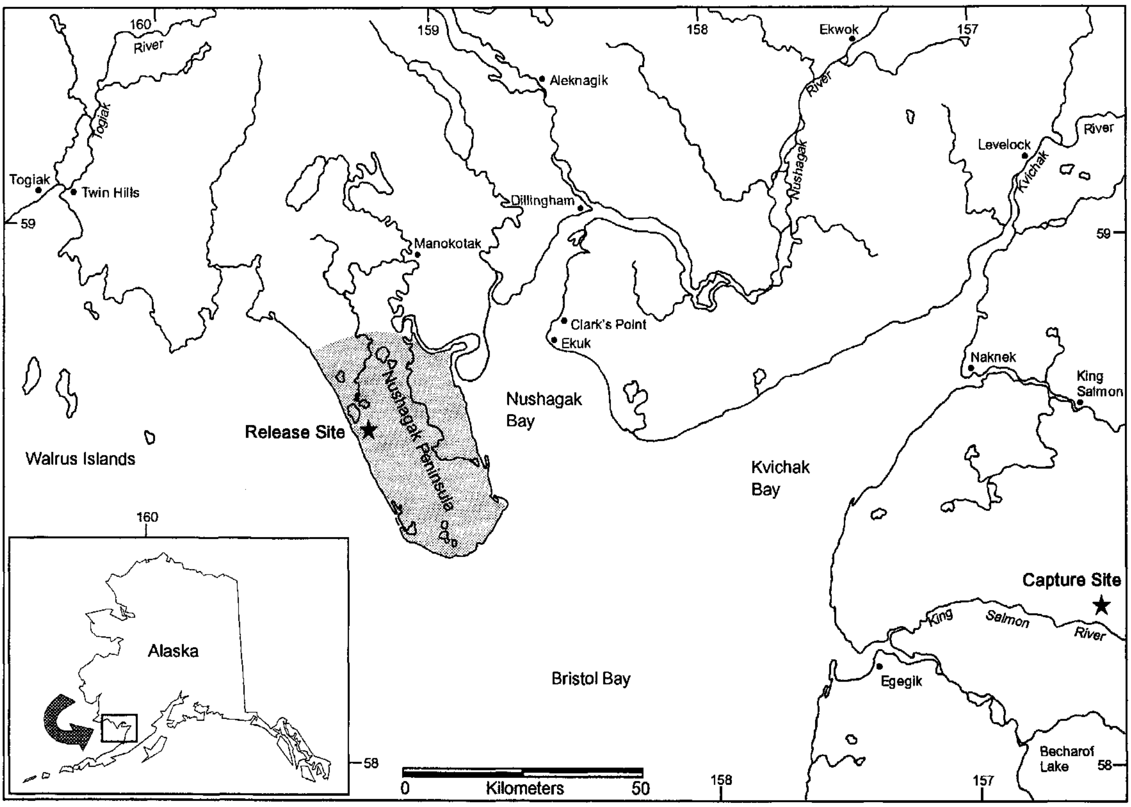

Fig. 1. Location of capture and release sites, and distribution(shaded area) for the reintroduced Nushagak Peninsula caribou herd, February 1988, southwest Alaska.

agreement between the U.S. Fish and Wildlife Service (USFWS), Alaska Department of Fish and Game (ADFG), and the residents of Togiak, Manokotak, Twin Hills and Dillingham. The reintroduction was intended to reestablish caribou in an area where local residents had been dependent on them for thousands of years. The principle goal was to establish a population large enough to sustain a subsistence hunt, while still allowing the herd to grow.

Methods

Reintroduction

Potential capture and release sites were evaluated to determine which would be most cost effective and would best support a caribou population during winter when forage is less available. Kikertalik Lake on the Nushagak Peninsula was chosen as the primary release site (Fig.1). The NAPH was selected as the donor population for this transplant because it was the closest herd and there was less chance the animals would return to their original range because of direct separation by Bristol Bay.

At Kikertalik Lake, we constructed a 10 m diameter, 2.5 m high corral of 1/2" plywood, supported by 2X4 braces. A smaller holding pen approximately 3 m diameter was constructed adjacent to the corral to hold caribou until they recovered from tranquilizer administered prior to or during transport.

The capture site was located 53 km SE of King Salmon, Alaska on a small unnamed lake 3 km north of the King Salmon River (Fig 1). Helicopter fuel, a four wheeler and sled, and 18 caribou transport crates were transported by Dehavilland Otter to the capture site. Twelve (3 sets of 4) individual holding pens 0.6 m X 1.2 m X 1.2 m with sliding doors at each end and numerous 2.5 cm diameter air holes were fabricated in Dillingham, disassembled and flown to the capture site where they were reassembled.

The capture effort began 4 February 1988 and was completed 16 February. Two USFWS Cessna 206 aircraft were used to transport field crews from King Salmon to the capture site daily. Field crews consisted of USFWS staff from Togiak and Becharof refuges, ADFG staff, and volunteers from the villages of Togiak and Manokotak. Selected students and teachers from Togiak, Manokotak, Naknek, Dillingham, and Egegik also participated in various stages of the project. A Hughes 500 helicopter with a skid-mounted net gun was used to capture caribou. The net gun was operated by the pilot and was capable of firing two 6 m X 6 m mesh nets a distance of approximately 10 m. Two capture teams of two biologists each sedated caribou after capture using either R51163 (an experimental drug supplied for testing by Wildlife Labs, Fort Collins, Colorado) or xylazine. Each animal was placed inside a canvas transport bag and a foam padded cloth hood was fitted over the head to protect the eyes. The neck was supported by a foam pad 7-10 cm to help keep the head upright during transport to the staging area. The canvas bag was then laced together and the sling rope was tied through the support loops at the end of the bag. A loop at the end of the rope was attached to the helicopter sling hook while it hovered over the caribou.

Transported caribou were lowered to the ground approximately 100 meters from the pens at the staging area to reduce disturbance to the animals already in the corral. They were loaded onto a sled pulled by 4-wheeler to the processing area where each was weighed, de-antlered, ear-tagged and fitted with a visual collar. Radio-collars were placed on 20 animals. Blood samples were taken to test for brucellosis, pack-cell volume and to add to the serum sample bank from the northern Alaska Peninsula herd. Each caribou was injected with 3 ml Ivermectin to reduce the possibility of the spread of parasites to new habitats. Temperature, heart rate, and respiration rate were monitored during the processing phase. After processing, caribou were either loaded individually in the holding pens, placed in transport crates or cargo nets and loaded onto the Otter for transport to the release area. Holding pens were generally used only for caribou held over-night before transporting them to the release site. Initially, either R51163 or xylazine was used to keep these animals sedated until transport. As the capture effort progressed however, all but the most active caribou were allowed to recover over-night from their initial sedation. Animals held over-night were sedated again prior to transport.

Caribou were transported in groups of 7-9 animals to the release site, a flight of 1.0 to 2.2 hours. Caribou were generally calm, although turbulence and engine noise caused them to struggle occasionally.

Weather conditions were generally poor at the release site during the operation. The snow drifted severely on the lake where the corral was constructed, and the lake surface inside the corral was very slippery. Efforts to increase traction (including covering the ice with straw and sawdust) were largely unsuccessful. Our intention was to hold transported caribou in the corral and release them in groups of 50 to facilitate group cohesion. However, because of the slippery surface and the danger of trampling, all but the first group were released outside the corral immediately after unloading.

Radio-collaring

In April 1992, an additional 23 caribou were captured on the Nushagak Peninsula and 16 more radio-collars were deployed. The purpose of the recollaring was to supplement the original 20 caribou radio-collars. We again used a Hughes 500D helicopter equipped with a skid-mounted net gun to pursue and capture female caribou. When the caribou became entangled in the net, we restrained them and immobilized them with 1.3-1.4 cc xylazine. We collected standard measurements and blood samples and bioelectrical impedance measurements were taken as an indicator of body condition (Gerhart *et al.*, in press).

Population Monitoring

Monthly flights to track radio-collared animals began February 1988. Weekly flights during the calving period were initiated in 1991. When possible, direct observations were made of each radio-collared caribou to determine if a calf was present. However, during post-calving aggregation this was not possible without major disturbance to calves. Monitoring radio-collared caribou allowed us to evaluate seasonal movements, distribution, dispersal, home range, calf production and survival, calving chronology, recruitment, and adult mortality.

A fall sex and age composition count was completed in October 1992 using a Bell 206 Jet Ranger helicopter. Groups of caribou were located first with the Cessna 185 fixed-wing aircraft which directed the helicopter to caribou to be classified.

Population estimates for 1988-1989 were based on the highest count obtained during a tracking flight. A population census was conducted during late winter each year since 1990 using a total-count technique. Transects were flown over the entire peninsula at intervals of 1.0-1.5 km depending on conditions. An attempt was made to census after fresh snow, during bright light conditions, and when winds were less than 25 kph.

Results and discussion

Reintroduction

Biologists captured 167 caribou from the NAPH between 4-17 February, 1988. Three were released at the capture site due to shipping delays and one escaped at the capture site. Mortality during the course of the project was 17 caribou (10.2%). Six died of injuries directly related to capture technique (broken necks and legs), 1 died from suffocation enroute to the holding pen, and 1 died in the holding pen. Of the 155 transported to the Nushagak Peninsula, 1 died enroute from suffocation, 6 died of capture myopathy at the release site, and 2, including 1 radio-collared animal, died within 24 hours of release. We successfully reintroduced 146 caribou to the Nushagak Peninsula. All were released at Kikertalik Lake except 1 group of 8 caribou which was released near Dillingham, approximately 40 km northeast of the release site, after poor weather conditions grounded the Otter in Dillingham.

Body measurements and condition

Nushagak Peninsula caribou captured in 1992 were larger and appeared to be in better condition than the caribou originally transplanted to the peninsula. The mean body weight of 2-yr-old caribou captured in 1992 was significantly ($P<0.05$; two-tailed *t*-test) heavier ($\bar{x}=100.5$ kg, n=5) than the 2-yr-olds captured in 1988 ($\bar{x}=87.7$ kg, n=18). Adult caribou (>4 yrs) captured in 1992 had somewhat greater mean mandible lengths (27.9 cm, n=5) than caribou captured in the parent NAPH (27.3 cm, n=17), however, these differences were not significant ($P>0.10$). Enhanced body condition is likely a direct result of the abundant high quality forage on the Nushagak Peninsula. It is also the probable reason for the preponderance of pregnant 2-yr-olds and contributing to the high calf survival we have seen in this herd.

Population size and growth

The NPCH has grown rapidly from 146 to over 1000 caribou in the 6 years since reintroduction (Fig. 2). The average growth was 38% (±7.3 s.d., n=6), or an exponential rate of increase $r = 0.317$. This growth rate exceeds the maximum theoretical potential of $r = 0.29$-0.30 or about 35% as described by Bergerud (1980), and Bergerud *et al.* (1983). Bergerud (1980) summarized that Alaska caribou herds without predators showed rapid growth approaching $r = 0.30$, while those with predators showed little or no growth. Davis *et al.*, (1991) however states that the growth of caribou herds seldom approach this level except in transplanted herds, and growth over 20% is uncommon even under optimum conditions. We attribute the impressive growth of the NPCH to the high percentage of females in the herd at reintroduction, in concert with high calf production and survival, pristine range conditions, few predators, and no hunting. When the current growth of the herd is modeled using average natality and mortality figures to reach the current population level, as expected,

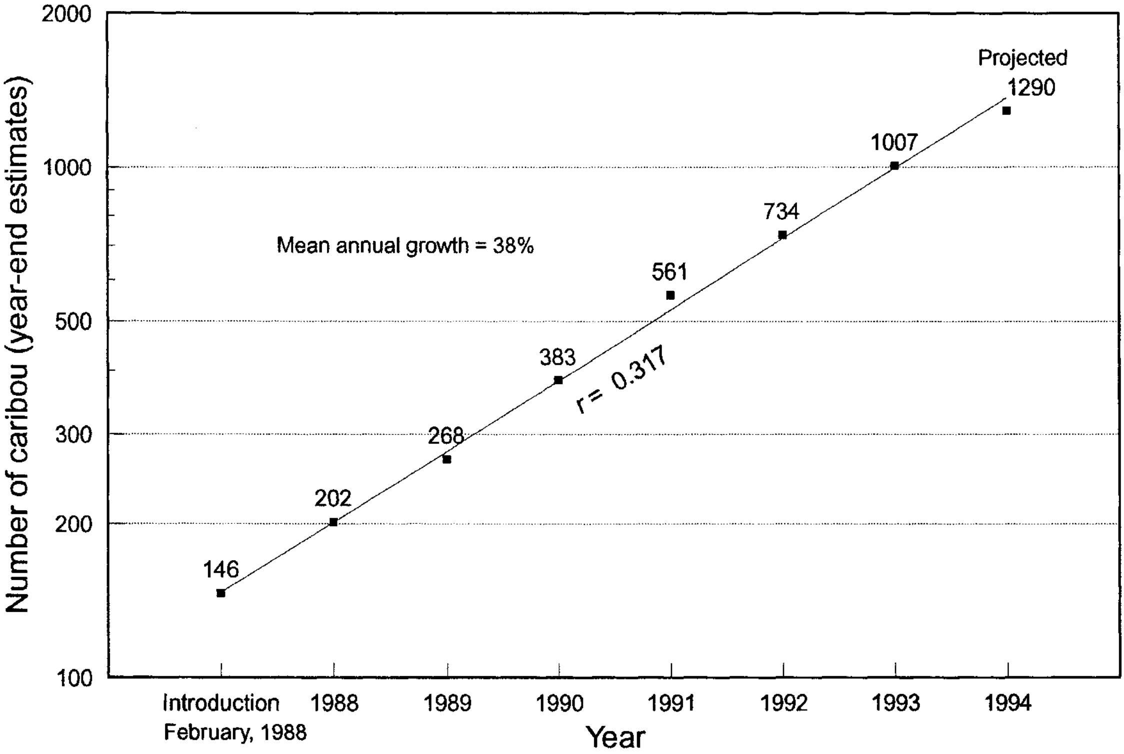

Fig. 2. Population growth of the Nushagak Peninsula caribou herd following reintroduction, southwest Alaska, 1988 - 1993.

the growth rate is highest at the time of reintroduction and steadily decreases.

The increase of the Nushagak herd is similar to that for reindeer when introduced into pristine range in the absence of other large herbivores and predators (Bergerud, 1980; Klein, 1987; Swanson and Barker, 1992). The average rate of increase on St. Matthew Island was possibly higher than 34% (Klein, 1968). Reintroduction of caribou in other areas of mainland Alaska has been less dramatic. Caribou transplanted to the Kenai Peninsula in 1965 and 1966 grew rapidly from 15 and 29 respectively to 335 in 1974 (Davis, 1978). An additional 80 caribou transplanted in 1985 and 1986, increased to 197 in 1990, 237 in 1991, and 272 in 1992; with annual rates of increase of 17% and 13% respectively (Spraker, 1992a; 1992b; 1993).

Sex and age composition

Sex and age composition at the time of reintroduction was skewed toward young females. Herd composition of the 146 caribou released and known to be alive at the end of the transplant operations was 111 adult females, 9 yearling females, 9 female calves, 6 adult males, 8 yearling males and 3 male calves. Estimated average age for the herd was around 5 years.

Herd composition changed dramatically in the first 4.5 years since reintroduction (Table 1). Although mortality rates in some Alaska herds have been found to be higher for males than females (Davis *et al.*, 1988, 1991), the percentage of males in the NPCH continued to grow.

The male component of the NPCH herd now exceeds those of most hunted Alaskan caribou herds which is generally less than 45 bulls:100 cows (Leib *et al.*, 1991; Van Daele, 1994) and even lower (27 bulls:100 cows) in herds with bull-only hunts (Davis *et al.*, 1990). Valkenburg *et al.* (1993) estimated a bull:cow ratio for the Western Arctic herd at 52 bulls:100 cows. Harvest of this herd is primarily by local subsistence users who usually do not select for bulls.

Calf production and survival

Natality estimates derived from radio-collared females were found to be similar to estimates from samples of the herd at large (Davis *et al.*, 1991). Natality rates for radio-collared females from the Nushagak herd ≥2-years-old have been high. In 1990, 1992 and 1993, all radio-collared females observed produced calves; 14 of 14, 27 of 27 and 28 of 28 respectively. No production data were collected in 1988, 1989 or 1991. Natality rates for most caribou are generally lower than the rates we observed, i.e. 82% average pregnancy rate for 8 herds and 86% parous females for 7 herds (Bergerud, 1980).

Caribou generally do not come into estrus until they are 28 months old (Skoog, 1968; Bergerud, 1971), and sometimes not until they are 41 months with poor nutrition (Bergerud, 1971). With good nutrition, caribou can conceive at 17 months (Bergerud, 1980). Davis *et al.* (1991) state caribou generally have to be at least 3 years old to be successful at producing and raising calves due to lower fat reserves, continued growth during their second winter, or immaturity which may effect mother-young bonding. All 5 females estimated to be 2-years-old from the NPCH radio-collared in April 1992 produced calves. Another 2-year-old which died during capture operations was also pregnant. Nutrition and body condition seems to be the most important factors affecting the natality rate of 2-year-olds. This agrees with Valkenburg (1991) who states "A small (relative to food supply) caribou herd within suitable habitat can be expected to be highly productive with most 24-month-old females producing calves."

Peak calving for radio-collared Nushagak caribou occurred in late May, similar to other caribou herds at similar latitudes in Alaska (Skoog, 1968; Hemming, 1971; Valkenburg *et al.*, 1991). Intensive monitoring of 27 radio-collared females in 1992 showed 4% had calved by May 17th, 32% by the 23rd, 66% by the 27th and 89% by June 4th. Eleven percent calved after June 4th. Results were similar

Table 1. Sex and age composition of the Nushagak Peninsula caribou herd, southwest Alaska.

Date	Bulls/[a] 100 cows	Calves/ 100 cows	% calves	% cows[b]	% bulls	Sample size	Estimated herd size
Feb, 1988[c]	12	10	8	82	10	146	146
Oct, 1992[d]	60	72	31	43	26	611	750

[a] Includes yearling males.

[b] Includes yearling females.

[c] Composition at time of reintroduction.

[d] Aerial estimate using a Bell 206 helicopter.

in 1993 for 28 radio-collared females; 6% calved by May 15th, 42% by the 23rd, 87% by the 27th and 100% by June 10th.

Calf survival and recruitment for the Nushagak herd has been high. Percent calves observed in fall 1990-1993 from radio-collared females averaged 64.3% (±9.8% s.d., n=4). If we use the ratio of 72 calves:100 cow estimated from a helicopter survey during fall 1992 composition count, the average would be even higher. Results are similar to the average ratio of 67 calves:100 cows when the herd is modeled to reach the current population level using observed mortality figures. Because all radio-collared females observed produced calves, these percentages represent actual calf (0-5 months) survival estimates. As with natality, fall calficow ratios for the Nushagak herd were higher than generally found in other caribou herds (Bergerud, 1980; Valkenburg *et al.*, 1991; 1993).

Studies of other caribou herds indicate that the greatest mortality occurs within the first few weeks of calving due primarily to predation (Skoog, 1968; Bergerud, 1971; 1980; Adams *et al.*, 1988; Leib *et al.*, 1991). Over-winter calf mortality can be high (Heard & Calef, 1986), however Bergerud (1971) found no evidence that calves died during winter at a higher rate than adults. Over-winter mortality of calves from the Delta herd was relatively low and no higher than cohorts ≥24 months (Davis *et al.*, 1988; 1991). Fall calficow ratios are often used by managers to evaluate population recruitment, and seems to provide a good index for the Nushagak herd.

Whitten (1991) suggested the survival rate of calves from 2-year-olds is lower then that of ≥3-year-olds. However, 4 of the 5 2-year-olds were still accompanied by calves in the fall.

Adult mortality

Annual mortality of radio-collared animals with known fates ranged from 0-6.7%, with a mean of 4.1% (n=6). Only 2 of 36 radio-collared caribou were bulls, and both died within the first 4 years. Bergerud (1980) estimates that adult mortality varies between 7-13% where predators are common, and 5-6% where they are not. Two of the 6 radio-collared caribou that died were males, the only 2 radio-collared bulls in the herd. One died within 24 hours of release and is not considered in the above estimate, and the other died when it locked antlers with another bull. One had a broken neck while the other probably died of starvation. The cause of death for the remaining 4 females is unknown. Ages of these animals were 3, 4, 6-7, and two 9 years-olds, suggesting no age-specific mortality. The extent of predation on the Nushagak Peninsula is unknown; however, we believe it is not a major factor. Brown bears are common on the peninsula and wolves are rare. The NPCH is currently closed to hunting, with only two caribou known to have been poached in March 1992, and possibly 1 in 1993.

Seasonal movements and distribution

Although the size of the NPCH has grown steadily over the past 6 years, no significant dispersal from its "core range" on the peninsula has occurred (Fig. 1). Of over 18 000 observations of caribou (1 486 radio-locations) during tracking flights and surveys, more than 99% were observed on the Nushagak Peninsula. The range of the herd on the peninsula as defined by a convex polygon that connected the outermost locations was 1 010 km^2. Two radio-collared females with several other individuals have been observed west of Kulukuk Bay and north of Twin Hills, an area of about 370 km^2. This movement began soon after reintroduction and has occurred primarily during the summer months, with the animals returning to the peninsula each time. Caribou observations have been plotted by month and season, with no detectable pattern of seasonal movements or distribution. Females were distributed throughout the peninsula during calving.

Caribou were observed in the upper Togiak River drainage in 1992 and 1993. These were probably members of the Kilbuck caribou herd which have been expanding southward onto the Refuge. However, no Kilbuck or Nushagak radio-collars were heard. Caribou observed near Dillingham during 1992 were believed to be members of the expanding Mulchatna herd. No overlap between these 2 herds and the Nushagak caribou is believed to have occurred at this time. As all 3 of these herds continue to grow and/or expand, overlap may occur.

Variations in mean group size were the only detectable seasonal changes for the NPCH. Group size was greatest in July during post-calving aggregation, and decreased through September. With the approach of rut, group size again increased and remained relatively stable throughout the winter months. As spring neared, pregnant females dispersed to calve, and group size again was at a low.

Home range

Mean home range for 32 radio-collared caribou was 447 km^2 (±168 s.d.), ranging from 239 km^2 and 799 km^2. Not included in this average were the 2 radio-collared caribou with ranges beyond the Nushagak Peninsula (1301 km^2 and 1458 km^2). These home ranges provide a rough estimate of the amount of habitat utilized. However, size of home range was correlated with the number of locations. For radio-collared caribou with 64-74 locations (those caribou collared in 1988), mean home range was 606 km^2 (±98 s.d., n=11), while those with 15-20 locations (collared in 1992) was 299 km^2 (±59 s.d., n=15). Mean home ranges for the Kilbuck caribou herd calculated using the same technique was 5 900 km^2 for 14 caribou with 16-38 locations each (Hinkes, 1989).

Habitat assessment

Range inventory and monitoring studies have been initiated in the years following reintroduction. Preliminary evaluation indicates the range of the Nushagak Peninsula to be in excellent condition, with an abundance of forage, including lichen. The range shows little sign of grazing. Although there are caribou trails in some areas, the impact does not appear significant.

Population Dynamics

The population dynamics of the NPCH are similar to those experienced by other caribou and reindeer herds introduced into, or occupying range with an abundance of high quality forage and few predators. In summary, the dramatic growth of the herd over the past 6 years was attributed to enhanced body condition, an initial high proportion of young females, high natality even among 2-year-olds, high calf survival and recruitment, and low adult mortality. An abundant high quality forage was probably the greatest factor effecting natality, while the lack of predators and hunting has allowed calf and adult mortality to remain low. Dispersal has not been a factor affecting the population dynamics of the NPCH.

Dispersal has been considered a major factor in the population dynamics of caribou herds in North America (Skoog, 1968; Bergerud, 1980; 1983; Haber & Walters, 1980). Haber & Walters (1980) suggest that competition for food when herds approach a density of 2.0 caribou/km^2 will cause caribou to disperse. This concept is supported by the decline and dispersal of the George River herd when it reached a density of 1.9/km^2 (Couturier *et al.*, 1990). The Avalon herd dispersed when it reached a density of 2.1/km^2 (Mercer *et al.*, 1986). However, there are several examples of caribou and reindeer herds that have reached densities and not dispersed (Bergerud, 1983). The south Alaska Peninsula herd apparently exceeded 2.0/km^2, did not disperse and declined dramatically (Pitcher & Johnson, 1989). Bergerud (1983) suggests that "caribou have not evolved intrinsic density-dependent limitations to growth at extreme densities to avoid catastrophic crashes."

The population density of the NPCH was estimated to be 1.0/km^2 in 1993. We believe the herd will continue to grow, and could reach a density 2.3/km^2 by 1998, even with a 10% harvest beginning in 1995. The NPCH provides an opportunity to examine the relationship of density to population growth and dispersal.

The NPCH is expected to exceed 2000 caribou by 1998. Whereas the current growth of the NPCH verifies the success of the reintroduction, the increasing density, lack of dispersal and potential for over-grazing, presents managers with hard decisions. Should the herd be allowed to continue to grow in hope that the herd will disperse into new range; alternately, should herd growth be limited through increased harvest to avoid range degradation?

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Use of summer habitat by caribou on the north slope of a mountain near the Macmillan Pass, N.W.T.

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Abstract: Habitat use by woodland caribou was investigated by counting pellet-groups, sampling phytomass, and evaluating topography in nine habitat-types on the north slope of an unnamed mountain near Macmillan Pass, N.W.T. Caribou pellets were most abundant in high elevation habitat-types, and pellet density was greatest in an alpine Lichen-Grass habitat-type with a slope of <1°. The high density of pellets in alpine areas may have resulted from of the use of cool, windy, alpine habitats by caribou seeking relief from insect harassment. There were no apparent relationships between pellet abundance, and phytomass of mosses, lichens, or graminoids, possibly as a result of caribou feeding and defecating in different habitats. The occurrence of pellets with a coalesced morphology in the barren Lichen-Grass habitat-type provided indirect evidence in support of a feeding cycle, whereby caribou visit lush habitats to feed, and return to open, alpine habitats to rest and ruminate.

Key words: woodland caribou, Mackenzie Mountains, Northwest Territories

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Introduction

Food preference and availability are important in the selection of habitat exercised by caribou (Kelsall, 1968; Skoog, 1968; White *et al.,* 1975; Skogland, 1980; Servheen & Lyon, 1989). Summering caribou are known to favor areas characterized by lush vegetation types, including forbs, sedges, and willows (Stelfox *et al.*, 1978; Bloomfield, 1980; Oosenbrug & Theberge, 1980; Skogland, 1980; Brown *et al.*, 1986).

On warm, calm summer days, the caribou's apparent preference for green, succulent plants can be compromised when harassment by insects in moist meadows, wetlands, and riparian areas reaches unbearable levels (Skogland, 1980; Roby, 1978). At these times, woodland caribou are known to retreat to sparsely vegetated areas such as windy ridge tops and snowpatches for relief (Downes *et al.,* 1986; Ion & Kershaw, 1989). Thus, it seems probable that selection of summer habitat by woodland caribou involves partitioning between those resources that provide relief, and those that provide forage (Bergerud, 1974).

The primary purpose of this study was to investigate the use of summer habitat-types by woodland caribou (*Rangifer tarrandus caribou*) in an alpine area of the Mackenzie Mountains, Northwest Territories. A comparison of caribou evidence with vegetation and physical characteristics in different habitat-types forms the basis for discussion.

Study Area

Research took place on an unnamed mountain 15 km east of the Macmillan Pass (Lat. 63° 18', Long. 130° 17'). The Pass is an east-west running corridor which traverses the Mackenzie/Selwyn Mountains above timber-line. Concentrations of woodland caribou, believed to belong to the Redstone herd, occupy the vicinity of Macmillan Pass between June and September, but are rarely seen at other times of year (Miller, 1976, Farnell & Nette, 1981). Other large vertebrates in the study area include moose (*Alces alces*), Dall's sheep (*Ovis dalli*), grizzly bears (*Ursus arctus*), wolves (*Canis lupus*), wolverines (*Gulo gulo*), and golden eagles (*Aquila chrysaetos*).

The Macmillan Pass area experiences a continental climatic regime modified by an alpine environment. Mean annual precipitation is 490 mm, and snow may fall during any month of the year. July, with a mean monthly temperature of 10°C, is the warmest month of the year.

With regard to vegetation, Erect Deciduous Shrub Tundra dominates at low elevation. Plant communities are characterized by birch (*Betula glan-*

dulosa) in association with lichens and mosses on drier sites, and several species of willow (*Salix* spp.) in association with mosses, sedges, and forbs on wetter sites.

Moderate to high elevation sites are frequently occupied by low-growing heath (*Cassiope tetragona*) interspersed within mats of lichens, particularly on rolling, moderately-sloped terrain. High elevation plateau areas appear as a rich, green mosaic of alpine and forb meadows, enriched by meltwater flowing from late-lying snowpatches. On the windswept dome of the study mountain, cobble-dominated sorted circles lie adjacent to a sparsely vegetated lichen-grass community.

Methods

Habitat-type designation

Transect blocks, each made up of six 100 m long transects, were flagged in nine habitat-types on the shoulder of the unnamed mountain. Sites were selected on the north face as caribou tend to favor cool, north-facing slopes in summer (Oosenbrug, 1976; Bloomfield, 1980; Skogland, 1980). Sites were located by walking up the fall-line of the mountain flagging transect blocks along an approximately evenly-spaced gradient between the base and summit, and deviating from a straight course only enough to include all prominent plant communities mapped by Kershaw & Kershaw (1983). Within each habitat-type, transects were oriented parallel to one another to maximize vegetation homogeneity. Descriptions of each habitat-type included aspect, slope, elevation, topography, and proximity of ecotones.

Phytomass collection

Above-ground phytomass samples were collected in early August using nine randomly-placed quadrats in each habitat-type. To speed sorting, a 10x10 cm quadrat was used for non-vascular plants while a larger 25x25 cm quadrat was used for all other live plants. All six transects within a habitat-type were sampled once, and three transects were sampled a second time based on the roll of a die. Phytomass samples were sorted into mosses, lichens, graminoids, forbs and shrubs. All samples were dried in a 60°C oven before being weighed.

Pellet-group counts

All transects were surveyed for pellet-groups twice, once in early July and again in early August. During the first survey, all fecal matter was removed from the 4 m-wide belt transects. Pellet-groups were categorized on the basis of morphology as either: 1. a single, coalesced mass, 2. a discrete, scattering of pellets, or 3. a transitional or intermediate character.

Data analysis

All phytomass values were converted to gm^{-2} and summary statistics were calculated for shrubs, forbs, graminoids, lichens, mosses, and total phytomass in each habitat-type.

The time between clearing of fecal matter and resurveying of transects was standardized to 38 days in order to equalize the opportunity for caribou to use each habitat type. All pellet-group counts were converted from a value based on the area of the transect (400 m^2) to pellet-groups per hectare.

Analysis of variance (ANOVA) based on habitat-type was performed on pellet-group data sets for both July and August. Similar ANOVA's were performed on the phytomass data for shrubs, forbs, graminoids, lichens, mosses, and total phytomass.

Results

Physical characteristics

Habitat-types selected for transect blocks occupied a range of plant communities and elevations from 1218 m to 1970 m (Table 1). The steepest study slope was on a late-lying snowpatch just below the summit dome; several other sites had slopes <1°. All habitat-types had northern aspects.

Vegetation characteristics

Variability within plant groups in a habitat-type was high - many standard deviations exceeded 70% of their associated mean values (Fig. 1a, 1b). This was a consequence of using a small sample size when variability inherent within the system was high. In order to make use of the data, values were assumed to reflect the grosser differences in phytomass among habitat-types. The least variability in phytomass occurred in the Forb Meadow, where the standard deviation was notably low for forbs.

With regard to relative amounts of phytomass, the Lichen-Grass habitat type had the lowest total phytomass, composed mainly of mosses and lichens (Fig. 1a,

Table 1. Gross characteristics of nine habitat-types surveyed for pellet-groups in July and August.

Plant Community	Terrain	Elev.(m)	Slope(°)	Aspect
Riparian willow	Riverbank	1218	<1	-
Birch-moss	Hillside	1316	5	N
Birch-lichen	Plain	1318	<1	-
Willow-forb	Lakeside	1328	<1	-
Lichen-heath	Rolling hills	1480	8	NE
Lichen-heath	Alpine slope	1650	5	NW
Forb meadow	Alpine plateau	1725	8	N
Snowpatch	Alpine slope	1880	22	NE
Lichen-grass	Summit plateau	1970	<1	-

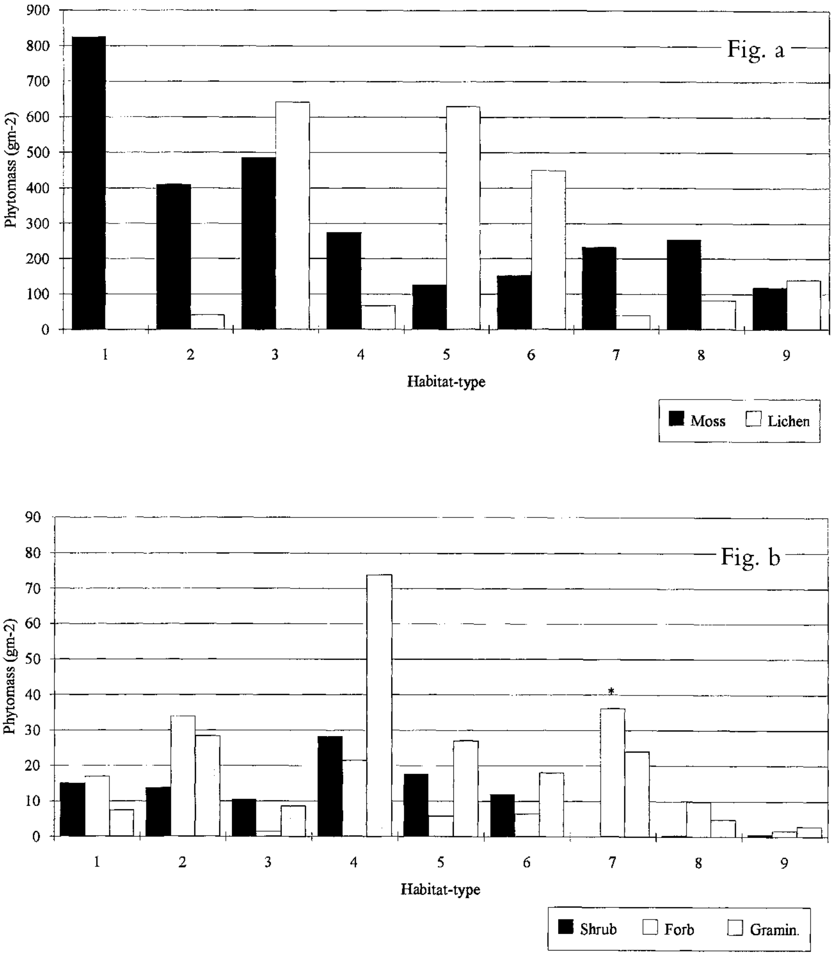

Fig. 1a, b.
Mean phytomass (gm^{-2}) of mosses, lichens, shrubs, forbs, graminoids in nine habitat-types, numbered from lowest to highest elevation. 1=Riparian Willow, 2=Birch Moss, 3=Birch-Lichen, 4=Willow-Forb, 5=Lichen-Heath, 6=Alpine Lichen-Heath, 7=Forb Meadow, 8=Snowpatch, 9=Lichen-Grass. Gram.=Graminoids. Standard deviation exceeds 70% of the mean value in all cases, except where * is shown.

1b). Woody plants were nearly absent from all the alpine habitats. Shrubs and graminoids were most abundant in the Willow-Forb habitat-type, despite a relatively low overall phytomass. Graminoids were also abundant in the Forb Meadow which also had the greatest forb phytomass. In contrast, forbs were most rare in the Birch-Lichen habitat-type even though this community had the highest overall phytomass, due to an abundance of shrubs, mosses, and lichens. Similarly, lichens in combination with shrubs constituted a large portion of the phytomass of both Lichen-Heath habitat-types. Between-group variance significantly exceeded within-group variance for phytomass of shrubs, forbs, graminoids, mosses, lichens and all plants (F=2.22 @ P=0.04, F=6.19 @ P=0.00, F=2.30 @ P=0.03, F=3.93 @ P=0.00, F=8.39 @ P=0.00, and F=4.83 @ P=0.00 respectively).

Pellet-group counts

There appeared to be a direct relationship between pellet-groups and elevation (Fig. 1c, 1d). In both early July and early August, the largest mean number of pellet-groups were recorded on the summit of the mountain while there was an absence of pellets in two low elevation habitat-types, specifically the Riparian Willow and Birch-Lichen.

Coalesced, scattered, and transitional pellet-groups were found in both July and August surveys; however, as pellets in the August survey were known to be deposited during July 1993, only these are presented in categories (Fig. 1d). Scattered and transitional pellet-groups were absent from low elevation habitat types while there appeared to be disproportionately large number of coalesced pellets-groups in the Forb Meadow habitat-type, which contained the greatest mass of forbs. Generally, the lower phytomass for all plants, and specifically shrubs, graminoids, mosses, and lichens in alpine habitat-types was accompanied by a higher abundance of pellet-groups (Fig. 1a, 1b, 1c, 1d). There was significant variability in the mean number of pellet-groups among habitat-types, with minimal variability within each habitat-type (F=30.44 @ P=0.00, F=45.94 @ P=0.00 for July and August respectively).

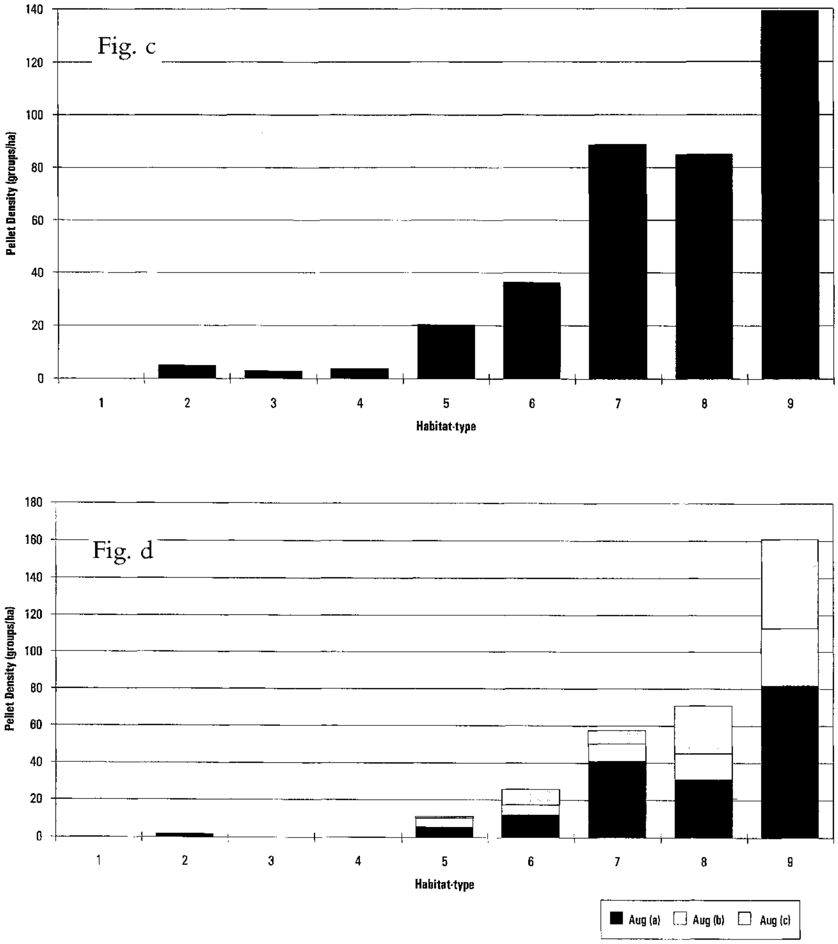

Fig. 1c, d.
Mean caribou pellet-groups per hectare counted in nine habitat-types during early July and August. August pellet-groups are subdivided based on morphology into coalesced pellet-groups (a), transitional pellet-groups (b), and scattered pellet-groups (c). Standard deviation is less than 50% of the mean value for habitat-types 5 - 9.

Discussion

Pellet-group counts

Unlike track counts, pellet-group counts are not dependent on the hardness of the ground surface, or on the difficulties of distinguishing between sign of separate animals (Fischer *et al.,* 1977). In contrast to both ground and aerial surveys, pellet-group counts can be an inexpensive way to assess the relative habitat use of an animal virtually in absentia. This technique is not without drawbacks, and chief among these is a fundamental and possibly-erroneous assumption that the number of pellet groups found within a habitat indicate of the amount of time an animal spends there (Robinette *et al.,* 1958). For this reason, previous caribou studies have been careful to qualify that the interpretation of pellet-group counts may be clouded by the high mobility of the subject animal (e.g. Fischer *et al.,* 1977).

Given this limitation of pellet group surveys, it is best to proceed cautiously from reporting pellet abundance to discussion of actual habitat use, particularly when habitat availability information is limited to a site description as in the present study. However, as cervids tend to follow an extremely regular cycle of consumption, rumination and defecation (Oldemeyer & Franzmann, 1981; Dinerstein & Dublin, 1982), pellet group counts inevitably provide some indication of the habitats utilized regularly by a species. Furthermore, the regular occurrence of an animal in a specific habitat for whatever purpose provides insight into the larger, more general question of habitat use. Because of this, ungulate pellet-group counts have been employed successfully by many researchers as an index of relative habitat use (e.g. Collins, 1981).

Because the study area is believed to be used exclusively as summer range by caribou, the early July pellet-group count is a survey of pellets dropped in previous summers, and the similarity between July and August pellet data implies a consistent trend in pellet deposition between the nine habitat-types (Fig. 1c, 1d). The only exception was in alpine Lichen-Grass habitat-type in which there were more pellets counted in August than in July. Most likely, this disparity was due to the greater age and exposure of the pellet-groups counted in early July which frequently appeared scattered by snowmelt run-off and animals, particularly in heavily-used habitats. This made it difficult to correctly identify discrete pellet groups, and may have resulted in an underestimation of the number of groups in the Lichen-Grass habitat-type in July. This reflects little on the relative number of pellet-groups among habitat-types.

Physical characteristics

If pellet-group density reflects habitat use, alpine habitat-types were used more than low elevation ones (Fig. 1c, 1d). However, this is not necessarily a valid assumption as an unbalanced distribution may be the result of many possible influences. As a simple example, the conical shape of a mountain will concentrate animals and their evidence into alpine areas while allowing them to disperse over greater areas in the subalpine. In light of this, it is better to approach discussion from a more functional perspective, and examine why high elevation habitats would contain high densities of pellets.

The Lichen-Grass habitat-type was on the flattened summit of the mountain. It supported the highest pellet-group densities, indicating it was regularly used by caribou (Fig. 1c, 1d). This habitat-type also had the highest elevation and a negligible slope (Table 1). An inverse relationship has been reported between elevation and insect activity, and thus summering caribou have been reported to avoid insect pests by utilizing high elevation areas in west central Alberta, central British Columbia, and the eastern Yukon (Stelfox *et al.*, 1978; Bloomfield, 1980; Downes *et al.*, 1986). Caribou have been witnessed to seek ridge tops and snowpatches in the Mackenzie Mountains to apparently take advantage of wind conditions that are unfavorable to blood-sucking insects (Gill, 1978; Ion & Kershaw, 1989). Both the exposed Lichen-Grass habitat-type and the neighboring Snowpatch habitat-type might have been attractive to caribou as sanctuaries from mosquitos and flies. Furthermore, Oosenbrug (1976) found caribou to have a preference for high elevations, but also for "flat-to rolling terrain" with slopes of <20°: topography similar to that of the Lichen-Grass habitat-type.

Vegetative characteristics

Gill (1978) conducted counts of individual caribou pellets in the Macmillan Pass and found little connection between pellet abundance and phytomass. This study achieved similar results concerning the lack of an obvious relationship between phytomass and the occurrence of pellet-groups (Fig. 1a, 1b, 1c, 1d). This may stem, in part, from the relatively small number of samples used. As well, it is entirely possible that the level of vegetative sampling selected for phytomass is inappropriate to the level of forage selection expressed by caribou. Sampling of plant groups from one point in time does not allow comparison to specifically sought-after species, nor change in preferential forage over the summer.

Nonetheless, certain generalizations can still be formed. In general, those communities with the least phytomass had the greatest evidence of use (Fig. 1a, 1b, 1c, 1d). To some degree, this is consistent with other studies which show that consumption of shrubs and lichens by caribou may reach its lowest level in summer (Stelfox *et al.*, 1978; Bloomfield, 1980). Skogland (1980) found a significant correlation between above-ground phytomass and time spent feeding in a vegetation type when animals were allowed to express selection uninterrupted by insect harassment. In contrast, insect harassment of caribou was frequently observed in the study area (Ion, 1986; Quayle, 1994).

Skogland (1980) found that forbs were the most selected of any plant in alpine areas, a finding reitterated by Stelfox *et al.*, (1978) and Bloomfield (1979). The relatively high density of pellets found in the Forb Meadow may also indirectly support use of forbs by caribou (Fig. 1d). The Forb Meadow habitat-type had the greatest forb phytomass (Fig. 1b), occurring at 1725 m on a moist plateau beneath a steep snowy slope. Caribou are opportunistic feeders, taking advantage of new growth as it appears, and such areas can be especially attractive to them (Gill, 1978; Stelfox *et al.*, 1978; Bloomfield, 1980; Skogland, 1980). August pellet data from the Forb Meadow may be indicative of regular visits by caribou. Many of the pellets present also showed a coalesced morphology which may be associated with the sort of lush forage found in this habitat-type (Fig. 1d).

Shrubs, particularly willow, have also been suggested as preferred summer forage for caribou; however, the results of this study indicate shrub phytomass was low or absent where pellet density was high (Fig. 1b, 1d). In fact, the only communities where both shrubs and pellets figure prominently were the Lichen- and Alpine-Heath habitat-types in which the dominant shrubs (*Cassiope tetragona* and *Vaccinium uliginosum*) were low growing. Differential pellet visibility between habitat-types is probably responsible to an extent for differences; however, given that both bear scat and numerous moose pellets were recorded in shrubby communities, visibility was likely not the only explanation.

As discussed earlier, a foraging cycle, in which animals browse on shrubs at low elevation, but ruminate and defecate in open, alpine areas would produce similar results.

A foraging cycle is given more indirect support by the morphology of the pellets found in the Lichen-Grass habitat-type. A large number of coalesced pellet-groups were found in the Lichen Grass habitat-type, despite an absence of any lush vegetation normally associated with this pellet morphology (Fig. 1b, 1d). This makes plain that pellet-group density is not always indicative of relative use between habitat-types. As well, although pellet density suggests that caribou consistently visit the Lichen-Grass habitat-type, they appear to feed elsewhere on more lush forage which is clearly not available on the windswept mountain-top. It is easy to speculate that the animals cycle back and forth between those habitat-types where they forage, and those where they ruminate, rest, and defecate. This would result in an abundance of pellets being deposited in alpine areas as animals defecate following periods of bedding, even though caribou may not necessarily spend more time in bedding habitat. Following this train of thought, the large number of coalesced pellets in the Lichen-Grass habitat-type may be from resting or ruminating animals, possibly seeking solace from insect harassment in windy, alpine areas after returning from feeding visits to more lush communities. Such behaviour patterns have previously been reported (Archibald, 1973; Ion, 1986; Quayle, 1994).

Conclusions

1. Woodland caribou pellet-groups were more abundant in habitat-types at higher elevations than those at lower elevations, with the greatest density of pellets occurring in a habitat-type with a slope of <1°. Assuming pellets are indicative of regular use by caribou, high elevations may be sought in summer for relief from insect harassment.
2. This study could not determine any relationship between pellet-group abundance and phytomass. This may be due to vegetative sampling which was inappropriate to forage selection by caribou in the study area; it may also be the result of caribou feeding and defecating in different habitats.
3. The abundance of coalesced pellets found in the dry, barren Lichen-Grass habitat-type suggested both that pellet-group densities were not always indicative of relative habitat use, and that caribou must have made feeding visits to more lush habitat-types. This suggests that the distribution of pellet-groups may be the result of a feeding-ruminating cycle, whereby caribou feed in lush habitats and retreat to open, high elevation habitats to rest, ruminate and, defecate.

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Post-calving photo-census of the Rivière George caribou herd in July 1993

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Abstract: A photographic census of the Rivière George caribou herd in Quebec and Labrador was conducted between 4-23 July 1993 during the post-calving period. The primary objective of the study was to obtain an accurate estimate of the current size of the herd to permit the monitoring of population trends and effective management of the herd. The census procedure consisted of (1) use of satellite and conventional radio-telemetry to locate and photograph post-calving aggregations during the period of optimal aggregation, (2) determination of the minimum population size by direct counts from photographs, and (3) estimation of the total population size using the Petersen Index method. This method allowed extrapolation of the data to caribou that were either not photographed or that were not aggregated at the time of the census. The minimum count indicates that the Rivière George caribou herd consisted of at least 358 460 adults (older than calves) at the time of the census. This count underestimates the total population size but is useful because it is virtually free of error. The total size of the Rivière George herd in July 1993 was estimated to be 540 040 adults within 90% confidence limits of ± 12.8%. Comparisons with previous estimates indicate that the size of the herd continues to be large, but that its growth has probably ceased. This study demonstrates that a photographic survey of post-calving aggregations is an effective method to census the Rivière George herd and possibly other large migratory caribou herds that are monitored by telemetry.

Key words: *Rangifer tarandus,* population estimate, minimum count, radio-telemetry, aggregation, Quebec, Labrador

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Introduction

The Rivière George herd of migratory caribou (*Rangifer tarandus*) occupies a vast annual range extending from the Labrador coast to Hudson's Bay and between 52° and 60° N latitude. The herd constitutes the most important sustainable wildlife resource in Northern Quebec and Labrador. The herd is a vital economic and cultural resource for aboriginal people in northern communities, who rely on caribou for a large part of their diet. It also supports a multi-million dollar sport-hunting industry and a developing commercial hunt.

The Rivière George herd has undergone at least three cycles of scarcity and abundance over the past 200 years, and the numbers have fluctuated from a few thousand to several hundred thousand caribou. Historical records suggest that the numbers peaked in the early and late 1800s (Elton, 1942), and recent data suggest that another peak may have occurred in the mid- to late 1980s (Messier *et al.,* 1988; Hearn *et al.,* 1990).

The Rivière George herd underwent a period of rapid population growth from the mid-1950s to the mid-1980s to become one of the largest caribou herds in the world (Williams & Heard, 1986; Messier *et al.,* 1988). Fall population estimates (including calves) ranged from 644 000 in 1984 to 283 000 in 1986 and to 682 000 caribou in 1988 (Crête *et al.,* 1991). However, the 1986 and 1988 censuses were relatively imprecise, with 90% confidence intervals of 36% and 39%, respectively.

Recent studies on productivity, body condition and survival rates suggest that the growth of the herd has ceased (Couturier *et al.,* 1988a,b; 1989; 1990; Hearn *et al.,* 1990; Messier *et al.,* 1988; Camps & Linders, 1989). Unfortunately, recent population estimates, determined by photographing caribou on the calving grounds, have suffered from technical problems and lack of precision (Messier *et* *al.,* 1988; Crête *et al.,* 1991). Due to historic fluctuations in population size and recent evidence of a decline in growth rate, it is important to obtain reliable population estimates at regular intervals to establish population trends. Such information, in turn, is essential for effective management of the herd.

We present the results and evaluate the methodology of a photographic census of the Rivière George herd conducted in July 1993. The method takes advantage of a brief phenomenon that occurs in July of most years as a part of the annual life cycle of large migratory herds of caribou (Valkenburg *et al.,* 1985). On calm, warm days most of the population aggregates in large groups, thus allowing photography of almost the entire herd in a cost-effective manner.

The technique relies on the presence of a large number of radio-collared caribou that disperse randomly within the population, thus facilitating the location of the aggregations. The majority of caribou can then be photographed and directly counted. An estimate of the total herd size is obtained by extrapolation to the (small) proportion of the population that could not be photographed. This method provides a high degree of accuracy and precision, and potentially allows frequent monitoring of herd size.

In the past, photography of post-calving or rutting aggregations has been used to successfully estimate the size of caribou herds in Alaska and Yukon (e.g. Whitten *et al.*, 1980; Whitten, 1985; Valkenburg *et al.*, 1985; Taylor, 1993), as well as in the Northwest Territories (McLean & Russell, 1988; Russell, 1990). A partial photographic census of the Rivière George caribou herd was carried out during the 1990 post-calving period (Russell & Jakimchuk, 1991). This census resulted in an imprecise population estimate, because less than 50% of the caribou were photographed during opportunistic surveys. The 1993 post-calving census represents a refinement of the 1990 census methodology.

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Study area

The study was conducted within the summer range of the Rivière George caribou herd in northern Labrador and northeastern Quebec (Fig. 1). The study area, about 120,000 km^2 in size, consisted of habitat used by caribou for post-calving aggregations as documented since 1990 (RRCS, 1990, 1992, 1993) and extended eastward from about 70° W longitude to the Labrador coast and northward from about 55°30' N latitude.

Pleistocene glaciations have shaped much of the geomorphology of the study area, which is underlain by the Canadian Shield (Sutton, 1972). Glacial and alluvial land-formations, including eskers and glacial drift plains, occur throughout the area, and deeply scarified bedrocks are a characteristic feature of the interior plateaus. Topography of the area is varied, ranging from the rugged Torngat Mountains (elevations up to about 1,500 m) and deep coastal fiords and valleys in the east to low coastal areas in the north. The vast Labrador Plateau, south of the Torngats, extends from the Rivière George eastward to the Labrador coast. The area west of the Rivière George is relatively flat and characterized by many large lakes and rivers, draining into Ungava Bay.

The terrain over most of the study area, excluding the Torngat Mountains, consists of rolling tundra plains, dominated by barren rock, lichens, mosses and grasses. Black spruce (*Picea mariana*) forest grows in the sheltered valleys along larger rivers. Scrub-forest associations, dominated by willows (*Salix* spp.) and alders (*Alnus* spp.), are found higher along valley slopes and along smaller rivers (Rowe, 1972; Meades, 1990; Sogeam Inc., 1992a,b). Open spruce-lichen woodland is present along the southern rim of the study area and westward from Rivière à la Baleine (Whale River).

The topography of most of the range provides terrain features, such as barren windy ridges, that are used by the caribou as insect-relief habitat during the post-calving period. Their movements within the traditionally-used summer range are governed largely by a response to harassment by blood-sucking and parasitic insects at this time. Suitable insect-relief habitats appear to be abundant on the Rivière George Plateau and in the barren tundra in the east (Juniper, 1982).

Methods

Location and photography of post-calving aggregations

The census began on 4 July, when monitoring by satellite telemetry indicated that the caribou were forming post-calving aggregations just east of Kuujjuaq. Two biologists, using either a twin-engine Partenavia aircraft or an amphibious float-equipped Cessna 206, conducted radio-telemetry surveys and took oblique photographs of caribou aggregations from the side windows of the aircraft. On July

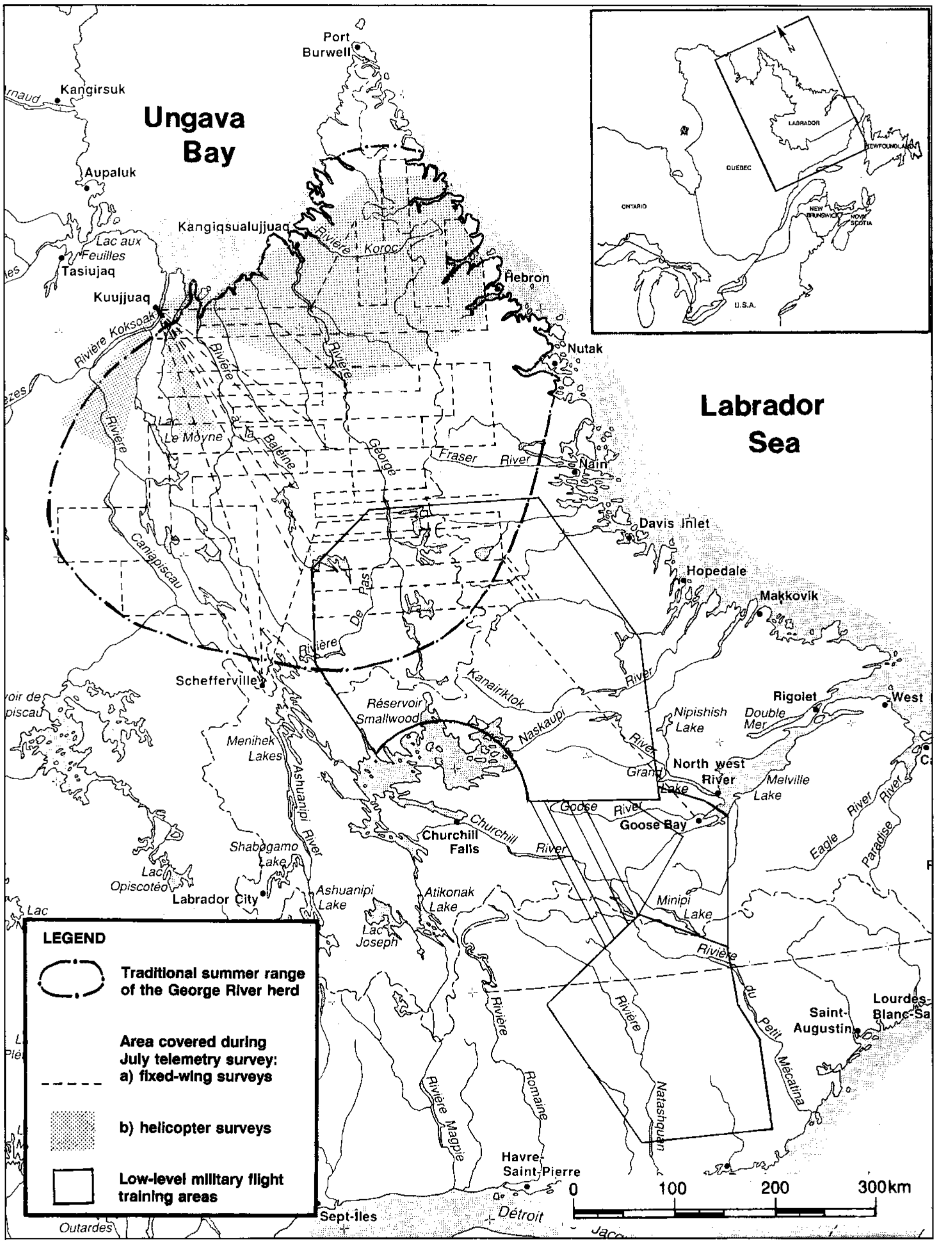

Fig. 1. Areas surveyed during the post-calving census of the Rivière George caribou herd between 4 - 23 July 1993, in relation to seasonal range use by the herd. Low-level training areas used by military flights originating from Goose Bay, Labrador, are also shown.

13, a second crew of two biologists in an A-Star helicopter joined the effort to ensure that as many aggregations as possible were located and photographed.

Each aircraft was equipped with two scanner receivers (either from Telonics Inc. or Lotek Inc.), which were used to locate VHF signals emitted by radio-collars. The receivers were connected to two H-shaped antennae, mounted on the wing-struts or fuselage of each aircraft. Both crews scanned at least 125 VHF frequencies, which were split between the two scanners of each aircraft.

Photographs of caribou aggregations were taken at oblique angles with motor-driven 35 mm single lens reflex cameras, equipped with a 50 mm (focal length) lens, on Kodachrome ASA 64 slide film. Minimum shutter speed was 1/500 second, but the speed of 1/1000 second was used whenever light conditions permitted. The lens was focused at infinity, and most photography was done at 250-300 meters above ground to minimize disturbance to caribou. Each exposed roll of film and each caribou aggregation was assigned a unique sequential number. To avoid confusion between the two survey crews, the crew using the fixed-wing aircraft began their number sequences from 1, whereas the helicopter crew began their sequences from 101.

Aggregations containing satellite collared caribou (i.e. collars equipped with Telonics Inc. platform transmitter terminals, PTT's) and conventional VHF radio-collars were monitored to determine the optimal time for photography. Systematic telemetry surveys over the entire summer range were conducted (Fig. 1). An attempt was made to photograph only highly aggregated groups, as indicated by their large size, high density and well-defined borders.

Under ideal conditions, a highly aggregated group of caribou is photographed during only one pass of the aircraft. This results in the least amount of time between overlapping frames and thus in the most precise counts. However, in cases when a very dense aggregation was not likely to develop, groups were photographed during more than one pass. If these aggregations were later observed under more suitable conditions, they were photographed again. Surveys and monitoring of the herd continued until all known groups were photographed or until caribou became too dispersed to warrant continued effort.

Counting caribou images on photographs and determining minimum population size

Caribou images were counted from slides projected onto a sheet of white paper taped to a sloping board. The projector (Leitz Pradovit R150) was aimed downward over the shoulder of the counter/interpreter onto the paper from a slanted stand. This arrangement allowed the greatest comfort for the counter to reduce fatigue over the extended counting period of several weeks. Each caribou image projected on the paper was marked with pencil, and a hand-held tally machine recorded each counted image. Images obtained in July could easily be assigned into two classes: calves and caribou older than one year (adults). A separate tally was kept for adults and calves. To determine the amount of overlap between two adjoining slides, at least two landmarks common to both slides were located. A straight line was drawn between these landmarks to eliminate counting images of the same caribou twice.

All counts were performed by the senior author, who has extensive experience in counting caribou images from slides (over a million images counted). To obtain an estimate of counting error, a second person recounted images on portions of slides, and the independent counts by the two persons were then compared.

The minimum number of adult caribou in the Rivière George herd was calculated by adding together the counts of photographed groups that did not contain repeated observations of individual radio-collared caribou. An exception was made in one case to account for caribou in a group that contained mostly new observations of radio-collared individuals (see "Results").

Unlike adult counts, calf counts in oblique photographs are biased and lower than the actual values, because some calves are likely to be eclipsed by the larger adults. Therefore, these counts are not presented.

Determination of population estimate and confidence interval Calculations

An estimate of the total population size, including caribou associated with radio-collars that were either missed or not highly aggregated at the time of photography, was calculated using the Petersen Index procedure, as applied to radio-telemetry data (White & Garrot, 1990):

$$(1)\quad \hat{N} = \frac{(M+1)(C+1)}{R+1} - 1$$

where $\hat{N}$ = estimate of population size at time of census
M = total number of radio-tagged animals present in the herd
C = total number of caribou observed in highly aggregated groups during the survey
R = number of radio-tagged caribou observed in highly aggregated groups

The 90% Confidence Interval for the estimate was determined as follows (White & Garrot, 1990):

$$(2)\quad \hat{N} \pm 1.645\ \mathrm{Var}(\hat{N})^{0.5}$$

where

$$(3)\quad \mathrm{Var}(\hat{N}) = \frac{(M+1)(C+1)(M-R)(C-R)}{(R+1)^2(R+2)}$$

Assumptions

An accurate estimate of population size using the above methodology is dependent on the following assumptions:

1. The population is closed.

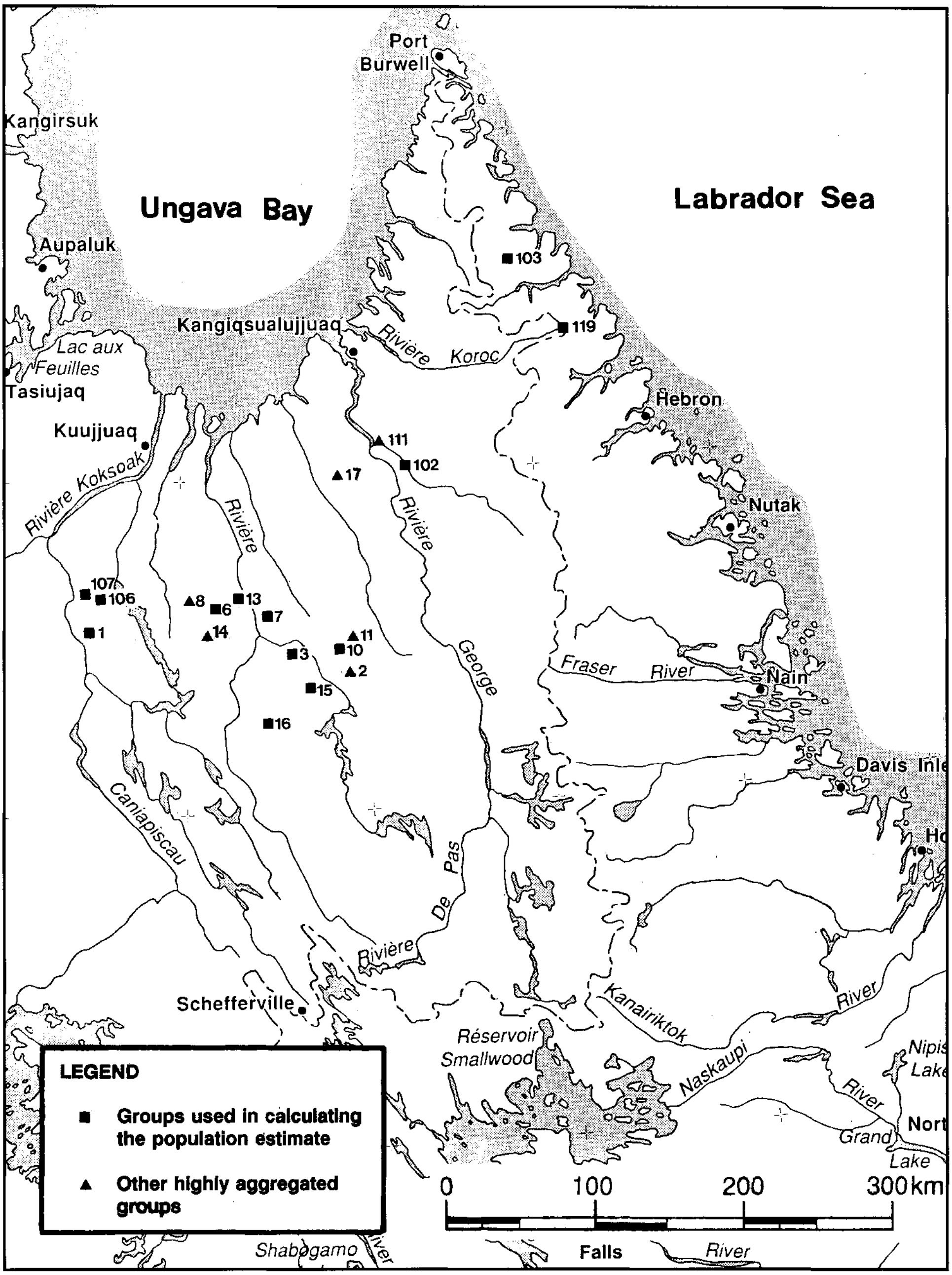

Fig. 2. Location of highly aggregated post-calving groups of the Rivière George herd, each containing more than 4 000 adult caribou, at the time of photography in July 1993.

2. All highly aggregated groups contain at least one radio-collar, and thus they can potentially be located.
3. The collared animals are randomly distributed throughout the herd during the time of census.
4. No significant movements of caribou between photographed groups used in the estimate occur during the time of census.

Results

Number and movements of photographed groups

A total of 50 groups in various stages of aggregation were photographed between 4-23 July 1993. Details of groups not used in the calculation of the minimum count and population estimate are presented elsewhere (RRCS, 1994). At the start of the census, several large aggregations, consisting of at least 300 000 adults, in total, were drifting around both east and west shores of Lac la Moinerie. These caribou moved southeast, reaching latitude 57°00' N and longitude 66°00' W on 11 July, and then turned westerly. Most of these caribou were highly aggregated between 12-18 July when they were photographed (Groups 3, 6-8, 14-16, 106, 107 in Fig. 2).

On 5 July, a group of about 50 000 adult caribou, consisting mainly of mature males, was photographed near Chute Calcaire (Limestone Falls) and the Rivière Caniapiscau, southwest of Kuujjuaq. This large aggregation (Group 1 in Table 1 and Fig. 2) had already started moving west toward the periphery of the traditional summer range and continued in this direction throughout the census period.

The remainder of the herd was located in an area that extended from just west of the lower Rivière George valley east to the Labrador coast and from the Collines Pyramid (Pyramid Hills) north to Abloviak Fiord. Within this large area there were several aggregations that appeared to be moving independently of each other. Caribou in the Torngat Mountains north of the Rivière Koroc were on the Quebec side of the border on 2 July, but by 10 July they were mostly on the Labrador coast. Caribou in this movement that were used in the estimate include Groups 102, 103 and 119 (Table 1 and Fig. 2). Near the end of the census, many of the animals on the Labrador coast had started moving back into Quebec in a southwesterly direction and were dispersing into many smaller groups. Most caribou had dispersed by 23 July, when the census was terminated.

Total number of functioning radio-collars in the herd

A total of 92 functioning radio-collars (31 PTT and 61 VHF) were determined to be present in the herd and on the summer range at the time of the post-calving census. These caribou consisted of 16 adult males and 76 adult females captured and collared between June 1987 and May 1993.

During the census, 84 individual radio-collared caribou were located. Five additional collars were located during surveys conducted by Couturier *et al.*, (1994) over the calving and summer range of the herd in June 1993. An additional three collars were estimated to be functional based on battery life of transmitters and survival probabilities of adults and calves.

Number of radio-collars in photographed groups

Most photographed groups (38 of 50) contained at least one radio-collar. The majority of unmarked

Table 1. Post-calving aggregations of the Rivière George herd photographed between 4 - 23 July 1993 and used in the calculation of population estimate.

Date	Group	No. of radio-collars	Adults	Calves	Total	Percent calves	Adults per radio-collar
July 5	1	9 (7)[a]	49 310	2 745	52 055	5.3	5 479
July 12	3	5 (1)	11 789	2 231	14 020	15.9	2 358
July 13	6	2	8 543	2 374	10 917	21.7	4 272
July 13	7[b]	4 (2)	8 779	1 551	10 330	15.0	2 195
July 14	10	2	16 585	5 576	22 161	25.2	8 293
July 16	13	10 (2)	66 448	11 032	77 480	14.4	6 645
July 16	15	5 (1)	16 278	3 897	20 175	19.3	3 256
July 18	16	6	55 773	11 576	67 349	17.2	9 296
July 14	102	4	14 082	4 950	19 032	26.0	3 521
July 14	103	2	4 678	1 835	6 513	28.2	2 339
July 16	106	2	11 498	1 088	12 586	8.2	5 749
July 16	107	4	51 187	9 401	60 588	15.5	12 797
July 20	119	3 (1)	27 656	11 132	38 788	28.6	9 219
Totals	13	58 (14)	342 606	69 388	411 994		

[a] value in parentheses shows the number of radio-collared males included in the total. Groups without parentheses contained collared females only.

[b] Group 7 contained 6 radio-collared caribou when it was photographed. However, two collared females were photographed also in Group 13. To avoid duplication, we reduced the count of Group 7 to two thirds of the original value (i.e. the original count was 13 168 adults and 2 327 calves).

Table 2. Image interpretation of a sample of census photographs by two observers, differing in experience. All photographs counted were taken from 250-300 m above ground.

	Observer 1 (experienced)			Observer 2 (inexperienced)			Difference in counts (%)	
	Adult	Calf	Total	Adult	Calf	Total	% Difference Adult Count	% Difference Total Count
Day 1	1 944	538	2 482	1 709	641	2 350	-12.1	-5.3
Day 2	47	–[a]	47	41	–	41	-12.7	–
	68	–	68	61	–	61	-10.3	–
	74	–	74	56	–	56	-24.3	–
	135	43	178	115	67	182	-14.8	+ 2.2
	114	40	154	118	50	168	+3.8	+ 8.3
Day 3	109	33	142	108	37	145	-0.9	+ 2.1
	82	26	108	81	36	117	-1.2	+ 8.3
Total	2 573	680	3 253	2 289	831	3 120	-11.0	-4.1

[a] calves were not counted in these samples.

groups (10 of 12) were relatively small, ranging in size from 389 to 1 859 adult caribou, and were most likely not photographed at the optimal state of aggregation. However, two large groups (Group 5: 23 615 adults, and Group 108: 7 175 adults) contained no radio-collars. These groups were probably photographed at another time during the census as a part of other larger groups containing radio-collars.

The size of groups containing only one radio-collar ranged from 59 to 2 770 adults ($\bar{x}$ = 967.5, SD = 895.5, n = 19). All 19 highly aggregated groups, as defined by their well-defined borders and large size (>4 000 adults), contained at least two radio-collared caribou. These groups ranged in size from 4 137 to 66 448 adults. Fig. 2 shows the location of these groups at the time of photography.

Accuracy of counting

The error associated with counting images from slides by the senior author, who performed all counts, was very small. Therefore, no correction was made to the actual counts. Portions of 8 slides (about 3 000 caribou) were selected to be counted independently by two observers. The counts obtained by the second person, inexperienced in counting caribou in oblique photographs, were lower in all but one case than the counts by the senior author, an experienced interpreter (Table 2). Because each person marked on paper the exact position of each image counted, it was possible to compare and verify these counts. By the end of the session, the counts and the classification of adults and calves by both observers agreed closely.

Minimum population size

A minimum count is useful, because it provides a measure of the population size that is relatively free of error. A total of 342 606 adult caribou were counted in 13 highly aggregated groups (Table 1). These groups, with the exception of Group 7, did not contain repeated observations of individual collared caribou. Group 7 contained six collared caribou, two of which were also photographed in another group. To avoid duplication, we reduced the count of Group 7 to two thirds of its original value.

An additional 15 854 adult caribou (corresponding to caribou associated with 14 radio-collars) were added to the above value, resulting in a minimum count of 358 460 adults. These caribou were associated with 72 of the total of 92 radio-collared animals. The remaining collars were found in groups that contained repeated observations of individual collared caribou and thus were not included in the minimum count.

Estimation of total population size

Groups used in estimating population size

Of the total of 19 highly aggregated groups, 13 were selected to be used in the calculations of population size (Table 1). Six groups were deleted (2, 8, 11, 14, 17 and 111 in Fig. 2), because one or more collared caribou in these groups were the same individuals photographed as part of another group. Counts of groups that were photographed under more suitable conditions (e.g. fewer animals obscured by trees, clearer images) were used in the calculation of population size in cases of repeated observations.

Population estimate

The total size of the herd is larger than the minimum count because not all caribou were photographed under optimal conditions of aggregation, and not all radio-collared caribou were photographed. Therefore, the total population size at the time of the census was estimated using the Petersen Index method (White & Garrot, 1990).

The Rivière George herd was estimated to consist of 540 040 ± 69 339 adult caribou (older than calves) in July 1993. The 90% confidence limits deviate by 12.8% from the mean.

Discussion

Evaluation of assumptions for the population estimate

Accurate estimation of herd size based on the Petersen Index method requires that the underlying assumptions are met. The analyses presented below indicate that all the assumptions outlined in "Methods" were satisfied with reasonable accuracy, although several potential sources of violation were identified.

Assumption 1: The population is closed

Due to the short period of the census (21 days), no significant adult mortality, immigration or emigration was likely to occur. Thus, the assumption is valid.

Assumption 2: All highly aggregated groups contain at least one radio-collar and can thus be located

Caribou aggregations were located primarily through radio-telemetry, and groups containing no radio-collars could potentially have been missed, thus resulting in an under-estimate of the total population size. The probability of a group containing at least one radio-collar decreases with group size, and thus an unknown number of smaller aggregations could have gone undetected during the census. However, the number of undetected groups was probably small for the following reasons:

(a) Migratory caribou, including the Rivière George herd, tend to aggregate in a few large groups during the post-calving period, rather than in numerous small groups, when environmental conditions are suitable (Western Arctic herd: Valkenburg *et al.*, 1985; Porcupine herd: Whitten *et al.*, 1980; Whitten, 1985; Bluenose herd: McLean & Russell, 1988; Qamanirjuaq herd: Russell, 1990; Rivière George herd: RRCS, 1990; 1992). Post-calving aggregations of the Rivière George herd can consist of more than 100 000 caribou (RRCS, 1990; 1992). Large groups are likely to contain at least one radio-collar, thus resulting in their location.

If the entire herd was composed of groups of equal size, then the probability of groups with no radio-collars (p) can be calculated as follows:

$p = (1-N_g/N)^n$,
where n = number of radio-collars
N_g = group size
N = population size

For example, if the entire herd (about 550 000 caribou) was composed of groups of 5 000 caribou at the time of the census, then the probability of groups with no radio-collars would be 0.43. If, however, the herd was composed of groups of 15 000 caribou, then the probability of groups with no radio-collars would be very small (0.08). Because suitable conditions for aggregation were present during July 1993 (warm, calm weather, abundance of mosquitoes), most aggregations were likely to be very large and thus have a low probability of being unmarked. Caribou in the Torngat Mountains may be an exception, because lower temperatures may have resulted in a relatively dispersed distribution during the census period.

(b) Visual surveys conducted during telemetry monitoring resulted in the location of two highly aggregated groups with no radio-collars. However, these groups were believed to be a part of larger aggregations, containing radio-collars, that were photographed on a different day during the census.

(c) Previous surveys, involving both visual and telemetry surveys and conducted as a part of the Wildlife Avoidance Monitoring Program sponsored by DND to protect caribou from aircraft disturbance, indicated that radio-telemetry was a very effective method for locating all or most post-calving aggregations of caribou (RRCS, 1992).

(d) Studies in Alaska, which combined intensive visual and telemetry surveys, showed that most caribou of several herds (87% to 90%) would have been located during the post-calving period based solely on telemetry (Valkenburg *et al.*, 1985).

Assumption 3: Radio-collared animals are randomly distributed throughout the herd

Several possible sources of violation of this assumption exist. The first source of violation may arise from the fact that caribou equipped with radio-collars do not represent a random sample of the population. However, given sufficient time, random mixing of radio-collared caribou in the herd is likely based on:

(a) random distribution of the collared caribou in highly aggregated groups (see below), and;
(b) evidence of random mixing of similarly collared animals in other migratory caribou herds (Valkenburg *et al.*, 1985; McLean & Russell, 1988; Russell, 1990).

We used the X^2-test to compare the observed number of radio-collars per highly aggregated group in Table 1 to the expected number, assuming random distribution of radio-collared caribou among groups. Smaller groups were combined to achieve expected values of at least 3, and the entire Group 7, which at the time of photography contained duplicate observations of some collared caribou, was deleted from the analysis. The distribution of radio-collared caribou among the highly aggregated groups did not deviate from random (X^2 = 9.78, df = 7, P = 0.2), thus supporting the validity of the assumption.

A second source of violation of the assumption may arise from independent movement of males and females during the post-calving period. The sexes were mixed unevenly throughout the various groups, as evidenced by the observation of two aggregations consisting predominantly of adult males and few calves. However, the ratio of adults/collar in Group 1, containing 7 collared males and 2 collared females, was very similar to the ratio in groups containing only collared females (5 479 adults/collar in Group 1 versus a mean of 6 610 adults/collar in 7 groups with two or more collared females and no males; data from Table 1). This suggests that the aggregation behaviour of each sex was similar. Furthermore, the data on collared caribou indicate that mixing of the sexes occurred in large aggregations: all nine groups with two or more radio-collars and with at least one collared male also contained one or more collared females. Thus, any possible differences in behaviour of the sexes was not likely to affect our estimate.

A third potential source of violation of the assumption may arise from non-random dispersion of the 13 caribou collared in 1993 (12 in March and 1 in May). All five caribou collared just north of the Fraser River travelled northward, but their relocation sites show a dispersed pattern within the northern portion of the post-calving range of the herd. The remaining seven caribou, collared at different locations in 1993, had moved considerable distances from their original capture sites and were relocated within a central area for post-calving aggregations.

Some non-randomness was possible based on the distribution pattern of the caribou collared in 1993. However, the collars deployed in 1993 represent a relatively small proportion of the total number of radio-collars functional in the herd during the census. Furthermore, the group of five caribou captured north of the Fraser River that showed unidirectional movement had dispersed within the area they occupied during the census.

Assumption 4: No significant movements of caribou between photographed groups used in calculating the estimate occur during the census

Independence of observations was achieved by excluding those groups that contained repeated observations of individual collared caribou from the analyses (except Group 7, the size of which was reduced in proportion to the number of repeated observations of collars; Table 1).

Because of the low proportion of collared individuals in the herd, groups of unmarked caribou could potentially have broken off from an already photographed group and joined another group yet to be photographed. Large scale movements (involving groups of several thousand individuals) would most likely have been accompanied by collared caribou and therefore should have been detected by telemetry.

Comparisons with the June 1993 calving ground census

Since 1984, population estimates of the Rivière George caribou herd have been derived by photographing caribou in calving areas (Crête *et al.*, 1991). To obtain a more robust estimate of the size of the herd, two independent photographic censuses were carried out in 1993: a calving ground census in June (Couturier *et al.*, 1994) and a post-calving census in July (this study).

Both the June calving ground census and the July post-calving census resulted in similar estimates of the size of the Rivière George caribou herd (566,800 versus 540,040 adults in the June and July censuses, respectively). The post-calving census provided a more precise estimate, with 90% confidence limits of ± 12.8% versus ± 34% in the calving ground census. However, the error associated with the post-calving census may be greater than indicated due to uncertainty surrounding the exact number of functional radio-collars in the herd and the possibility that some highly aggregated groups did not contain radio-collars and hence were not included in the estimate.

Advantages and disadvantages of the post-calving photo-census methodology

The main advantages of a photographic census of post-calving aggregations are that;

(a) few assumptions regarding population structure are necessary, and;
(b) most caribou are counted directly from photographs, requiring extrapolation to only a relatively small segment of the population.

Radio-telemetry was used to locate post-calving aggregations during this census, and the presence of an adequate number of radio-collars in the herd is essential for a successful use of this method. The timing of photography is also critical, and caribou must be photographed when aggregated in well-defined, high-density groups.

The Petersen Index method, used to estimate population size, circumvents the two main drawbacks of photographic censuses of caribou aggregations:
(1) uncertainty regarding whether all caribou in the herd are located, and;
(2) problems associated with caribou that are not aggregated sufficiently for photography (Heard, 1985).

The Petersen Index method has been previously used to estimate the size of the Qamanirjuaq herd (Russell, 1990) and the Rivière George herd (Russell & Jakimchuk, 1991). Unlike these studies, we provide a measure of the error that is associated with the population estimate.

Potential problems associated with the application of the post-calving census methodology to the Rivière George herd result from the large population size and large summer range of the herd, necessitating extensive survey and photographic interpretation effort. In addition, forested terrain in parts of the range decreases the visibility of caribou on photographs. The caribou may also not aggregate sufficiently each year to enable efficient photography. Uncertainty regarding the number of functional radio-collars in the herd at any one time may also bias the estimate. However, the 1993 post-calving census shows that this method is a viable census method for the Rivière George herd, and that these potential problems are outweighed by the advantages of the method.

The precision of the population estimate derived from future post-calving censuses can be improved by two measures: First, caribou movements should be monitored closely throughout the month of July to ensure that all photographs are taken during the period of optimal aggregation. For example, post-calving aggregations began to form unusually early in 1993 because of an early spring, whereas the best photographs in 1990 were taken on 27-28 July (Russell & Jakimchuk, 1991).

A second measure to improve the accuracy of future post-calving censuses is to deploy more radio-collars in the herd. In 1993, we monitored 125 frequencies, but 33 of these were found to be inactive. The above measures should result in the photography of a high proportion of the herd under optimal conditions, thus reducing the error associated with the estimate.

Implications for herd management

Recent population estimates suggest that the size of the Rivière George herd has been stable within the past decade (Table 3). However, various other para-

Table 3. Recent population estimates for the Rivière George herd, 1984 - 1993.

Year (month or season)[a]	Census type	Adults[b]	90% Confidence limits Lower limit	Upper limit	Percentage	Source
1984 (fall)	calving	517 454[d]	388 091	646 818	±25%	Crête *et al.*, 1991
1986 (fall)[c]	calving	225 038[d]	137 273	312 803	±39%	Crête *et al.*, 1991
1988 (fall)	calving	564 895[d]	361 533	768 257	±36%	Crête *et al.*, 1991
1990 (July)[c]	post-calving	465 000	-	-	-	Russell & Jakimchuk, 1991
1993 (fall)	calving	566 800	374 655	758 945	±34%	Couturier *et al.*, 1994
1993 (July)	post-calving	540 040	470 701	609 379	±13%	This study

[a] time of year for which estimate was calculated.
[b] animals older than calves.
[c] these censuses were not complete.
[d] Crête *et al.* (1991) do not present directly the number of adults in the population. We computed the adult numbers from their data (total population size) and from the proportion of calves observed in the fall (see Table 12 in Crête *et al.*, 1989).

meters (e.g. physical condition, productivity) indicate a decline in the growth rate of the herd. Due to these uncertainties, caution should be exercised when developing management programs.

Because the 1993 post-calving census provides an accurate and precise estimate of the size of the adult population, herd size over the next several years can now be monitored with greater confidence by measuring the gross recruitment rate of juveniles in spring and the annual mortality rate of adult caribou. This requires that the annual harvest of caribou from the herd and the overall mortality rate of adults be accurately monitored.

We recommend that the total adult population be censused every 3-4 years, because the error associated with estimating population size solely from recruitment and mortality data is likely to increase over time. The results of this study indicate that oblique photography of post-calving aggregations is a cost-effective and precise technique for census of the Rivière George herd and should be considered for future censuses.

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Prevalence of *Echinococcus granulosus* and *Taenia hydatigena* in caribou in north-central Canada

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Abstract: There are few data on the prevalence and infection intensity of parasites in large samples of caribou (*Rangifer tarandus*). Therefore, differences related to sex, age, and season are unknown. The effect of parasites on the health and condition of caribou also is poorly known. From 1980 through 1987, 1258 barren-ground caribou (*R.t. groenlandicus*) were collected from the Beverly herd in north-central Canada. The prevalence in lungs of cysts of the hydatid tapeworm (*Echinococcus granulosus*) increased significantly with age of caribou. Prevalence in females was 2% in the 2-5 year class and 8% in older individuals. Cysts were more prevalent in young females compared with young males. Reductions in physical condition and fecundity were not statistically significant. The prevalence of *Taenia hydatigena* cysts in livers increased significantly with age of host but not with sex and condition of the hosts. The use of parasite prevalence as an index of predation rate is discussed.

Key words: caribou, *Rangifer tarandus*, parasites, *Echinococcus granulosus*, *Taenia hydatigena*

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Introduction

Most information on the prevalence and intensity (number and size of cysts/animal) of internal parasites of barren-ground caribou is based on small sample sizes and is not specific to sex, age, season, or condition of the hosts. Furthermore, the debilitating effect of these parasites, if any, is virtually unknown. Are they a limiting factor by lowering fecundity or increasing mortality? Some significant negative relationships occurred between the intensity of warble (*Oedemagena tarandi*) larvae and condition indices of caribou (reviewed by Huot & Beaulieu, 1985; Thomas & Kiliaan, 1990). Fecundity is inextricably linked to condition in caribou (e.g., Thomas, 1982). Therefore, any debilitating effect of parasites could reduce condition and, in turn, reduce fecundity. Mortality rate also is linked to condition.

The purpose of this paper is to report the prevalence and intensity of larval stages of *Echinococcus granulosus* and *Taenia hydatigena* in relation to sex, age, pregnancy rate, and physical condition of caribou, an intermediate host for these tapeworms. Additionally, I speculate on use of these parasites as indices of predation.

Data in this paper came from samples of migratory barren-ground caribou of the Beverly herd obtained in December and March. The Beverly herd uses forested winter range in northwestern Manitoba, northern Saskatchewan, and the Northwest Territories as far west as central Great Slave Lake. Information on parasites were obtained incidental to primary objectives related to evaluating effects of forest fires on caribou and their winter range. More details are in an unpublished report (Thomas & Kiliaan, 1994).

Methods

In cooperation with the Fort Smith Hunters and Trappers Association, 1258 caribou were collected from 1980 through 1987. Prior to 1985, there was no systematic search of lungs and livers for cysts. Some small hydatid cysts may have been overlooked by the hunters who were asked to report anything unusual about caribou while skinning and evicerating them. Beginning in March 1985, I visually inspected the lungs of all caribou and palpated them for internal hydatid cysts. The diameters of cysts were measured with a ruler. I also checked the surface of the liver for larvae and sections 3 mm apart enabled examination of most of the liver tissue.

Whole body weights were obtained with a dial scale and tripod. Depth of back fat was measured at its maximum thickness along a cut anterio-lateral to the base of the tail. Weights were obtained for the kidneys and for surrounding fat trimmed flush with

Table 1 Prevalence of lung and liver cysts in caribou sampled from the Beverly herd from March 1985 - 1987.

Month/ Year	*Echinococcus granulosus* Sample size	Caribou w/ cysts	Prevalence (percent)	*Taenia hydatigena* Sample size	Caribou w/ Cysts	Prevalence (percent)
Mar 85	162	8	4.9	162	25	15
Dec 85	78	2	2.6	77	23	30
Mar 86	150	7	4.7	149	32	21
Dec 86	49	1	2.0	49	11	22
Mar 87	49	1	2.0	40	9	23
Totals: Dec	127	3	2.4	126	34	27[a]
Totals: Mar	361	16	4.4	351	66	19[a]
Totals/ave.	488	19	3.9	477	100	21[a]

[a] Samples from all age classes and from December and March should not be pooled but the data are presented to facilitate comparisons with results for herds where age and season were not partitioned.

the ends of each kidney. A first incisor and first molar were used for age determination. Age was rounded to the next birthday; e.g., 5.5 became 6 years.

Data for all years were pooled for sex and age classes for comparisons with other pooled data even where grouping was not justified statistically. The significance of differences were tested with χ^2 where α was 0.05.

Results

Echinococcus granulosus

The range in prevalence was 2.0%-4.9% in five samples obtained from 1985 through 1987 (Table 1) (X^2=1.8, p>0.8). The age distribution of infected females differed from their age structure in the sampled population (Thomas & Barry 1990) but not when calves were excluded (X^2=14.8, p=0.11). Number of infected females in the 2-5 year and >5 year classes differed from that expected by the age structure (X^2=36, p<0.001). In females >1 year of age, a correlation of prevalence with age was significant (Spearman r=0.96, p<0.01). A plot of cumulative cyst volumes with age was not significant but average diameter of cysts was correlated with age (Spearman r=0.66, p<0.01). No cysts >4 cm in diameter occurred before age 6 years.

Table 2: Prevalence of *Echinococcus granulosus* in the lungs of caribou by sex and age classes, 1985 through 1987.

Age class (years)	Females Sample size	Prevalence (percent)	Males Sample size	Prevalence (percent)	Both sexes[a] Sample size	Prevalence (percent)
1[b]	10	0	6	0	16	0
2	26	0	27	0	53	0
3	57	2	53	0	110	2
4	59	3	19	0	78	1
5	40	3	16	0	56	2
6-11	143	8	12	8	155	8
>11	26	8	0	0	26	8

[a] Data pooled for comparisons with data from other studies.

[b] Cysts take several months to develop and therefore seldom appear in calves.

There were more infected females than expected from the 2 female:1 male ratio in the sampled population (X^2=4.7, p<0.05). The higher prevalence in female caribou was confined to the 3-5 year class (Table 2). The prevalence in caribou >5 years old was 8.3% in both sexes.

There were no statistical differences in prevalence for season (December vs. March) or for years (1985 vs. 1986 vs. 1987). Therefore, the data were pooled.

Data on parasite intensity and condition indices of 10 caribou with the most intense infections are presented in Table 3. The only caribou with a massive hydatid infection was considerably leaner than average for its age class (Table 3). An analysis of individuals whose condition indices were outside the confidence limits (CL) revealed the following: for weight, 5 lower than the CL and 9 higher; for depth of back fat, 11 lower and 7 higher; and for weight of kidney fat, 10 lower and 5 higher.

The prevalence of *E. granulosus* in females 2-5 years old did not differ between individuals with less than and greater than median back fat: 2% in each case (n=182). Nor was the difference significant in females >5 years old (prevalence 8% vs. 12%; n=172; p=0.4).

The pregnancy rate of infected individuals was 72% (n=18); that of non-infected females was 84% (X^2=0.9, n=279, p=0.33). However, only 1 of 10 females that were most-intensely parasitized was not pregnant (Table 3).

Table 3. Condition indices of the 10 caribou most intensively infected with *Echinococcus granulosus* and average condition indices for their sex and age class.

						Fatness: individual vs. average					
						Back fat (mm)			Kidney fat(g)		
Sex	Age (Yr)	Preg?	No. of cysts	Ave. dia (cm)	Cyst vol. (cm^2)	Indiv.	Ave[b]	CC[c]	Indiv.	Ave[b]	CC[c]
F	10	Y	6	2	11	5	12.2	2.7	102	101	12
F	9	Y	2	3	12	18	12.2	2.7	138	101	12
F	4	Y	1	4	13	22	18.9	4.8	84	64	23
M	7	Y	1	5	20	0	1.0	12.7	62	73	>99
F	14	Y	2	5	39	18	20.8	11.5	132	76	39
F	8	Y	1	7	39	40	18.4	2.7	131	123	11
F	6	Y	1	8	44	9	12.2	2.7	101	101	12
F	10	N	3	6	85	2	15.0	4.5	46	91	16
F	6	Y	7	4	88	11	4.6	3.3	125	65	15
F	6	Y	12	5	235	12	19.7	2.9	37	124	11

[a] Volume in cm^2.

[b] Average for age class.

[c] CC is basis for calculating the approximate confidence limit (CL) where CL = mean ± CC and CC = $SE\ X\ t_{.05}$ for N-1 samples (2 tail).

Taenia hydatigena

There was no difference in prevalence between males and female caribou even where age and season were taken into account. Data for prevalence were homogenous within the 2-6 and >6 year groups. Prevalence declined 30% and 25% from December to March in 2-6 year old and >6 year old caribou, respectively. These data are for females in 1985/86 and 1986/87, respectively, where sample sizes were largest. There was no change from December to March in 1986/87 when both sexes and all ages were combined (Table 1).

There was an age difference in prevalence in December samples: 0% (n=4), 23% (n=89) and 40% (n=30) in 1, 2-6, and >6 year old caribou respectively ($X^2=42$, $p<0.001$). The same trend, with lowered prevalence, continued in those age classes in March samples: 0% (n=12), 16% (n=257), and 30% (n=82) ($X^2=30$, $p<0.001$).

Prevalence of *T. hydatigena* in March samples was similar in pregnant females (PF) and non-pregnant females (NPF) >2 years old: in December samples, 31% in PF (n=59) vs. 26% in NPF (n=19); in March samples, 20% in PF (n=196) vs. 16% in NPF (n=31). Prevalence of cysts in March samples was also similar in females with greater than (>) and less than (<) median depth of back fat: in females 2-5 years old, both 14% (n=65, 64); in females >5 years old, 27% (>) vs. 23% (<) (n=59,61).

Discussion

Are E. granulosis *and* T. hydatigena *debilitating?*

These data are inconclusive for the hydatid tapeworm. The only caribou with a massive infection was relatively thin. If caribou with massive infections fall prey to wolves, there is little chance of sampling them. Massive infections of large hydatid cysts may make caribou more vulnerable to wolf predation where chases are long. However, light and moderate infections do not reduce condition and fecundity significantly. There was no indication that *T. hydatigena* was debilitating.

Parasite prevalence and intensity as an index of predation?

Information on the effect of predators on wild populations is exceedingly difficult to obtain. Because *E. granulosus* and *T. hydatigena* have obligate, definitive, canid hosts for the adult tapeworm, the incidence of these species in caribou may provide an index to predation rate. They may cycle primarily through wolves (*Canis lupus*) as opposed to coyotes (*C. latrans*) and foxes (*Vulpes vulpes*; *Alopex lagopus*) (Holmes & Podesta, 1968; Addison *et al.*, 1988). The prevalence of *E. granulosus* in caribou was 6.3% in the Qamanirjuaq herd (Broughton & Choquette, 1969); 3.9% in this study (Table 1); and 1.3% in the George River herd (Parker, 1981). Wolf abundance was subjectively rated as relatively high (Parker, pers. comm.), relatively low-moderate (Thomas, unpubl. data), and relatively low (Messier *et al.*, 1988; Parker, pers. comm.) in the relevant periods in the three herds.

The prevalence, mean number, and mean total weight of *E. granulosus* in moose in Quebec was related to moose density and in turn to wolf predation rate (Messier *et al.*, 1989). Pybus (1990) inferred a relationship between the prevalence of hydatid cysts in moose and wolf densities in Alberta. The required large number of caribou samples and accurate surveys of wolf numbers and predation rate are not available for any caribou-wolf system.

The prevalence of *T. hydatigena* in caribou also fits subjective evaluations of wolf abundance. Cysts occurred in 25% of 809 caribou sampled in 1966-68 in the Qamanirjuaq herd (Broughton & Choquette, 1969) and in 17% (n=159) and 43% (n=30) of caribou in the George River herd in April 1981 and 1984, respectively (Parker, 1981; Huot & Beaulieu, 1985). Except for the 43% in the small sample in 1984, prevalence fits subjective evaluations of relative wolf abundance among those caribou populations. Adult *T. hydatigena* occurred in 27-80% of wolves (Holmes & Podesta, 1968; Samuel *et al.,* 1978).

There are problems with using parasite prevalence as an indicator of predation rate in hunted populations. Biases may result from infections obtained from viscera left by hunters and wounded animals that die, fall prey to wolves, or are scavenged by wolves.

Age and sex differences

Data for parasite prevalence and intensity should be presented specific to age and sex classes. Comparisons with grouped data for other populations may be invalid unless age and sex structures are similar and sample sizes are adequate. Changes with age and sex may reflect lags between infection and expression of the larval stage; different distributions of age and sex classes relative to sites of exposure; behavioral (e.g., foraging) differences that affect ingestion of eggs; and acquired resistance to the parasite.

Whereas the prevalence of *E. granulosus* and *T. hydatigena* tended to increase with age, the prevalence of *Parelaphostrongylus andersoni* in caribou of the Beverly herd declined progressively with age (Lankester & Hauta, 1989). Also, *T. hydatigena* was more prevalent in yearling white-tailed deer (*Odocoileus virginianus*) compared with fawns and deer >2 years old, although intensity tended to increase with age (Addison *et al.*, 1988).

The intensity of warble (*Oedemagena tarandi*) larvae declined with age in female caribou in the Beverly herd (Thomas & Kiliaan, 1990) and in the George River herd (Parker, 1981). Acquired resistance was one of several possibilities (Thomas & Kiliaan, 1990).

Season and year differences

Little seasonal or annual variation in prevalence should occur for hydatid cysts that develop slowly and persist for years. The low infection prevalences also largely preclude statistically significant differences. In contrast, the decline of 25-30% from December to March in the prevalence of *T. hydatigena* may indicate annual infection in summer and constant resorption. The higher prevalence and lower seasonal decline in prevalence in caribou over 6 years old may implicate slower resorption.

Management implications

Forest exploitation in the boreal and cordilleran forests may increase the prevalence of *E. granulosus* in caribou. The parasite could become more prevalent with extensive forestry that produces more early-succession stages and greater densities of moose, wapiti, deer, and wolves. Whether such increases reduce the fitness of caribou remains to be seen. Research should focus on the effects of parasites and disease on population parameters such as condition, fecundity, and mortality.

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The diet of woodland caribou populations in west-central Alberta

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Abstract: The diet of woodland caribou (*Rangifer tarandus caribou*) populations in the foothills and Rocky Mountains of west-central Alberta was estimated by microhistological analyses of feces collected in winter and summer. In winter, terrestrial lichens averaged 60-83% of fecal fragment densities in both areas. In the mountains, decreasing proportions of terrestrial lichens and increasing proportions of conifer needles and moss indicated decreasing accessibility of forage because of deeper/harder snow. Apparent diets in summer were dominated by *Salix* spp., sedges, and lichens. However, forb inflorescences and stems were largely undetected by the microhistological technique and results for summer samples must be interpreted accordingly. We conclude that the conservation and management of forest ecotypes of caribou must include options of lichen-rich habitats as a major component of management plans.

Key words: alpine, boreal, cordillera, forestry, subalpine, microhistology, *Rangifer tarandus caribou*

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Introduction

Knowledge of diet is fundamental to definition of a species niche, habitat, and ecology. Dietary information for woodland caribou is scanty in boreal and cordilleran forests of western Canada east of the Continental Divide. Such information is needed to help conserve caribou in the southern commercial forest, which will be permanently altered by forestry and other developments. The primary habitat concern is reduced proportions and sizes of post-rotation forests and fragmentation. Furthermore, managers of protected ecosystems, such as Jasper National Park, are responsible for vegetation management that affects food supplies of caribou and the ecology of all species. What sorts of habitats should be safeguarded? Are lichens essential to the viability of forest-alpine ecotypes of caribou in western Canada?

Our primary objective was to assess and compare the winter diet of populations of caribou in west-central Alberta in relation to season, snow characteristics, and geographic location. One group of fecal samples came from winter ranges on the "east slopes" of the Rocky Mountains and are termed the "foothills" group. In winter, there are two subpopulations within each population of mountain (forest-alpine) and woodland (forest) ecotypes of caribou in the foothills (Edmonds, 1988) (Fig. 1). The forest-alpine ecotype migrates into alpine areas of the Willmore Wilderness, northern Jasper National Park, and adjacent British Columbia to calve and spend the summer. In addition, composite samples were obtained from a forest ecotype that occupies habitat year-round in the boreal forest. The second group of samples came from caribou wintering in the Rocky Mountains, mostly in watersheds of Jasper National Park. These caribou, in three subpopulations, traverse alpine, subalpine, and montane regions over short distances.

We also examined feeding craters dug in the snow by caribou in both areas. The purpose was to obtain independent information on diet by examining plant species present at feeding sites. Another objective was to obtain insights into forage selection by caribou by comparing data from the microhistological technique with the relative frequency of plant species found in feeding craters. Additionally, we checked the accuracy of the microhistological technique on plant species mixed by dry weight in proportions that simulated winter diet. We also assessed the ability of the technique to detect plants in the summer diet.

Methods

Pellets were obtained throughout the year from several locations on the ranges of the caribou populations. Fresh pellets from 5-30 groups were pooled into a composite sample by taking about equal amounts (2-

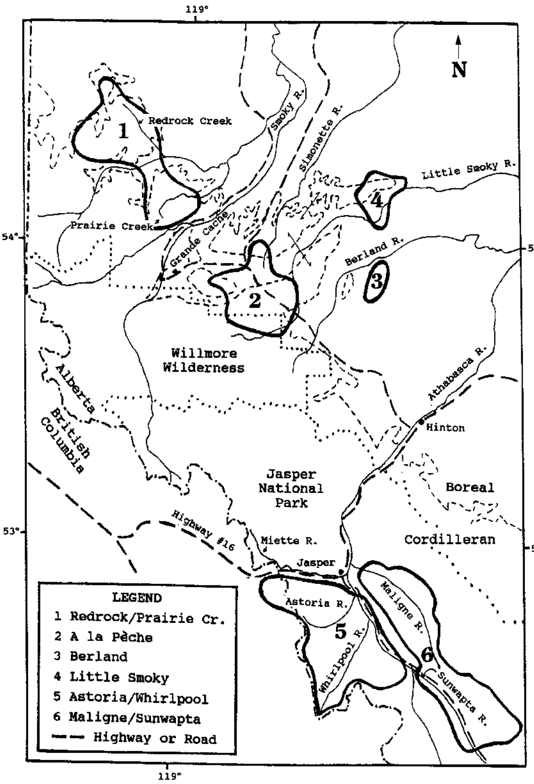

Fig. 1. Locations where fecal samples were obtained for this study of caribou diet.

Table 1. Plant fragment densities in caribou fecal pellets collected in winter from 1979-80 through 1982-83 in the Alberta foothills[a].

	Fragment densities (%)			
	1979-80	1980-81	1981-82	1982-83
No. of samples	7	23	37	12
Ave. snow depth: openings	60	<45	91	<45
Ave. snow depth: craters	41	15	62	25
Terrestrial lichens[b]	60	71	79	72*
Arboreal lichens	<1	<1	2	<1
Graminoids	6	5	3	4
Conifer (*Pinus & Picea*)	22	16	14	13
Equisetum spp.	<1	1	1	NA[c]
Shrubs	6	5	1	4
Moss	2	<1	0	2
Other species	3	1	0	4

[a] A la Peche, Prairie Creek, and Little Smoky River regions.

[b] *Cladonia*-type, *Cetraria*-type, and *Peltigera* spp. lichens.

[c] Data not available.

* indicates significant variation in row (Chi-square $p<0.05$).

5 pellets depending on size) from each group. Microhistological analyses at the Composition Analysis Laboratory in Fort Collins, Colorado, consisted of 20 fields in each of 5 slides. Percent relative densities of discerned plant fragments was shortened to "fragment densities" in this report, and termed "apparent diets" to facilitate presentation of results.

Plant species present at the bottom of snow craters dug by caribou were recorded and converted to frequency of occurrence. Those data reveal little about relative consumption of forages by caribou. However, inferences can be made about plant selection by comparing occurrence in craters with fecal analyses and by observing plant composition in craters and peripheral to them. Snow depths and hardness were recorded at a minimum of 10 points at crater peripheries and in openings in the forest. Caribou were observed feeding in summer and the frequency occurrence of grazed plants (parts removed) were tallied. Two mixtures of plants with dry weights that simulated winter diets were sent to the laboratory and the results compared.

All comparisons of plant species composition in fecal samples among seasons, areas, and years were tested using Chi-square and Kruskal-Wallis tests. Data for months, years, and locations were pooled where there was no statistical difference ($p>0.05$) between or among them. Comparisons between the two major study areas were made after results were adjusted by the amount of conifer needles and moss. We assumed that both of those plant groups were ingested incidentally with lichens and diet comparisons were best made on species selected by caribou.

Results

Apparent Winter Diet in the Foothills

Seventy-nine composite fecal samples were obtained from the A la Peche, Prairie Creek, and Little Smoky River drainages (Fig. 1) throughout the winters (October-April) of 1979/80 through 1982/83 (Edmonds & Bloomfield, 1984). The apparent diets were almost identical for all three areas and winter months. Therefore, data were pooled. The apparent diet of caribou on winter ranges in the foothills varied little over four winters in spite of pronounced differences in snow depth (Table 1).

Winter diet in the Rocky Mountains

Apparent diets were similar among years within watersheds (Thomas, 1993) but species composition

Table 2. Plant fragment densities in caribou fecal pellets collected from October through April, 1988-89 and 1989-90, in the Rocky Mountains[a].

	Fragment densities (%)						
	Early winter				Late winter		
Month	Oct	Nov	Dec	Jan	Feb	Mar	Apr
No. samples	7	7	8	6	8	9	8
Terrestrial lichens	79	78	83	79	71	70	67
Arboreal lichens	1	1	1	1	1	1	1
Graminoids	5	2	2	2	1	1	2
Conifer needles	4	7	6	9	13	12	18*
Equisetum spp.	3	2	2	2	0	1	2
Ledum spp.	3	4	3	4	6	7	5
Moss	2	3	3	2	7	6	4
Other species	3	3	0	1	1	2	1

[a] Maligne, Astoria, and Sunwapta river valleys of Jasper National Park.

* indicates significant variation in row (Chi-square $p<0.05$).

changed over the winter (Table 2). In comparisons of early and late winter, proportions of terrestrial lichens, graminoids, and *Equisetum* spp. declined while proportions of conifers, *Ledum* spp., and mosses increased.

Variations in apparent diets were slight in early winter among three regions in the mountains: Maligne, Astoria, and Sunwapta watersheds (Fig. 1). In late winter, plant species compositions were similar in caribou feces from those watersheds. However, proportions of terrestrial lichens were lower in two watersheds (Miette & Whirlpool, Fig. 1), near the Continental Divide, and in areas south of Jasper National Park. Increased proportions of *Ledum* spp. and moss accounted for most of the difference.

Winter dietary information for the Rocky Mountains (Table 2) excluded results from two areas where atypical foraging occurred in winter. Caribou foraged on the Medicine Lake drawdown delta, where fresh pellets collected during the winter contained mostly fragments of *Equisetum variegatum*. At a second location of the Maligne Valley, caribou fed mostly on arboreal lichens (*Bryoria* spp. and *Alectoria* spp.) in forests older than 400 years and with an easterly exposure. Long-strand lichens grew on widely spaced large and tall fir (*Abies lasiocarpa*) and spruce (*Picea englemanni*). That protein-poor diet (Nieminen & Heiskari, 1989) was supplemented with *E. scirpoides*.

The two species of horsetails that were eaten by caribou in winter were winter-green forms. Samples of *E. variegatum* and *E. scirpoides* obtained in July contained 10.2% and 9.2% protein, respectively. Three samples of *E. scirpoides* collected in March in Saskatchewan contained 6.8% protein.

Table 3. Mean relative densities of plant fragments in winter feces of two populations of caribou in Alberta and the densities adjusted by the proportion of conifer needles and moss.

	Foothills[a]			Rockv Mountains[b]		
	Unadjusted		Adjusted[c]	Unadjusted		Adjusted[c]
Plant group	Mean	SD	Mean	Mean	SD	Mean
Terrestrial lichens	69.9	(10.4)	85	74.3	(11.7)	87
- *Cladonia* type	41.1	(8.7)	50	69.7*	(11.6)	82
- *Cetraria* type	25.0	(6.3)	30	2.5*	(2.2)	3
- *Peltigera* spp.	3.8	(5.6)	5	2.0	(3.3)	2
Arboreal lichens	1.1	(1.1)	1	0.9	(1.0)	
Low shrubs	4.4	(2.9)	5	5.5	(7.8)	6
Graminoids	4.7	(3.2)	6	2.0	(2.3)	2
Equisetum spp.	0.7	(0.7)	1	1.2	(1.9)	
Other species	1.4		1	1.2		3
Conifer needles	17.1	(7.9)		10.7	(7.6)	
Moss	0.7	(1.4)		4.2	(4.9)	

[a] A la Peche, Prairie Creek, and Little Smoky River watersheds (n=79 composite samples).

[b] Maligne, Astoria, and Sunwapta valleys (n=53 composite samples).

[c] Adjusted by the proportion of conifer needles and moss to reflect forages selected by caribou and not consumed incidentally with lichens.

* Significant difference (Chi-square and *t* test).

Alpine areas with adequate food supplies were used in the foothills and the mountains in winters when the slopes were windswept. *Dryas* spp. was the most consistent item in the diet. In a sample from northern Jasper National Park, *Vaccinium* spp. (mostly berries) and *Dryas* spp. comprised 88% of the fecal fragments.

Apparent diet in the foothills and the Rocky Mountains

There was no statistical difference in the results for major forage groups between the two major wintering areas (Table 3). There were significant differences within plant types, such as less *Cladonia*-type lichens and more *Cetraria* spp. and conifer needles in the foothills samples. Other differences not reflected in Table 3 were more *Vaccinium/Empetrum* and less *Ledum* spp. in fecal samples from the foothills compared with those from the mountains.

Frequency of occurrence of plant species in craters

Frequency of occurrence (presence-absence data) in craters revealed high occurrences of *Cladonia* spp.,

Table 4. Frequency of occurrence of abundant plant species in snow craters dug by caribou throughout winter in the foothills and Rocky Mountains.

Species or group	Frequency of occurrence (%) in craters[a] Foothills (n=478)	Maligne (n=105)	Cavell (n=132)	Sunwapta (n=79)	Poboktan (n=52)
Cladonia type	63	90	89	92	67
Cladina mitis	64	79	86	28	19
Peltigera spp.	19	71	45	61	56
Stereocaulon spp.	12	20	19	3	2
Graminoids	23	30	4	42	94
Ledum spp.	52	36	43	11	12
V. vitis idaea	61	75	64	58	25
Moss	47	66	58	65	71

[a] 50% means that the plant was detected in half of the craters examined. These are presence-absence data.
Note: Variation significant (Chi-square, $p<0.05$) in rows except moss.

Cladina mitis, *Peltigera* spp., moss, *Ledum* spp., and *Vaccinium vitis-idaea* (Table 4). There was significant regional variation in the proportion of *Cladonia*-type lichens and a major component, *C. mitis*. The consistency of winter diet (Table 3) in contrast to the significant variation in major vegetation species in the craters (Table 4) indicated that caribou were selecting for *Cladina*-type lichens and selecting against low shrubs and moss.

Summer diet in the Rocky Mountains

Terrestrial lichens, *Salix* spp., and graminoids comprised 84-91% of apparent diets of the mountain populations of caribou (Table 5). Proportions varied significantly over the 3 months, reflecting changing preferences and, perhaps, dietary variation among groups of caribou. Sedges were eaten as early as mid-April in valley bottoms. Forb meadows, in seepage areas and along alpine streams, were used extensively in summer. In mid-August, caribou consumed at least 19 species of forbs in alpine areas that went undetected in the fecal samples collected concurrently

Table 5. Plant fragment densities in caribou feces collected from June through August, 1989-90, in alpine areas of the Rocky Mountains.

Month	Fragment densities (%) June	July	August
No. comp. samples	3	10	10
Terrestrial lichens[a]	55	29	40
Salix spp.	16	45	25
Graminoids	14	10	26
Conifer needles	7	<1	3
Moss	3	5	2
Equisetum spp.	1	4	2
Ledum spp.	2	3	2
Arboreal lichens	1	<1	<1
Other	1	3	0

[a] *Cladonia*, *Cetraria*, and *Peltigera* types.
Note: These data are biased by absence of forbs (see text).

Table 6. Percent composition (dry weight) of plant species in two mixtures simulating the apparent diet of caribou in the mountains in early and late winter and microhistological ("micro") fragment relative densities of the undigested mixture.

Plant species	Composition (%) Sample #1 Mixture	Micro	Sample #2 Mixture	Micro
Cladonia type[a]	75	75.8	65	70.5
Cetraria nivalis	3	2.3	2	0.3
Bryoria spp.	1	3.1	1	6.0
Usnea spp.	0	1.0	0	0.1
Peltigera apthosa	2	2.2	2	2.6
Ledum spp.	4	5.6	6	7.2
Pinus contorta	6	0.9	12	4.3
Picea englemanni	1	0	2	0
Carex spp.	3	2.7	3	1.1
Poa spp.	0	0.9	0	0.2
Pleurozium schreberi	3	4.4	6	6.5
Equisetum scirpoides	2	1.1	1	1.0

[a] Proportions (%) in samples 1 & 2, respectively: *Cladina mitis* 40, 34; *C. rangiferina* 10, 9; *Stereocaulon* spp. 10, 9; *Cladonia uncialis* 5, 4; Other *Cladonia* spp. 10, 9 (*Cladonia cornuta* and *Cladonia ecmocyna* in a 1:1 ratio).
[b] Dead, brown needles in the litter.

(Thomas, 1993). Therefore, apparent diets in summer may be highly biased using the microhistological technique, as cautioned by others (e.g., Boertje *et al.*, 1985).

The only data for the population that wintered in the foothills was for August in alpine areas north and northwest of Jasper National Park. There, the apparent diet was 54% terrestrial lichens, 38% shrubs, 5% graminoids, 2% forbs, and 1% arboreal lichens (Edmonds & Bloomfield, 1984). By late September and October, in the same area, the lichen component increased to 73% and shrubs decreased to 16%.

Plant proportions versus fragment relative densities

The microhistological results for two non-digested mixtures that simulated diet revealed close correspondence except for Pinus contorta needles and *Bryoria* spp. (Table 6).

Discussion

The winter diet of caribou in west-central Alberta did not change appreciably, either spatially or temporarly, provided the snow cover was soft, regardless of depth. The differences in apparent diet among locations in the mountains reflected, for the most part, variations in relative forage availability caused by deep snow containing hard layers, including ice. High evergreen shrub and moss content in the winter diet were indicators of poor range condition or poor availability, as found in Alaska (Boertje, 1984).

The diet of three subspecies of caribou that winter in boreal and cordilleran forests, where soft snow generally is <60 cm deep, were remarkably similar (Thomas & Barry, 1991; Russell *et al.*, 1993, this study). This similarity points to caribou "lichenophilia" and a high degree of consistency in surface vegetation under mature and old-growth pine forests over wide geographic areas.

The genus *Rangifer* is a lichen specialist although other herbivores eat lichens opportunistically. Caribou can survive on graminoids, forbs, and low shrubs in certain environments. These generally are insular, non-migratory populations not subject to much predation or severe insect harassment. The large herds of caribou exploit terrestrial lichens without exception. All species except *Peltigera* spp. occurred more frequently in caribou craters than in random snowplots used as controls (Edmonds & Bloomfield, 1984). Paradoxically, the other lichen genus with high protein content, *Stereocaulon*, is eschewed by caribou where it is abundant (Thomas, 1994).

Terrestrial lichens, when damp and where available, are consumed in summer by caribou (rev. by Boertje, 1984; Thomas, 1993). They are a high energy source and their continued use in summer may be necessary to maintain a microflora that is efficient at digesting them.

Winter-green forms of *Equisetum* spp. are selected by caribou in winter as indicated by high use of *E. variegatum* on the Medicine Lake delta and cratering for the sparse, wiry *E. scirpoides*. Moose (*Alces alces*) also cratered for the same species. *Equisetum* spp. generally have protein levels of 8% to 10% (range 5% to 15%) and are rich in minerals (Nieminen & Heiskari, 1989). Winter-green grasses and sedges are also important sources of protein in winter.

Management implications

Caribou dietary information and field observations in the study areas indicated the need for winter habitats where terrestrial lichens were relatively abundant. These generally were open, pine-dominated forests older than 80 and 100 years in the Foothills and Rocky Mountains, respectively. In winters with deep and crusted snow, some caribou moved to areas of more-favourable snow. Those were old spruce/fir dominated forest (>130 years in the Foothills and >200 years in the mountains) with high arboreal lichen biomass; alpine ridges with little snow cover; or subalpine and montane valleys with relatively shallow snow.

Alternative wintering areas may become important or critical to caribou in only 1 winter of 10 or 20. There are at least three reasons why caribou need optional areas to forage at regional and local scales. (1) They need optional regions to travel to when environmental conditions are unfavourable in parts of the traditional winter range. (2) They need alternate areas to prevent overgrazing and to allow grazed areas to recover lichen biomass. Caribou appear to rotate use of winter range by using one area for several winters and then shifting to another area. (3) They need optional habitat types locally when snow precludes them from using other types. These options must be left open for caribou in planning their habitat needs in managed forests.

Conclusions

The apparent winter diet of caribou populations was similar among foothills and Rocky Mountain regions in spite of significant regional variation in the vegetation at feeding sites. Diet changed involuntarily as vegetation became increasingly inaccessible because of thick snow containing icy layers.

Summer diet was dominated by graminoids, *Salix* spp. (leaves), terrestrial lichens, and an unknown proportion of forbs that went undetected by the microhistological technique.

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A fire suppression model for forested range of the Beverly and Qamanirjuaq herds of caribou

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Abstract: A fire suppression model was developed for forested winter range of the Beverly and Qamanirjuaq (formerly Kaminuriak) herds of barren-ground caribou (*Rangifer tarandus groenlandicus*) in north-central Canada. The model is a balance between total protection, as voiced by some aboriginal people, and a let-burn policy for natural fires advocated by some ecologists. Elements in the model were caribou ecology, lichen recovery after fire, burn history, community priorities for caribou hunting, and fire cycle lengths. The percent ratio of current productive caribou habitat to the goal for that habitat determines whether fire should be suppressed in a specific area. The goals for productive caribou habitat, defined as forests older than 50 years, were scaled by fire cycle length and community priority ranking. Thus, the model is an example of co-management: traditional knowledge combined with science in a joint forum, the Beverly and Qamanirjuaq Caribou Management Board.

Key words: caribou management board, co-management, fire, *Rangifer*

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Introduction

Caribou flesh is an important staple in the diet of aboriginal people living within the ranges of the Beverly and Qamanirjuaq herds in north-central Canada. The herds' combined economic-cultural value is incalculable. Understandably, then, fire suppression has always been a major concern of caribou hunters and those who speak on their behalf within the Beverly and Qamanirjuaq Caribou Management Board. Developing a fire management strategy has resulted from the successful marriage of traditional knowledge with government science and policies (co-management).

Co-management began with the Board's inception in June 1982; in 1992 its mandate was renewed for another 10 years. It is composed of five representatives from governments and eight members from aboriginal communities. The structure and functions of the Board are detailed in several reviews (Beverly and Kaminuriak Caribou Management Board, 1986; 1987; Scotter, 1991; Thomas & Schaefer, 1991; Usher, 1991). The Board is strictly advisory but its advice generally is accepted by the relevant jurisdictions.

The two caribou herds that the Board oversees occupy range west of Hudson Bay that includes winter habitat in the transitional boreal-tundra forest in northern Manitoba, northern Saskatchewan, northeastern Alberta, and the south-central Northwest Territories (NWT) (Fig. 1). Summer range is on the tundra in the NWT to about 66° N and some caribou spend all or part of the winter there as well.

Population estimates in June 1988 were 190 000 for the Beverly herd and 221 000 for the Qamanirjuaq herd (Heard & Jackson, 1990a; 1990b). The Beverly herd was estimated at about 286 000 in June 1994 (A. Gunn, pers. comm.).

The two herds are used by 12 000-15 000 people in 19 communities (Fig. 1). The annual kill is 14 000-18 000 caribou but an estimated 26 000-33 000 caribou would be killed if the herds were fully accessible to all communities in any 1 year (Thomas, 1994). There is concern that future needs for caribou will increase because human populations on the range are doubling in 16-20 years and new roads into the region potentially will expose the herds to hunters from outside the range of the herds.

The economic value of the two herds in the 1980s, in terms of the replacement value of meat, was about $13.5 million (Government of the

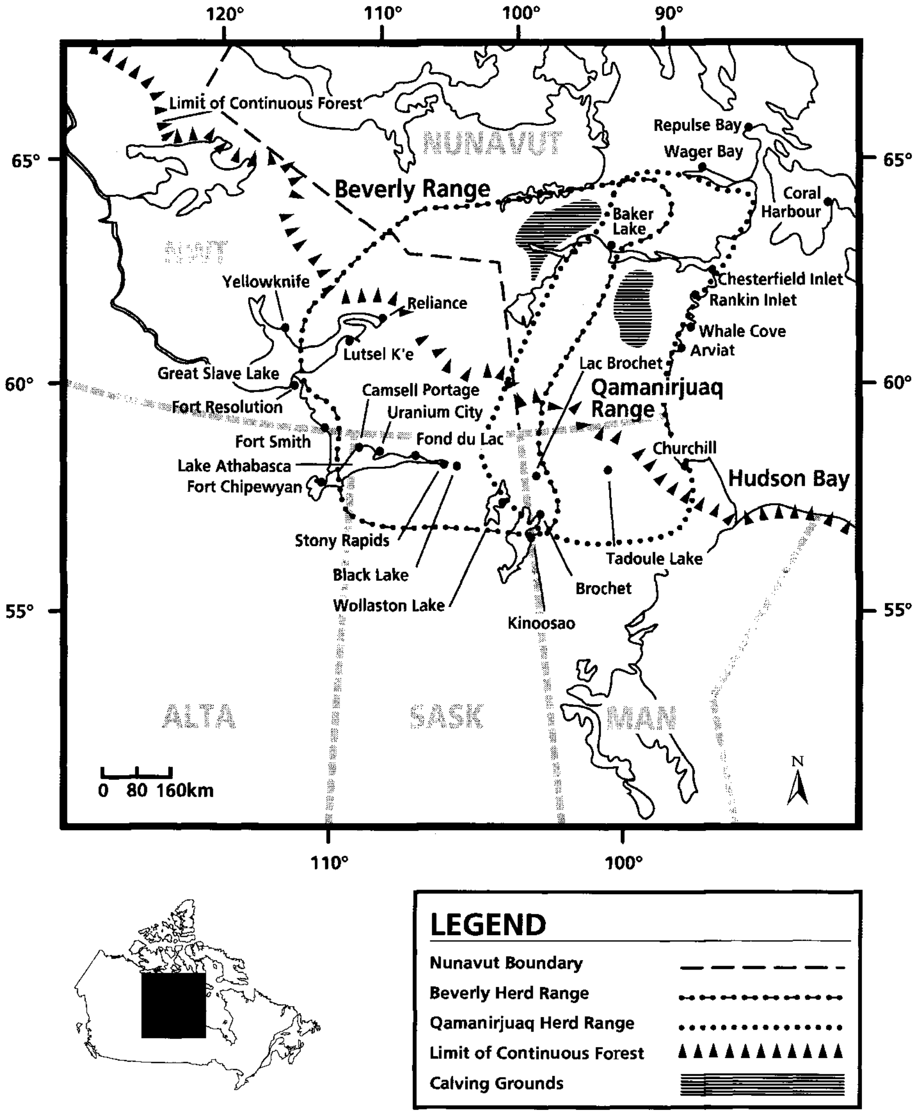


Fig. 1.
Ranges of the Beverly and Qamanirjuaq herds of caribou and caribou-using communities. Generalized ranges, since about 1955.

Northwest Territories, 1990). In Manitoba, the average harvest is valued at $1.9-2.4 million annually in replacement value of red meat. Corresponding numbers for Saskatchewan and the NWT are $2.5-3.1 million and $7.6-9.5 million. These values would double or triple if caribou were accessible to all communities and the herds could be managed at a higher sustained yield. With effective caribou and land management, the resource is sustainable at present population sizes of caribou and humans. However, the optimum and maximum sustained yields are not known and they would vary according to the weather.

The cultural, social, and spiritual value of the caribou in the two herds is incalculable but it is immense in the opinion of the Board. Other economic and cultural activities such as trapping and fishing are closely linked to caribou hunting. The herds also have considerable intrinsic value not only to Canadians but to the people of all nations.

Fire suppression relates directly to Objective 3 of the Board's management plan:

> *Access and availability: to ensure that caribou are accessible and available to traditional users. (Beverly and Kaminuriak Caribou Management Board 1987).*

It also concerns Principle 8 of that Plan:

> *The maintenance of suitable caribou habitat, including preservation of calving grounds and*

migration routes and pursuit of improved fire management, is essential.

Usher (1991), in a review of the Board, found that fire management was of high priority for hunters and trappers in forested portions of the range. Progress in development of fire suppression guidelines was too slow.

There is no justification for fire suppression based on the natural ecosystem, fire suppression capabilities, or caribou conservation. Fire is a natural component of the ecosystem as almost all of the burned area is lightning-induced (Johnson & Rowe, 1973; Johnson, 1979). The justification for fire suppression is based strictly on the food and socio-economic requirements of local communities.

The purpose of this report is to provide background information on two caribou populations and the Board established to help manage them, to outline the steps that were necessary to develop a fire suppression strategy, and to briefly report the recommendations that resulted.

Methods

The development of fire management recommendations occurred in several stages.

1. Scientists and aboriginal people jointly conducted a study of the winter ecology of the Beverly herd of caribou with emphasis on: (a) the adequacy of the forested winter range to support the population (Thomas & Kiliaan, 1994a); (b) the effect of burns on the regional and local distribution and movements of the herd (Thomas, 1991); (c) the recovery sequence of "caribou lichens" after fire; and (d) relative use of forests at time periods after fire (Thomas & Kiliaan, 1994b).
2. The burn history in the preceding 50-60 years was mapped from: a) burn maps provided by each jurisdiction and various other sources; (b) satellite imagery first obtained in 1972; and (c) dating of burns in field studies (Beverly and Qamanirjuaq Caribou Management Board, 1994a; 1994b).
3. The BQCMB sponsored a survey by the Prince Albert Tribal Council to obtain priorities for fire suppression on traditional hunting areas of 13 communities (Dantouzie, 1991; 1992).
4. The burn history, priority hunting areas, fire suppression priority areas and current proportions of productive caribou habitat and goals for such habitat within them were incorporated into a Geographic Information System (GIS - SPANS).
5. Fire suppression recommendations were developed after a technical review (Beverly and Qamanirjuaq Caribou Management Board, 1994a) examined the winter ecology of caribou, fire history of caribou ranges, past fire suppression on the range of the herd, fire management policy in each jurisdiction, and community priorities for hunting areas.
6. A brief report was drafted (Beverly and Qamanirjuaq Caribou Management Board, 1994b) containing all the information that was needed to implement the recommendations.
7. A fire suppression priority map was drafted that simplified information necessary for fire agencies to address goals for productive caribou habitat within each fire suppression area (Beverly and Qamanirjuaq Caribou Management Board, in prep.).
8. Consultation took place with communities and fire managers. As stated previously, communities within the forested range of the two herds mapped priority areas for caribou hunting and fire suppression. Board representatives discussed the draft recommendations and priority areas, and provided fire history maps and the fire management zones at scales of 1:250 000 and 1:1 million (National Topographic Series). Fire managers were provided draft reports for review and met with the Board to discuss the recommendations.

Some of those steps require further elaboration. The maps for 13 communities were simplified to one map by removing overlapping zones, simplifying the priority ratings, and accepting the highest rating for any area of overlap. The resultant composite map of community priority ratings was modified into fire suppression areas by: (1) adding fire cycle boundaries; (2) adding jurisdictional boundaries; (3) including only areas within the limit of continuous forest; (4) subdividing large community-priority areas and grouping small areas into larger ones and averaging the priorities; and (5) removing small areas created by fire cycle boundaries within fire suppression areas and including them in the adjacent area.

Fire cycles of three lengths (short = <80 years, medium = 81-140 years, and long = >140 years) were mapped (Fig. 2) to account for widely different fire return intervals across the range. The mapping was based on field observations of the return interval of fire and fire statistics over the past 20-40 years (Beverly and Qamanirjuaq Caribou Management Board, 1994a). The boundaries are arbitrary, however. These fire cycles are viewed as average, centuries-long disturbances and they cannot

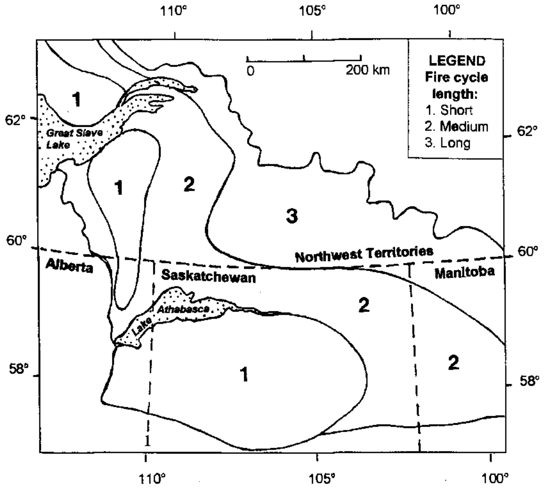


Fig. 2. Fire cycle lengths on the forested range of the Beverly and Qamanirjuaq herds of caribou as estimated from fire statistics and observed fire return intervals.

Table 1. Goals for the proportion of forest older than 50 years (productive caribou habitat) by communities' priority rank for caribou hunting and by length of the fire cycle.

	Goal for proportion of forest >50 Years (%)		
Communities' priority rank	Short cycle (<81 years)	Medium cycle (81-140 years)	Long cycle (>140 years)
1	35	60	85
2	30	55	80
3[a]	25	50	75
None	20	45	70

[a] Goals in this line correspond to the estimated long-term, average proportions of productive caribou habitat in each fire cycle zone.

be estimated by just using burn statistics for the past 20 or 30 years.

Goals for productive caribou habitat were established for each priority rating. These goals are proportions of productive habitat for caribou feeding (herein shortened to "productive caribou habitat" and defined as forests older than 50 years). Lowland spruce bogs and small lakes (<10 km^2) were included in the forest category. The original goal for maximum percentage of productive caribou habitat was arbitrarily set at 80% and decreased by absolute units of 10% as community priority rankings decreased from 1 to 4 and as the fire cycle length decreased from long to short. The 80% maximum value was predicated on maximum use by caribou of forests older than 150 years, the relationships between fire cycle length and percentage of productive caribou habitat (Beverly and Qamanirjuaq Caribou Management Board, 1994a), and the need to maintain forest diversity.

The preliminary goals were found to place too much emphasis for fire suppression on caribou range outside the core and commonly-used areas and in areas with a short fire cycle. Therefore, they were revised. The estimate for the long-term, average proportions of productive caribou habitat was set as the goal for community priority rank #3 within each fire cycle zone, and the goals were scaled upward and downward from there (Table 1).

Goals were scaled to long-term, average fire cycle lengths recognizing that any attempt to greatly modify fire cycles is not ecologically tenable. Moreover, it would be prohibitively expensive and perhaps counterproductive. Recent burns act as fire breaks and forests, particularly pine forests, are more susceptible to fire as they age and fuel builds (Rowe *et al.*, 1975). Successful fire suppression over a long period could result in loss of diversity and loss of large areas of productive caribou habitat in a severe-fire-year.

Decisions on whether fires should be suppressed depends on the present proportion of productive caribou habitat (P) relative to goals for productive caribou habitat (G) in a particular zone. The ratio of the two percentages determines suppression priority. For example, the notation "30P/70G" in a fire suppression area means that 30% of the range presently is productive foraging habitat for caribou and the goal is 70%. In theory, all fires would be suppressed in that area. A notation of 80P/70G means that goals are exceeded and no suppression is required.

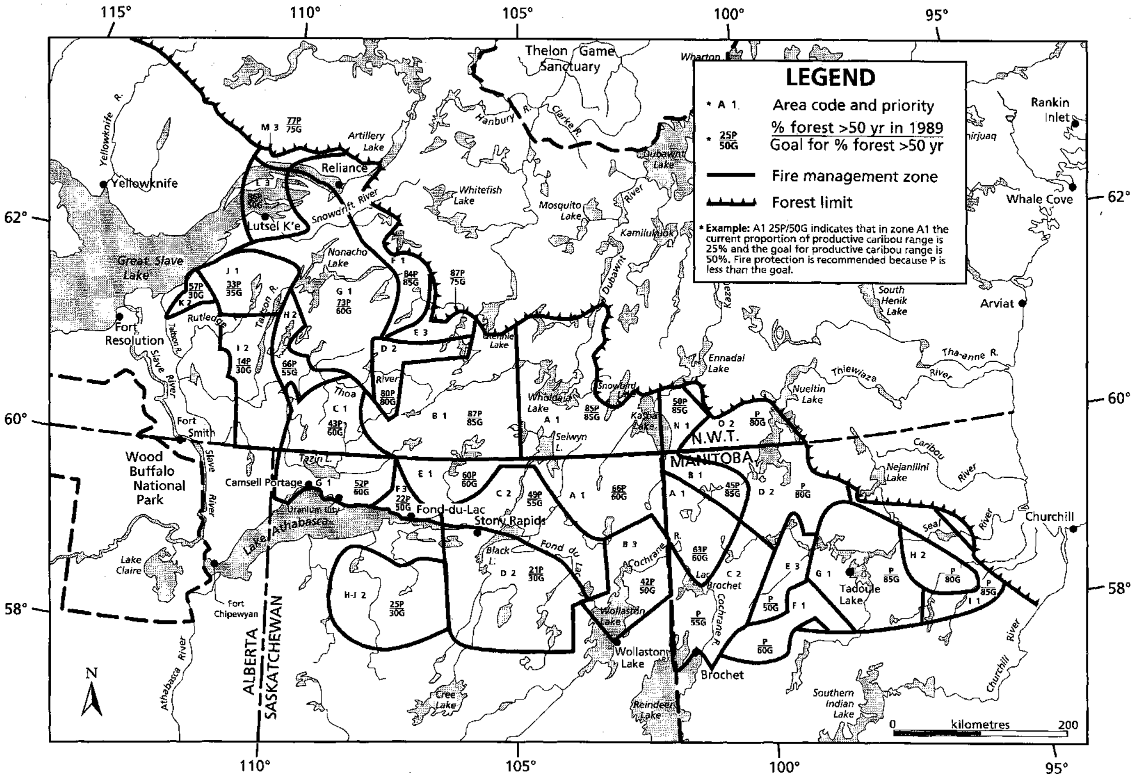
Results

Recommendations were developed to guide fire suppression on the range of the Beverly and Qamanirjuaq herds (Beverly and Qamanirjuaq Caribou Management Board, 1994a; 1994b).

1. That fire management agencies in each jurisdiction attempt to meet goals for productive caribou habitat within fire suppression areas (Fig. 3).
2. That fire management agencies attempt to meet goals for productive caribou habitat within caribou habitat protection areas beyond the community priority areas, if new data indicate the need. In future, the Board may recommend different boundaries and priorities for fire suppression as:

(1) the herds are managed more intensively at a higher population size; or (2) new data indicate overuse of winter range by caribou; or (3) conservation of the herds becomes a concern.

3. That fire management agencies develop administrative structures that will permit cooperative and cross-jurisdictional fire suppression operations. Agreements should be established between and among jurisdictions such that detection and suppression operations are shared. For example, reciprocal agreements could mean that suppression costs by one jurisdiction in another would be repaid in kind at a later date.
4. That fire management agencies enhance resource user participation in fire suppression. Greater participation by caribou hunters is requested for all stages of fire suppression within the caribou range. Enhanced roles include the setting of priorities in their chosen areas, suppression strategies, training of crews, and local management. Experienced crews trained in initial attack should be available in each large community. Such crews could attempt to suppress fires within hours of their detection, if warranted.
5. That fire management agencies obtain burn maps annually and that the fire history be updated periodically in a Geographic Information System.The updating interval for fire history will depend on discussion and negotiation among fire management agencies. The updating interval for present proportions of productive caribou habitat could range from 1 to 10 years but every 5 years is feasible.
6. That field checks be made to establish ages of all burns of unknown age and that attempts be made to map and classify mature (51-100 year), old (101-200 year), and ancient (>200 year) forests.
7. That for all large fires (>10 000 ha), data be obtained on burn characteristics, including percentage of unburned inclusions within each burn.



The present (P) (in 1989) proportions of productive caribou range and the goals (G) for each fire management zone, which were delineated from grouped community priority zones, fire cycle boundaries, jurisdictional boundaries, and forest limits, then simplified.

Fig. 3. Coded (A, B, etc.) simplified fire management areas based on composite priority (1, 2, etc.) areas of communities, fire cycle lengths, jurisdictional boundaries, forest limits; each containing preliminary estimates percent of productive (P) (>50 year forests) caribou habitat in 1989, and preliminary goals (G) for productive caribou habitat.

Discussion

The objectives, goals, and principles of fire suppression were defined in the detailed technical report (Beverly and Qamanirjuaq Caribou Management Board, 1994a). The recommendations call for recognition of cultural values by fire managers and greater participation by local caribou resource users at all stages of fire suppression. However, the recommendations also reflect the realization that fire is necessary to sustain the existing ecosystem. In the long term, fire can be modified only slightly by human intervention in remote, fire-dependent forests. A system of priorities is necessary to focus fire suppression activities.

Although the recommendations were passed by the Board, support was not unanimous. Opposition to the model was expressed by some aboriginal members, and Manitoba was not prepared to suppress fires on the range of the Qamanirjuaq herd. Consensus is highly unlikely for an issue as complex and emotional as fire suppression. However, the Board was committed to developing a strategy. The result is a balance between attempts at complete suppression of all fires on the forested range, as advocated by some aboriginal members and community residents, and no suppression, as proposed or inferred by some ecologists (e.g., Johnson & Rowe, 1973; 1975; Rowe *et al.*, 1975). Winter habitat was considered to be adequate in the mid-1980s and the local and scientific evidence suggests that, if one area is extensively burned, the caribou will use adjacent less-burned areas.

Some elements of the strategy are still being developed. For example, the Board is reviewing the goals for productive caribou habitat and is considering ways to simplify the model for greater understanding of it by the communities and fire managers. One map expresses, by colours, three levels of the departure of current proportions of productive caribou habitat from the goal within each fire suppression area. There is still debate whether priority for fire suppression should be proportional to the degree of deviation from the goal. There is need to update the burn map and statistics as they are 5 years out of date and many large burns occurred on the range in 1994.

When should a fire be suppressed? For fire management agencies it depends on the values that may be lost if the fire is allowed to burn naturally. Scale is important. In the case of caribou, values may be partitioned into regional values of the herds and local values within traditional hunting areas. Some tangible values are known for the herds as a whole, by jurisdiction, and by community based on the average number of caribou killed. If winter range limited herd numbers, it would be possible to calculate the value of winter habitat that burned in terms of the reduced sustainable yield of caribou. The herd was not limited by the quantity and quality of the winter range in the 1980s so no such losses can be calculated.

The value of caribou to a community is a local issue related to the distribution and movements of the caribou. Absence or scarcity of caribou for part or all of a winter causes nutritional, economic, and social hardship. It may be due to natural variation in movement patterns of the herds, reduced caribou population size, and/or loss of winter range because of fire. In the latter case, the values are partly economic due to increased travel (time and money) and loss of cabins and equipment. But there are also largely unmeasurable social costs. Costs could include hardships that influence the social fabric of a community, as well as some loss of cultural identity.

The fire model provides guidance to maintain sufficient winter range within traditional hunting areas such that, potentially, the caribou resource can be sustained in the traditionally-hunted areas of each community. A key point is the weight given to the cultural value of caribou in assessments of values-at-risk. Such values cannot be expressed in conventional cost-benefit analyses. Nevertheless, the Board has requested that they be given considerable weight.

Conclusions

The fire suppression model is a first attempt by the Board at welding scientific and local knowledge on caribou, caribou ecology, caribou-fire relationships, caribou hunting, fire history, and fire suppression into a strategy that will focus fire suppression into areas of socio-economic importance to communities dependent on caribou for sustenance. The model is still being revised and it will require periodic updating. Whether there will be sufficient funds or human resources to implement the strategy remains to be seen. Fire suppression generally is allocated to other areas where values-at-risk are perceived to be higher. However, a fire suppression strategy was an essential first step. And thanks to the involvement of hunters in the caribou-fire studies, the use of local knowledge in the setting of priorities, and a co-management forum that allowed the strategy to be developed, such a model was successfully created.

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Genetic survey of caribou populations using microsatellite DNA

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Abstract: Microsatellite loci are highly variable regions of eukaryotic DNA that consist of tandemly repeated sequences of one to six nucleotides in length. The use of microsatellites and the Polymerase Chain Reaction (PCR) are powerful tools for quantifying genetic variation within and among individual populations. Recently, we have developed primers for caribou that amplify 4 microsatellite loci. These microsatellite loci were used to survey the genetic variation in populations of Barren-ground caribou (*Rangifer tarandus groenlandicus*), Peary caribou (*R.t. pearyi*) and Woodland caribou (*R.t. caribou*) of Canada. The four loci examined were all polymorphic, revealing high levels of heterozygosity (> 0.74) in all of the study populations.

Key words: microsatellites, DNA fingerprinting, population level analysis, *Rangifer tarandus*

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Introduction

DNA fingerprinting was first introduced in 1985 by Jeffreys *et al.*, which involved the analysis of highly variable regions of DNA (tandem-repetitive 'minisatellite' regions of 10-50 bases). Variation observed at these regions arises very rapidly relative to other types of DNA and the high levels of heterozygosity at these regions have been utilized to identify relatively unique genotypes in individuals, dubbed 'DNA fingerprints'. The use of DNA fingerprinting has provided valuable information in the analysis of genetic diseases, forensics and ecological genetics (Jarman & Wells, 1989). This technique has been applied to study genetic variation in wildlife populations. For example, Gilbert *et al.* (1990) were able to show population differentiation using DNA fingerprints among Channel Island fox (*Urocyon litoralis*) from isolated islands, and Gibbs et al. (1990) revealed multiple paternity in families of polygynous red-winged blackbirds (*Agelaius phoeniceus*). However, there are limitations to the standard methods of DNA fingerprinting and their application to population level analysis. For example, multi-locus minisatellite analysis may reveal bands of varying intensity and comparisons between gels may lead to subjective and possibly incorrect decisions about band identities. Similarly sized alleles from different loci make the estimate of genetic parameters much more difficult. Furthermore, slight variation in the experimental conditions can produce erratic results, such as samples that vary in the amount of DNA and gels run under slightly different conditions (Queller *et al.*, 1993).

In 1989, Weber & May introduced a new technique of DNA fingerprinting, known as microsatellite analysis, which was first developed to facilitate genetic mapping in humans. Microsatellites are simple sequence loci that are widely dispersed in eukaryotic genomes and are highly polymorphic due to variation in the number of repeat units (1 to 6 base pairs in length) . The large number of microsatellite loci combined with their high variability make them ideal markers for genetic analyses at the level of populations. Microsatellites provide many advantages over other methods of genetic analysis, including: single locus analysis - providing for ease of interpretation (Weber & May, 1989), comparisons may be made across gels for loci, the genotypes of 36 individuals at as many as 3 loci can be determined from a single gel (Edwards *et al.*, 1991), and microsatellites developed in one species can used in related taxa thereby saving time and effort in the development and screening of genomic libraries. For example, microsatellites developed for the long- finned pilot whale (*Globicephala melas:* Odontoceti) were found to be useful in the analysis of variability in other whale species, including all toothed and baleen whales (*Mysticeti*) (Schlötterer *et al.,* 1991). In addition, amplification of microsatellite loci through the Polymerase Chain Reaction

(PCR) allows for use of small samples of DNA. Large amounts of specific DNA fragments can be synthesized from a small amount of initial DNA template. The template is amplified by repeated cycles of heat denaturation, annealing of oligonucleotide primers (short specific sequences of single stranded DNA) to the complementary strands of the template DNA, and the synthesis of DNA (White *et al.*, 1989). A single copy of a nucleotide sequence of interest can be amplified over a million times in only a few hours. With the use of PCR it is possible to obtain DNA from single hairs (Higuchi *et al.*, 1988) and fecal samples (Höss *et al.*, 1992) for use in DNA fingerprint analyses.

Here we report data from the analysis of four microsatellite loci in populations of Peary caribou (*Rangifer tarandus pearyi* - Western Queen Elizabeth Islands), Barren-ground caribou (*R.t. groenlandicus* - Beverly and Bathurst herds) and Woodland caribou (*R.t. caribou* - George River herd and Mount Revelstoke and Glacier National Parks).

Materials and methods

Caribou samples were obtained through the DNA Repository at the University of Alberta maintained by Parks Canada. The distribution of caribou populations used in this study is represented in Fig. 1. Caribou genomic DNA was isolated from blood or tissue samples using an Applied Biosystems Genepure 341 Nucleic Acids Purification System.

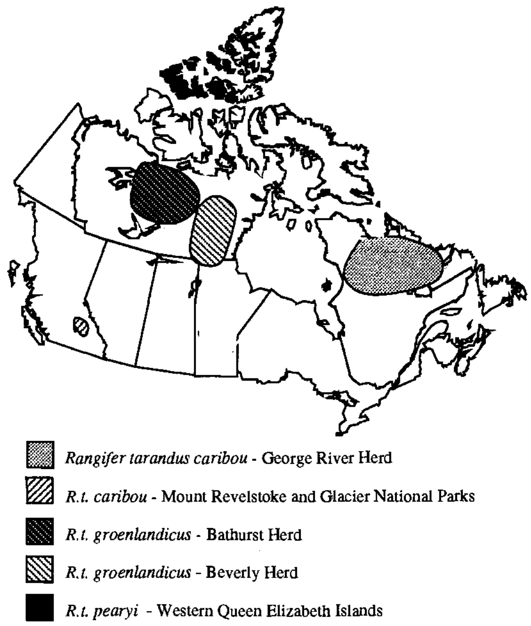

Fig. 1. Study populations of caribou (*Rangifer tarandus* sp.) in Canada.

Four microsatellite loci were developed within our laboratory for caribou. Random segments of caribou genomic DNA were cloned into M13mp18, and the resulting library was screened with a biotin-labeled oligonucleotide which would hybridize to a microsatellite repeat [AC] . The nucleotide sequences of the positive clones were determined and primers that bound to the DNA flanking uninterrupted repeats were chosen (Coffin & Strobeck, unpubl. data). Subsequently, one primer for each clone was flourescently labeled by incorporation of FAM-amidite (Applied Biosystems) during synthesis.

Microsatellite loci were amplified using Taq polymerase and the fluorescently labeled primers in a Perkin-Elmer 9600 Thermal Cycler. Alleles of the four loci were separated by polyacrylamide gel electrophoresis using a Model 373A Automated DNA Sequencer (Applied Biosystems) and scored using 672 Genescan PCR Analysis software (version 1.2, Applied Biosystems). DNA size standards (Genescan 2500 ROX, Applied Biosystems) were run on all gels to provide a reproducible standard at every base position and to allow for comparisons to be made across gels.

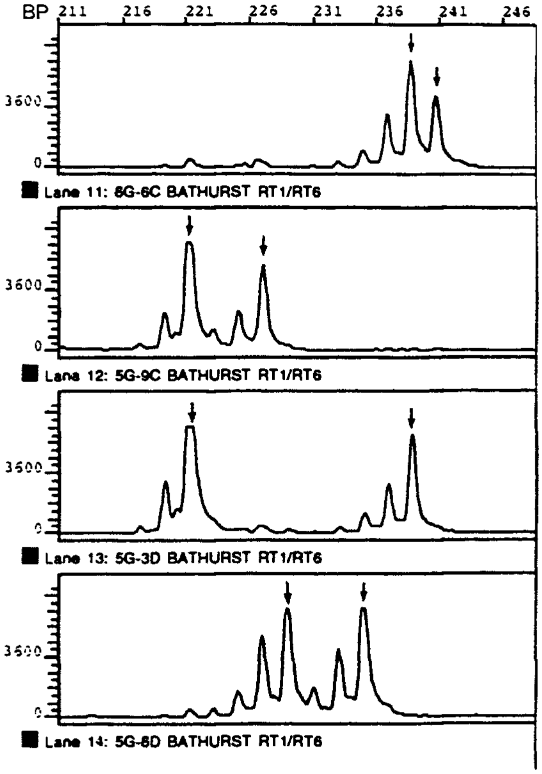

Fig. 2. Electrophoretogram revealing 6 alleles at microsatellite Locus RT 1 (resolution of alleles differing by as little as one base pair).

Heterozygosity and probability of identity were calculated using the formulae:

$$1-\sum_{i} p_i^2, \text{ and } \sum_{i} p_i^4 + \sum_{i}\sum_{j>l}(2p_ip_j)^2$$

respectively, where p_i and p_j are the frequencies of the ith and jth allele.

Results and discussion

The 4 loci used to survey caribou were all highly polymorphic. Alleles were sized according to the length of nucleotide base pairs (Fig. 2), allowing for precise allele identification at all loci. A minimum of 5 alleles were identified for any given locus in all of the caribou populations (Table 1). A total of 12, 13, 12 and 11 alleles were identified for microsatellite loci RT 1, RT 6, RT 7 and RT 9, respectively. Loci reveal considerable variation of alleles within and among caribou populations. For example, locus RT 1 in *R.t. pearyi* (WQ) exhibits a relatively high frequency of alleles 1 and 6, and at locus RT 7 in *R.t. caribou* (MG), alleles 3 and 12 are observed with relatively high frequency in comparison to other caribou. Also, the George River herd (*R.t. caribou*) exhibits a high frequency of allele 11 which is not present in any other of the study populations. These data suggest that caribou populations have significant differences in allele frequency distributions at microsatellite loci. With the sensitivity exhibited at loci, it may be possible to determine from which population a caribou originated. An unknown caribou could be assigned to a population in which its genotype (across many loci) is most common, with a minimal margin of error.

Expected heterozygosity is a standard measure of genetic diversity that estimates the probability that an individual in a random mating population will be a heterozygote (two randomly chosen gametes are different). Heterozygosity indices of the 4 loci combined range from 75% in the Western Queen Elizabeth Islands herd (*R.t. pearyi*) to 82% in the Bathurst herd (*R.t. groenlandicus*) of the Northwest Territories (Table 2). Individual loci had a minimum heterozygosity of 66% (RT 7, WQ), indicating that microsatellite loci are highly variable in caribou. These results are consistent with the levels of heterozygosity found in other large mammal populations. For example, Amos et al. (1993) found 54 alleles at a single microsatellite locus in long-finned pilot whale (*G. melas*) pods. Also, Paetkau & Stobeck (1995) found a mean heterozygosity level of 60% in Canadian polar bear populations (*Ursus maritimus*), whereas previous genetic studies of such populations using allozymes and mitochondrial DNA sequence have consistently found little or no variation.

Probability of identity estimates the probability that two randomly chosen individuals in a population have identical genotypes (Paetkau & Strobeck, 1994). The probability of identity was approximately 1:25,000, 1:60,000, 1:132,000, 1:1,600 and 1:14,000 for QW, BE, BA,GR and MG caribou populations , respectively (Table 2). The ability to identify individuals in a given population has many applications for use in wildlife forensics and management. The low

Table 1. Allelic variation at microsatellite loci in caribou populations of Canada. WQ - *R.t. pearyi* - Western Queen Elizabeth Islands (n=10), BE - *R.t. groenlandicus* - Beverly herd (n=9), BA - *R.t. groenlandicus* - Bathurst herd (n=9),GR - *R.t. caribou* - George River herd (n=13), MG - *R.t. caribou* - Mount Revelstoke & Glacier National Park (n=18).

	Number of Alleles at Microsatellite Loci																			
	Locus RT 1					Locus RT 6					Locus RT 7					Locus RT 9				
Allele	WQ	BE	BA	GR	MG	WQ	BE	BA	GR	MG	WQ	BE	BA	GR	MG	WQ	BE	BA	GR	MG
1	4	–	1	1	–	–	–	1	–	–	–	–	1	–	–	–	–	1	–	–
2	–	3	4	–	–	1	–	2	–	–	–	2	–	–	–	–	1	–	–	–
3	–	–	–	–	1	1	–	–	1	–	1	6	7	1	14	–	1	1	–	–
4	2	2	–	9	3	1	1	–	1	–	2	1	3	1	1	–	1	1	–	3
5	–	–	2	1	–	–	–	–	1	–	1	1	1	–	1	6	5	1	–	5
6	3	–	1	–	–	1	–	–	–	1	3	–	–	1	–	4	2	4	–	11
7	–	–	–	1	8	3	1	4	1	6	11	3	4	8	7	–	1	–	–	7
8	1	1	1	1	3	7	4	3	1	7	–	2	1	6	7	1	4	1	–	2
9	2	6	2	–	9	2	5	4	5	13	1	2	1	2	–	3	1	4	–	5
10	6	3	2	2	–	2	6	1	11	3	1	1	–	–	–	2	2	4	–	1
11	–	2	4	5	–	–	1	1	5	1	–	–	–	6	–	–	–	1	–	–
12	–	1	1	6	12	–	–	2	–	1	–	–	–	1	6	–	–	–	–	–
13	–		–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Table 2. Heterozygosity and probability of identity indices for caribou populations.

	Heterozygosity					Probability of Identity				
Locus	WQ	BE	BA	GR	MG	WQ	BE	BA	GR	MG
RT 1	0.784	0.802	0.850	0.778	0.762	0.077	0.064	0.038	0.080	0.094
RT 6	0.815	0.753	0.840	0.740	0.740	0.045	0.101	0.046	0.101	0.104
RT7	0.655	0.815	0.760	0.787	0.744	0.123	0.055	0.090	0.076	0.105
RT 9	0.742	0.833	0.833	–	0.798	0.095	0.047	0.048	–	0.068
4Loci	0.749	0.801	0.821	0.768	0.761	4.0xl0^{-5}	1.7xl0^{-5}	7.6X10^{-6}	6.1x10^{-4}	7.0xl0^{-5}

values for four loci combined in QW, BA and MG indicate that microsatellite analysis has a very high potential for identifying individuals in respective populations, considering recent caribou population estimates (Ferguson & Gauthier, 1992).

In conclusion, the high levels of variation observed at microsatellite loci in caribou could be potentially useful for analyzing caribou at the level of populations. The hyper-variability of fragments containing microsatellites make it possible to uniquely identify individuals in a population, useful for forensics and studies of paternity and reproductive success, as well as distinguishing populations that have only been recently separated. Spatial distributions of alleles can be used to study local gene flow and the recent history of large scale migrations. A temporal dimension could also be added by utilizing PCR to amplify ancient DNA that may be degraded (Thomas *et al.*, 1990). It may also be possible to obtain DNA from gut cells in fecal pellets (Höss *et al.*, 1992), allowing for non-intrusive sampling of caribou. We are presently refining the fecal analysis technique in caribou to make it a more efficient method of processing large sample sizes.

Microsatellite analysis will provide considerable resolution to the measurement of variation and population structure in caribou. Analyses of population differentiation and sub-structuring are currently under way in our laboratory.

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Attributes of Woodland Caribou Migration Habitat in West-Central British Columbia

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Abstract: We examined sites used by 73 caribou located by radio-tracking during spring migration through a forested travel corridor. The physical and botanical characteristics of these sites were described to find what features (if any) distinguished them from the forest at large. Raised and open aspect, sparse tree cover, free-draining soils, and a simple flora with abundant lichens were features common to all the sites, but were lacking in the denser forest around. Scores for these attributes were ordinated by multidimensional scaling of similarities and differences from site to site. Separate scalings for (i) terrain features, (ii) tree cover attributes, and (iii) floristic content each yielded a single cluster of points with few outliers and no particular pattern or trend. The inference is that the sites conformed to a single type with limited variation. A profile of the distinguishing characteristics was compiled and then applied to transects through the general migration area by persons unfamiliar with it beforehand. Sites which matched the profile proved easy to identify, even though they comprised only a small proportion of the area. Sites with high scores for the most distinctive attributes had more caribou at the time of radio-tracking.

Key words: habitat descriptors, ordination, lichens, radio-tracking, forest management, *Rangifer tarandus*

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Introduction

The Tweedsmuir-Entiako woodland caribou herd contains about 500 animals (Cichowski & Banner, 1993). Until recently, these were some of the least studied caribou in British Columbia. In the mid-1980s, using radio-tracking, Marshall (1986) defined the range of the herd and its seasonal pattern of use. The animals summer in northern Tweedsmuir Park, and winter in the Entiako drainage south-east of Tetachuck Lake (Fig. 1). The Chelaslie River drainage serves as a connecting travel route, and in certain years part of the herd may winter within that route, rather than continuing on to the Entiako (Steventon, 1994).

Cichowski (1989) described habitat preferences on the Entiako range, but site selection during migration was not well understood. As logging and other land uses begin to encroach on the range of this herd, the need to know more about habitat usage was becoming urgent.

We examined a sample of sites used by the herd during spring migration in 1993, and compared their physical and botanical characteristics. The aim was to find what features, if any, were shared amongst these sites, and distinguished them from other parts of the travel corridor. The study was done as part of a forest management plan for the area.

Study area

The Chelaslie corridor (61 000 ha) is a gently sloping plateau with undulating terrain, from 850 m elevation at Tetachuck Lake to 1430 m at the Tweedsmuir Park boundary. It lies within the driest part (subzone *dk*) of the Sub-boreal Spruce (SBS) biogeoclimatic zone of British Columbia. Treeline (westward within Tweedsmuir Park) is about 1600 m. The forest cover is mostly lodgepole pine (*Pinus contorta*) and hybrid white spruce (*Picea glauca* x *engelmannii*). Small raised periglacial features (drumlins, eskers, and fluvial terraces) are scattered throughout the area. These alternate with numerous meandering sedge meadows and willow swamps, fringed with black spruce (*Picea mariana*). The forest cover has a long history of wildfires, resulting in a patchwork of even-aged stands at various stages of maturity.

Methods

Sample sites

In April and May 1993, 42 radio-collared cow caribou were tracked from the air, approximately twice weekly by the BC Forest Service and BC Parks. Most of the

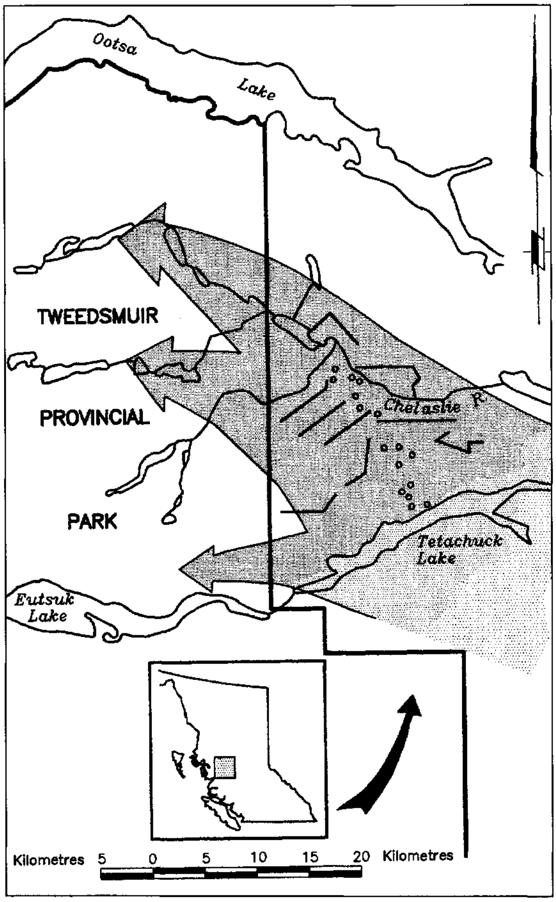

Fig. 1. Project area adjoining the northeast portion of Tweedsmuir Park, west-central British Columbia, showing the general spring migration route of the caribou (arrowed band). Redrawn from Marshall (1986). Circles show the approximate location of 16 habitat sampling sites; zig-zag lines represent 10 habitat survey transects.

herd travelled in small groups, usually less than 10 animals per group but sometimes up to 20. Radio-locations were recorded either as Global Positioning System readings, or Universal Transverse Mercator coordinates. All were considered accurate to within 200 m, and many were confirmed by direct sighting.

From the full set of 153 radio-locations (Steventon, 1994), we chose a sample of 16 to visit on the ground. These were chosen without regard to location-date, identity of the caribou concerned, or any site attribute except that all 16 were from places considered to he within the main path of migration through the corridor (Ministry of Forests, 1992).

Some of the 16 sites had more than 1 radio-collared caribou at the time the site was radio-located. Other sites were occupied more than once by different collared individuals at different dates. Together they represented the locations of 23 collared caribou. A further 50 uncollared ones were sighted along with these, bringing the total up to 73. Others which were screened by trees may well have been missed, however, and so this total was a minimum.

When migration ended, the 16 sites were plotted onto forest cover maps and located on the ground by compass. Each was described by terrain, soil, and floristic criteria, with special attention given to the terrestrial lichen flora. Physical and floristic descriptors (Tables 1 and 3) were from the list by Luttmerding *et al.* (1990) for assigning sites to ecosystem type within the biogeoclimatic classification of British Columbia. The flora for each site was compiled by walking the length and breadth of the site, recording the species present and estimating their percentage ground-cover. Species represented by just a few scattered plants were given a cover score of 1. A few species with scant cover may have been overlooked, and a few plants lacking flowers could not be identified with certainty. The list in Table 3 is thus conservative. However, common species tended to be common at most sites, and species with sparse cover were consistently sparse at each site where they were found.

Tree descriptors (Table 2) were as used by the BC Forest Service (Ministry of Forests, 1994). Mean height, crown closure, and live crown percentage were estimated visually for the stand as a whole. Diameters were tape-measured at 1 or 2 large trees and 1 or 2 small trees according to the range of sizes in the stand. Stem density and merchantable volume (a function of tree numbers and size) were estimated by standard timber cruising methods (Ministry of Forests, 1994). Ages were taken by increment bore and ring count for 1-3 trees in the stand. As most stands were of fire-origin, most of the trees within them were of the same age-*class* (defined in the Notes below Table 2). One sample tree was usually enough to determine age-class.

Signs of caribou use of the sites (tracks, trails, droppings etc.) were noted as they occurred, as was the general context of the site itself (adjoining forest types; other habitats nearby). 'Beard lichen' loadings (*Bryoria* and *Alectoria* spp.) on trees at the site were scored on a scale of 0-5 by the method of Armleder *et al.* (1992).

Data analysis (sample sites)

The data in Tables 1-3 (for all tables, see Appendix) were converted to standardized scores expressing the similarity or difference in each attribute, site by site. Scores were compiled separately for the three types of attribute (soil and terrain, tree cover, and flora). For soil and terrain: a pair of sites with the same attribute scored 1, or zero if the two sites differed. Summing these scores over all attributes gave the net difference in soil and terrain for that site-pair. Tree attributes were scored the same way as for soil and terrain. For the rest of the flora, the species list for all 16 sites combined was compared to the lists for each site-pair. A species which was present at both sites scored 1. Likewise a species absent from both sites. A species which was present at one but absent at the other scored zero. These scores were then summed to express the net difference in flora, in the same way as for soil/terrain and trees. For each of Tables 1-3, these steps generated a matrix of net differences for all possible site-pairings (120 pairs).

The three sets of differences were ordinated by monotonic multidimensional scaling (MDS) for indications of clustering or segregation into site-groups, or evidence of a linear or other gradational trend. Scaling was done first in two dimensions and then in three (where each dimension represents a different combination of variables in the dataset - here, the matrix of net-difference scores among the 16 sites). Dimensions beyond 3 or 4 seldom account for much of the variation in a dataset (Wilkinson, 1990). In the present case, adding the third dimension explained only 5% more of the variation in scores. Therefore, only the first two dimensions are plotted in Figs 2-4.

Transect strips

Attributes which best defined the 16 sample sites were then checked for consistency and occurrence in the area at large. Ten transects (Fig. 1) totalling 65.4 km were run through places having a mixture of merchantable and non-merchantable timber types, so that value as timber and value to caribou could be compared. When a site was found which fit the profile of the sample sites, its size, tree density, crown closure, and lichen cover and moss cover were scored in classes of 1 to 4, corresponding to quartiles of the range of values shown by the 16 sample sites. One of us (BM) surveyed 2 of the transects and supervised the other 8, which were done by three people with no previous knowledge of the sample sites or the rest of the area. This allowed us to test the criteria in Table 4 for their ability to indicate habitat sites without needing prior experience or data on caribou themselves. The surveys also allowed us to roughly estimate the extent and distribution of such sites throughout the migration corridor.

Number of caribou at the 16 sample sites

The number of caribou seen per site during the radio-tracking period ranged from 1 (5 sites) to 20 (one site). Numbers per site were compared with site attributes singly and in combination, under the assumption that numbers at a site were a measure of caribou use of that site, and that level of use was a reflection of site suitability - specifically, the state of the forest cover and lichen supply. The analysis was therefore confined to six variables: (1) lichen abundance (all spp.), (2) percentage *Cladina* spp., (3) stem density, (4) tree size (merchantable volume), (5) crown closure, and (6) percentage slash. These were compared by step-down multiple regression. There was no *a priori* reason to reduce these variables in any particular sequence, and so they were deleted by size of effect in simple regression, largest first. As well as to find whether caribou numbers did vary with these attributes, the aim was see which of them had most potential for ranking sites in value to caribou.

Results

Sample sites

Each of the 16 sample sites differed distinctly from its surrounds. This was apparent as soon as the site was located on the ground. Their similarity to each other was obvious as well. Raised and open aspect, coarse free-draining soils, sparse tree cover, little or no large woody debris, and a simple ground flora with abundant lichens were characteristics shared by all. Most of the sites were small and narrow (less than 100 m in width), but some extended for more than 1 km atop eskers and glaciofluvial terraces next to sedge meadows and willow swamps. Tables 1-3 show the attributes of each site. Together, these attributes contrasted sharply with the denser forest around. Indeed: just the combined presence of juniper, *Arctostaphylos uva-ursi*, *Shepherdia canadensis*, and a *Cladina*-dominant lichen flora beneath a sparse cover of lodgepole pine, is sufficient to distinguish these sites from all other types within the *SBSdk* biogeoclimatic subzone (DeLong *et al.*, 1993).

The results of multidimensional scaling confirmed the similarity of the sites. Separate scalings for (i) terrain features, (ii) tree cover attributes, and (iii) ground flora each yielded a single cluster of points with few outliers and no linear or other systematic trend (Figs. 2-4). The inference is that the 16 sites conformed to a single type with limited variation. A composite profile of the sites is shown in Table 4.

Numbers of caribou at the sites

Total lichen cover, percentage *Cladina*, tree density, canopy closure, merchantable volume, and debris cover, together explained nearly 60% of the difference in caribou numbers from site to site (Table 5). Fig. 5 compares numbers seen and numbers predicted from these attributes combined as an

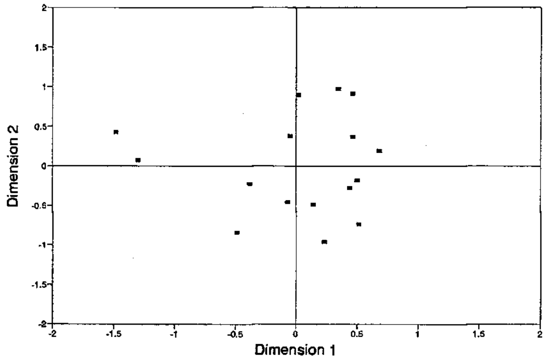

Fig. 2. Multidimensional scaling (MDS) of soil and terrain attributes at the 16 sample sites. Dimensions 1 and 2 represent combinations of attribute scores which account for the largest and the next largest amount of variation among the sites.

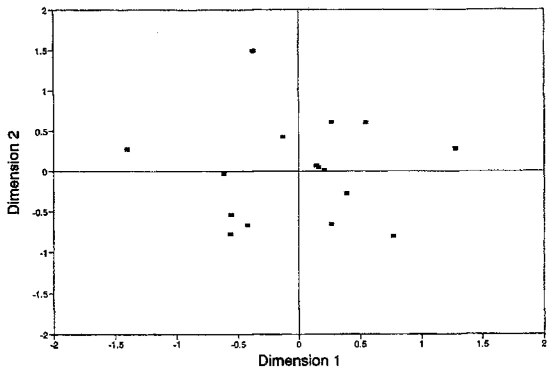

Fig. 4. Multidimensional scaling (MDS) of floristic attributes at the 16 sample sites. See note below Fig. 2.

index of the 'habitat value' of the site. With only 9 degrees of freedom available, the index was not statistically significant. Individually, however, crown closure and merchantable volume had a quite substantial effect: when these two factors were dropped from the index, R^2 fell by more than half. Stem density and lichen cover appeared to have only a small effect, and slash cover none at all, even though caribou tend to avoid dense timber clogged with slash, and lichens are their dietary mainstay. However, all but one of the 16 sites had stem densities less than 2000 per ha, and none of the sites had much slash (Table 1). Lichen cover varies with crown closure and stem density (next Section).

Transect strips

The 10 transects through the wider study area identified 64 sites which fit the general profile in Table 4. Every transect had at least 2 such sites; the most was 11 (Table 6). All but one of the 64 sites were in forest cover composed of mature semi-open lodgepole pine, mostly less than 2000 trees per ha - the density used by the BC Forest Service to define a stand of timber which was 'passable' for travel by this caribou herd (Ministry of Forests, 1992). All but three sites had densities less than 1500 trees per ha, and ninety percent had a canopy closure of 25% or less.

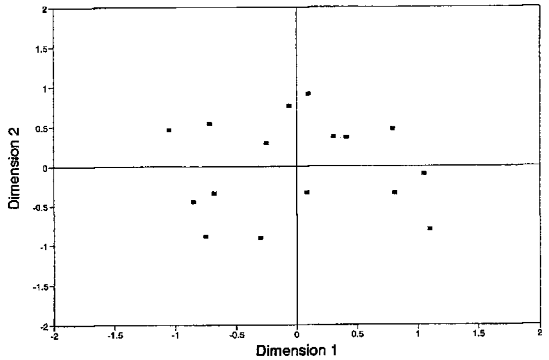

Fig. 3. Multidimensional scaling (MDS) of tree attributes at the 16 sample sites. See note below Fig. 2.

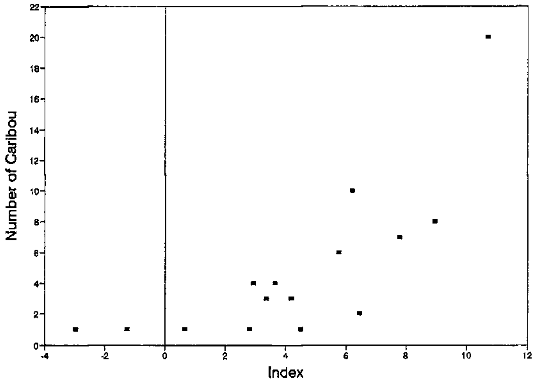

Fig. 5. Index of site attributes *I* versus number of caribou seen at the sites.

$I = 11 + .11TL - .06Cl\% + 4\text{EXP}3SD - .04MV - .49CC\% + .41S\%,$

by multiple linear regression. *TL* = total lichen cover, *CL%* = percent *Cladina* spp., *SD* = stem density (ha^{-1}), *MV* = merchantable timber volume (m^3), *CC%* = percent crown closure, and *S%* = percent cover of large woody debris (as in Tables 2 and 3).

Lichen ground coverage ranged from 5% to 50%, with most sites having 5-25%. Moss cover (mostly *Pleurozium schreberi*) varied inversely with this (Kendall τ = -0.57). The sparser the timber and the more open its canopy overhead, the higher was the ground-coverage by lichens underneath (Kendall τ = -0.36 and -0.35 respectively) and the lower was the cover by moss (all τ values significant at $p < 0.001$). Lichen:moss ratios showed no relationship to site size, and so the sites were merely summed rather than weighted by size when calculating the extent of 'lichen habitat' on the transect strips.

The sum of the widths of the 64 sites where they intercepted the transects was 4700 m. This was 7.2% of the total transect length. Most of the sites were roughly 2.5 times longer than wide; hence the sum of the lengths was at least 11 600 m (17.7%, ignoring very elongated sites whose total length was unknown (pursuing these sites to their full length would have required long deviations from the transect route)). By simple division, the mean of these two percentages was 12.5.

Associations with other habitat types

Eleven of the 16 radio-sample sites were within 200 m of treeless lakeshores, meadows, or swamps. Most of these openings were crossed by game-trails with caribou tracks or droppings. Some trails led from one dry lichen site, through a nearby meadow, to another lichen site nearby. Along the 10 transect strips, sites with lichens tended to occur in scattered groups interspersed with low-density timber and meadows or swamps. The pattern as a whole appeared to consist of series or clusters of feeding sites linked by trails through semi-open timber and treeless ground.

Discussion

The 16 sample sites resembled each other and differed distinctly from their surrounds. When being approached through the surrounding timber, most of the sites were readily visible some distance ahead as openings in the forest with little or no understorey and a carpet of lichens on the ground.

Assuming that their extent on the transects reflected proportion by area, sites of this type comprised at least 12.5% of the migration corridor - probably more, since the unknown length of very long sites was ignored. Thus, any one of the 23 radio-collared caribou had at least a 12.5% chance of finding such a site at random. However, the chances of all 23 doing so were less than 1 in 2^{21} (ie, 0.125^{23}). This degree of consistency was not likely accidental. (Four sites had more than one radio-collared caribou. If these are treated as just one location per site, the likelihood is still only 1 in 3^{14} that caribou found all 16 sites by chance (ie, 0.125^{16})).

State of the tree cover was better than lichen cover at predicting the number of caribou seen at a site. However, the estimates of lichen cover were rather crude, were correlated with the tree cover, and were made after the caribou had already grazed the site. Also, the caribou seen at a site were not necessarily all of the caribou present at the time. Thus, the coefficients in Fig. 5 do not necessarily express the actual relationship between caribou numbers and site attributes. Nonetheless, a trend was apparent, and was strong enough to suggest that the degree of site usage does vary with differences in these attributes. (The presence of some caribou at a site might have attracted others to it. However, if 'herd behavior' instead of site attributes determined the size of the group, Fig. 5 should not have shown a trend).

The floristic features in Table 3 resemble the 'dry lichen' and mixed 'lichen/moss' vegetation types which Cichowski & Banner (1993) described as important to this caribou herd on the winter range. Among the sites studied by us, lichen cover and moss cover alternated with each other in a gradational way rather than discretely, and the sites as a whole suggested a continuum of differences rather than a set of disjunct types (Fig. 4). Level of use by caribou appears to vary likewise.

After this study had ended, Steventon (1994) plotted the full set of 153 radio-locations onto forest cover maps which rated each part of the area in timber-production terms. He found that the percentage of locations on sites rated 'low' or 'poor' exceeded the extent of these sites on the area. The opposite held for sites rated 'medium' or 'good'. The apparent preference of the caribou for less-productive forest may lower the risk from logging within their range. On poor dry sites with approximately 2000 stems per ha or less, the timber becomes sparse enough for lichens to occur, but is usually too low in volume for logging to be worthwhile.

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Staff of BC Environment, BC Parks, and various volunteers, caught and marked most of the radio-collared caribou during the 1980s..J.D. Steventon (BC Forest Service) and D.B. Cichowski (BC Parks) did the radio-tracking in spring 1993, accompanied by one of us (ANL) during an early flight. We thank them for the use of these data for choosing the sample sites. B.Barry, A.Jankowski, & D.Routledge (Industrial Forestry Service) did most of the fieldwork at the ten transects. George Danilec re-drew Fig. 1. The BC Forest Service, Burns Lake, funded the flights for radio-tracking, and Fraser Lake Sawmills Ltd funded the fieldwork.

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Appendix: Tables 1-6

Table 1. Terrain and soil attributes of the sample sites.

Attribute	Site															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
landform[a]	FG	M	M	FG	M	MR	M	FGM	FG	M	M	MFG	FGM	M	M	FG
edatope[b]	B2	B3	B2	B2	B2	B3	B3	B1	B1	B2	B2	B1	B3	B2	B2	B2
slopeclass[c]	G	G	G	G	G	G	M	S	G	M	G	5	G	M	G	G
aspect	S	S	S	S	S	S	N	S	S	S	N	S	S	N	S	S
slope position[d]	M	M	M	U	C	C	C	C	C	C	C	C	M	C	C	C
soil group[e]	B	P	B	B	P	B	B	P	B	B	B	B	P	B	B	B
soil type[f]	G	G	G		G	GC	G	G	G	G	G	GC	G	G	G	G
soil texture[g]	LS	SCL	SCL	S	SL	SL	SL	SL	LS	LS	SL	SL	Si	SL	SL	5
coarse fragment content[h]	M	M	H	L	M	M	H	H	H	H	H	M	L	M	M	L
duff type[i]	X	H	X	X	X	X	H	X	X	X	X	X	H	X	X	X
duff depth (cm)[j]	3.5	5	2	2	4	3.5	3	3	3	4	2	2	3	3		
% woody debris cover[k]	0	1	1	3	2	5	5	1	3	6	1	0	4	1	1	2
woody debris depth (cm)[l]	0	10	20	20	10	20	30	10	20	30	10	0	40	30	10	20

Notes: (categories from Luttmerding *et al.*, 1990).

[a] F fluvial; G glacial; M morainal; R ridge.

[b] B nutrient-poor (A very poor; E very rich); Moisture regime: 1 xeric; 3 submesic (6 hygric).

[c] G gentle; M moderate; S steep.

[d] M midslope; U upper slope; C crest.

[e] B brunisol; P podzol.

[f] G gravel; C cobble.

[g] L loam; S sand; C clay; Si silt.

[h] H high; M moderate; L low.

[i] X xeromor; H hemimor.

[j] Depth to first mineralized horizon.

[k] Logs, dead branches etc.

[l] Size (diameter) of debris, or height elevated above ground surface (whichever was greater).

Table 2. Tree attributes at the sample sites.

Attribute*	Site															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Leading species[a]	Pl	Pl	Pl	Pl	Pl	PlSx	Pl	PlSx	Pl	Pl	PlSx	Pl	Pl	Pl	PlSx	Pl
Ageclass[b]	5	5	3	5	8	8	8	8	8	8	6	7	4	6	3	4
Mean DBH[c] (cm)	20	25	15	20	25	25	25	20	25	30	15	20	15	25	15	30
Range DBH[d] (cm)	10	15	5	15	10	20	10	20	10	20	15	20	10	10	10	10
Mean Height[e] (m)	15	20	10	15	20	20	20	15	15	20	20	15	15	15	15	10
Crown closure[f] (%)	15	5	5	5	15	10	15	10	5	10	10	15	20	10	5	5
Live crown[g] (%)	40	50	60	70	30	50	50	80	60	50	80	60	40	50	80	80
Stem density[h]	850	330	1000	1600	900	600	300	1750	430	450	370	1500	2700	600	1800	150
Merchantable volume[i] (m^3)	150	105	110	100	225	120	90	180	140	150	60	200	170	220	115	70

[*] Sample size (n) varied with attribute and site. Age, DBH, and height were determined from 1-3 trees which typified most trees in the stand. Crown closure, Live crown %, Stem density, and Merchantable volume were visual estimates for the entire stand.

[a] The dominant/co-dominant tree species at the site. Pl = lodgepole pine (*Pinus contorta*); Sx = hybrid white spruce (*Picea glauca* x *engelmannii*).

[b] BC Forest Service age-classes: 3 = 41-60 yrs; 4 = 61-80; 5 = 81-100; 6 = 101-120; 7 = 121-140; 8 = 141-250.

[c] DBH = diameter at breast height, to the nearest 5cm.

[d] Max. minus Min. for the sample trees, to the nearest 5cm.

[e] Visual estimate for the sample trees, to the nearest 5%.

[f] Percent ground cover, to the nearest 5%.

[g] Proportion of total stand height comprised of live tree crowns, to the nearest 10%

[h] Number of live trees per hectare.

[i] Volume of timber available (m^3 per ha) from sound trees of commercially harvestable size and age.

Table 3. Plant species content (percentage cover) of the sample sites.

	Site																All	% of
Species[a]	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	sites	sites
Arboreal lichen																		
Total arboreal lichen[b]	0	2	0	0	2	1	1	1	0	1	2	2	0	1	1	1		
Terrestial lichen																		
Cladina mitis	30	5	20	10	14	20	5	13	60	15	7	50	4	5	4	2	16	100
Cladina rangiferina	1					1		1	1	1		15	1	2		1	9	100
Cladonia cornuta	1		3	7	1	2	1	1	2	5	4	1	1	1			13	81
Cladonia pixidata															1	1	2	13
Cladonia bellidiflora				1												1	2	13
Peltigera apthosa	6	3	1	2	2	5		1	10	1	3	1		10	1	3	14	88
Stereocaulon spp.	1	1	1		1	1		1	2	1	1	1	1	1	1	1	14	88
Total terrestrial lichen	39	9	25	20	18	29	6	17	75	23	15	68	7	19	7	9		
% *Cladina*	80	56	80	50	78	72	83	82	81	70	47	96	71	37	57	33		
Mosses																		
Pleurozium schreheri	1	80			5	15	50		1	60	30	2	10	20			11	69
Polytrichum spp.																1	1	6
Dicranum fuscescens	1											1					2	13
Total moss	2	80	0	0	5	15	50	0	1	60	30	3	10	20	0	1		
% *Pleurozium*	50	100			100	100	100		100	100	100	67	100	100		0		
Vascular plants																		
Shepherdia canadensis	1	2	3	3	1	1	3	2	1	2	2	1	10	15	5	8	16	100
Arctostaphylos uva-ursi	20	5	5	30	1	1	10	25	5	3	3	1	3	20	15	5	16	100
Rosa acicularis	1	1	1	3	1	1		1		1	1	1	1	1	1	1	14	88
Juniperus communis	3		3	2			1	20		5	4	3		1	1		10	63
Spiraea betulifloria	1	2	2	2	1		1						1	1	1		9	56
Oryzopsis pungens	1	1			1			1	1			1					6	38
Arnica cordifolia							2	1		1	1	1	1				6	38
Cornus canadensis					1	1			1		1	1				1	6	38
Lycopdium complanatum		1				1					1			1	1		5	31
Vaccinium membranaceum						1	1			1			1	1			5	31
Linnea borealis					1							1	1		1	1	5	31
Empetrum nigrum		1				1					1			1			4	25
Calamagrostis rubescens				2							1	1			1		4	25
Geocaulon lividum									1				1		1		3	19
Vaccinium caespitosum			1							1					1		3	19
Chimaphila umbellata			1								1						2	13
Pyrola asarifolia				1							1						2	13
Achillea millefolium			1								1						2	13
Salix spp.		1												1			2	13
Petasites palmatus							1										1	6
Fragaria virginiana															1		1	6
Vaccinium vitis-idaea														1			1	6
Aster conspicuous													1				1	6
Calamagrostis canadensis																1	1	6
Epilobium angustifolium													1				1	6
No. of vascular species	6	8	8	7	7	7	7	6	5	7	12	9	10	10	11	6	25	
Total ground flora	13	12	12	11	12	13	10	11	11	13	17	16	15	16	15	13		

[a] Species represented by >1 individual at a site. Species occuring as a few scattered individuals were given a score of 1.

[b] Virtually all *Bryoria* spp. ('horsehair lichen'), but occasionally with small amounts of *Alectoria sarmentosa* ('witch's hair lichen'). Scored on a geometric scale of 0 to 5, after Armleder *et al.* (1992). Plant names after MacKinnon *et al.* (1992).

Table 4. Key-feature summary of the sample sites.

Feature	Attribute	Criteria
Landform	**Glacial deposition**	**Fluve, moraine, esker, or mounded blanket till**
	Terrain	Hummocky, undulating, ridge or bench
		Sloping or raised, giving an outlook over surrounds
	Aspect	Variable, but most often SE, S, SW
	Slope position	Midslope & upward
Substrate	**Mineral soil**	**Free-draining** sandy clay loam
		Coarse fragment content (gravel or cobble) 20% or more
	Duff layer	**Xeromor** <5cm thick (occasionally hemimor)
Tree Cover	**Dominant species**	***Pinus contorta***
	Sub-dominant species	*Picea glauca* x *engelmannii*
	Age	Variable between (and within) sites, but usually >60 years
	Crown closure	**<20% (usually <15%)**
	Height	Variable between (and within) sites, but seldom <15m
	Stem density	**<1600/ha** (rarely >2000)
	Dead woody debris	**Sparse to nil** (usually <5% ground cover)
Flora	**Terrestrial lichens**	**>10% total ground cover** (may be less if site has been grazed)
	***Cladina* spp.**	**>50% of total lichen cover**
	Arboreal lichen	*Bryoria* Spp. usually present, but sparse
	Mosses	Variable (0 - 90% cover); inversely related to Lichen Cover
		Pleurozium schreberi dominant
	Vasculars	**Simple flora:** Max. No.of species = 25
		Number[*] at any one site is usually 12 or less
	constants:	*Shepherdia canadensis*
		Arctostaphylos uva-ursi
	present at most sites:	*Rosa acicularis*
		Juniperus communis
		Spiraea betulifolia
	cover-dominants:	*Arctostaphylos* (up to 30%)
		Juniper (up to 20%)
		Shepherdia (up to 15%)

Boldface type denotes the most characteristic attributes.

[*] Number of species with significant ground cover (1% or more). Other definitions: see Tables 1-3 and text.

Table 5. Percentage of variance explained by the site attributes in Fig. 5.

Regression	Crown closure	Merch. volume	Stem Density	Cladina%	Total lichen	Slash%
simple[a]	31.7[*]	11.9	3.6	3.7	1.5	0
multiple[b]	14.4	20.4	11.9	9.3	1.5	0

[a] The variance explained by each attribute in simple regression with caribou numbers.

[b] The reduction in explained variance when the attribute was deleted during step-down multiple regression.

[*] $p<0.05$.

Table 6. Score-frequencies of four main site attributes on 10 survey transects.

	Strip length (m)	No.of sites	Tree density				Lichen cover				Moss cover				Canopy closure			
Strip		Score[a]:	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
1	5000	11	8	3	0	0	1	10	0	0	1	9	1	0	8	3	0	0
2	5640	2	0	1	1	0	2	0	0	0	0	0	2	0	2	0	0	0
3	7600	7	1	0	6	0	5	1	1	0	1	1	5	0	1	5	1	0
4	6366	3	1	2	0	0	0	2	1	0	1	2	0	0	1	2	0	0
5	6360	5	5	0	0	0	2	3	0	0	2	3	0	0	1	4	0	0
6	5740	4	4	0	0	0	4	0	0	0	4	0	0	0	1	2	1	0
7	6950	11	1	8	2	0	1	8	2	0	8	2	1	0	2	9	0	0
8	8600	5	0	2	3	0	2	3	0	0	1	1	3	0	1	3	1	0
9	6923	9	4	5	0	0	2	5	2	0	3	3	3	0	5	4	0	0
10	6220	7	1	5	1	0	2	4	1	0	0	2	3	2	0	5	2	0
All	65399	64																
% All[b]			39	41	20	0	33	56	11	0	33	36	28	3	34	58	8	0

		Tree density (stems/ha)	Lichen cover (%)	Moss cover (%)	Canopy closure (%)
[a] Score-classes	1	< 1000	< 5	< 5	< 10
	2	1000-1500	5-25	5-25	10-25
	3	1500-2000	25-50	25-50	25-50
	4	>2000	>50	>50	>50

[b] % All = percent of the 64 sites.

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Seasonal habitat use and movements of woodland caribou in the Omineca Mountains, north central British Columbia, 1991-1993

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Abstract: From 1991 to 1993, 30 woodland caribou were captured and fitted with radio-collars west of the Williston Reservoir in north central B.C. Monthly radio-telemetry location flights revealed that caribou in the Northern Area, characterized by a complex of mountain ranges, moved greater distances to calving areas than did those in the South, where only one major mountain range exists. In the year of record heavy snowfall for the area, all collared caribou wintered on windswept alpine slopes, while during the below average snowfall year, many caribou remained in forested habitats. In winter, caribou were found to forage on terrestrial lichens in both lowland lodgepole pine flats and on windswept alpine slopes, and on arboreal lichens in upper elevation Engelmann spruce and subalpine fir forests. There are at least 600-700 caribou in the Omineca Mountains.

Key words: *Rangifer*, snow depths, mortality, population dynamics, habitat use, migration

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Introduction

Woodland caribou on the west side of the Williston Reservoir in north central B.C. are faced with substantial increases in road development and forest harvesting over the next ten to twenty years. With the flooding of the Reservoir in the late 1960's, an extensive area of wildlife habitat and forest resources was lost, placing increased pressure on surrounding lands.

Conflicts with forest harvesting in the range of the mountain caribou ecotype, have focused most habitat use studies of caribou primarily in the southeastern part of B.C. (Stevenson, 1991). Mountain caribou inhabit areas with deep snowpacks and forage primarily on arboreal lichens during winter. The northern caribou ecotype which resides in areas with low to moderate snowdepths and forages primarily on terrestrial lichens, has been the subject of only two major studies in the province (Hatler, 1986; Cichowski, 1989). Only the caribou of the latter study, in west central B.C., are presently subject to forest harvesting concerns.

The objective of Phase 1 of the Omineca Mountains Caribou Project is to describe the seasonal movement patterns, habitat use, and ecology of these caribou by monitoring radio-collared animals over a three year period (1991-1994). These data will aid in designing a caribou/forestry management strategy for the area. Phase 2, which began in 1994, will focus primarily on the use of forested habitats by caribou. In this report, I present data from the first two years of Phase 1.

Study area

The Omineca Mountains study area lies to the west of the Williston Reservoir in north central B.C., and encompasses 21,000 square kilometres (Fig. 1). A diversity of habitats exists within this forest transition area which is reflected by the variety of biogeoclimatic subzones (Meidinger & Pojar, 1991). Biogeoclimatic zones occurring below 1100 metres are the Sub-Boreal Spruce (SBS) in the southern portion of the study area, and the Boreal Black and White Spruce (BWBS) in the north. These zones have extensive wildfire histories (Parminter, 1984), and forests are dominated by lodgepole pine (*Pinus contorta*) and white spruce (*Picea glauca*). Between 900 and 1600 metres, the Engelmann Spruce Subalpine Fir (ESSF) zone occurs in the south, and the Spruce Willow Birch (SWB) zone in the north. Climax tree species in the ESSF are the Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Both white spruce and subalpine fir are found at lower elevations in the SWB, with subalpine fir

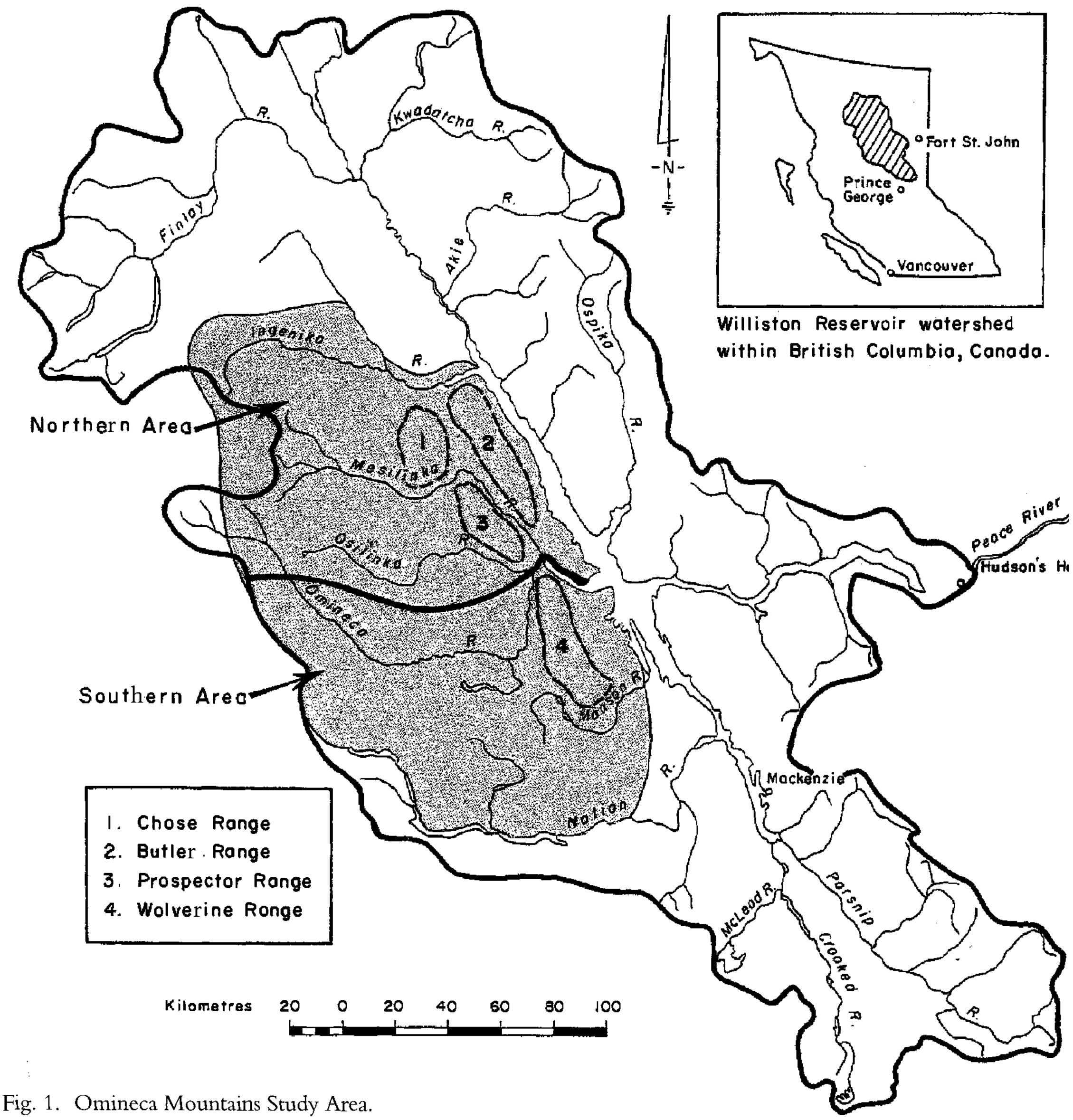

Fig. 1. Omineca Mountains Study Area.

dominating on higher slopes. Extensive lodgepole pine stands in the ESSF and SWB are uncommon as wildfires are less frequent. Alpine Tundra (AT) exists at the highest elevations which extends from 1600 to 2300 metres. Gentle, windswept alpine slopes are common.

I have divided the Omineca Mountains study area into Northern and Southern Areas (Fig. 1); to date, radio-collared caribou in these two areas have remained separate. The Northern Area is characterized by a complex of mountain ranges which extend westward into broad high elevation scrub/parkland plateaus. Clearcut forest harvesting has been extensive in the BWBS zone in the three major river valleys that divide these mountain ranges. The Southern Area is less mountainous, with one primary mountain range, the Wolverine Range, and a few smaller mountain ranges interspersed with broad expanses of lower elevation ESSF, BWBS and forest and meadows. The Wolverine Range is one of very few mountain ranges in the area with gently sloping windswept terrain suitable for wintering caribou in deep snow years. To date, forest harvesting activities in the Southern Area have been minimal and are concentrated on the east side of the Wolverine Range, primarily at low elevations. Some harvesting has also occurred in the ESSF zone.

Other common ungulates in the Omineca Mountains study area include moose (*Alces alces*) and mountain goat (*Oreamnos americanus*), while mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), elk (*Cervus elaphus*), and Stone's sheep (*Ovis dalli stonei*) are present in small numbers. Potential predators of caribou include wolves (*Canis lupus*), wolverine (*Gulo gulo*), black bears (*Ursus americana*), grizzly bears (*Ursus arctos*), and lynx (*Lynx canadensis*).

Methods

Capture and Radio-Collaring

Between February 1991 and January 1993, 30 caribou (10 females and 4 males in the Northern Area; 13 females and 3 males in the Southern Area) were captured using a handheld net-gun fired from a Bell 206 Jet Ranger helicopter, and fitted with radio-collars equipped with mortality sensors (Model LMRT-4, Lotek Engineering, Newmarket, Ontario). Blood samples were taken from females for analysis of serum progesterone levels.

Radio-Telemetry

Twenty-two radio-location flights from a Cessna 182 fixed-wing aircraft were conducted over a two year period hereafter referred to as 91/92 (April 1991 - March 1992) and 92/93 (April 1992 - March 1993). Monthly flights were attempted, although poor weather conditions prevented flights in some winter months. Three flights were conducted in May 1992 during spring migration. Forest cover type, slope, aspect, elevation and if possible, group size, were recorded for each caribou located. An attempt was made to locate every radio-collared caribou on each flight.

Seasonal Movements and Ranges

Discrete areas used by caribou during different seasons of the year were delineated using geographic (primarily rivers) and elevational boundaries, and referred to as "ranges". Twenty ranges were delineated in the Southern Area, and 25 in the Northern Area ranging in size from 82 to 293 km^2, with a mean range size of 160 km^2 (SE=8.5).

Seasonal movements of collared female caribou were measured as straight-line distances between known seasonal locations. Spring movements were measured between late winter ranges (using February capture locations for 1991, and March locations for 1992) and late May/early June calving locations. Pre-rut movements in both years were measured between summer ranges (using mid-July locations) and rutting areas (using mid-October locations), while post-rut movements were measured between the October rutting locations and late winter ranges (February locations). Differences between spring, pre-rut and post-rut movements between years, and between Northern and Southern Areas, were tested using a two-way analysis of variance for each season (Proc. GLM, SAS, 1988). Differences between the mean pre-rut and post-rut distances moved in each year in each Area were tested using Student's *t*-test.

Habitat Classification and Use

Caribou locations were plotted onto 1:50,000 Forest Cover Polygon Maps (Ministry of Forests, 1990-1993), which when combined with the description of the forest type observed at the time an animal was located, aided in placing each radio-location into a broad Forest Cover Type category. Six Forest Cover Types based on primary tree species, elevation, and seral stage were defined:

1) *Alpine/Subalpine:* alpine and upper elevation subalpine parkland;
2) *Balsam/Spruce: ≥1300 metres:* upper elevation climax stands with subalpine fir and Engelmann spruce dominating;
3) *Pine: >1300 metres:* upper elevation seral stands with lodgepole pine dominating;
4) *Pine: ≤1300 metres:* lower elevation seral stands with lodgepole pine dominating;
5) *Pine/Spruce: ≤1400 metres:* lower elevation mixed stands of lodgepole pine and Engelmann spruce and/or white spruce, interspersed with meadows and black spruce (*Picea mariana*);
6) *Spruce: <1300 metres:* lower elevation climax stands of Engelmann and/or white spruce dominating.

Low elevation early seral stages of immature lodgepole pine (<80 years), trembling aspen (*Populus tremuloides*), non-productive brush and meadow sites were included with *Pine ≤1300 metres.* The proportion of radio-collared caribou locations in each Forest Cover Type was determined for five periods: spring migration (Apr/May), calving/summer (Jun/Jul/Aug), fall/rut (Sep/Oct), early winter (Nov/Dec/Jan), and late winter (Feb/Mar). Data from females and males were pooled, as were locations of caribou in both the Northern and Southern Areas. Snow depths and densities were based on B.C. Environment data from the Germansen Station (B.C. Environment, 1991-1993). At 1500 metres elevation, this station was selected to best represent the Omineca Mountains study area. Other snow stations in the study area and throughout the Williston watershed revealed the same annual trends as the Germansen Station.

Winter Diet

Composite fecal samples were collected from each of four low elevation lodgepole pine sites prior to the initiation of this study (February 1990), and from five windswept alpine slope locations (three in February 1991, one in February 1992, and one in March 1992). Composite samples were comprised of about five pellets from each of 10 different fecal pellet groups. Samples collected from low elevation lodgepole pine flats were pooled for analyses and called "Pine Flats". Four of the five alpine samples showed similar vegetation composition and were lumped as "Alpine 2", while one sample with a very different composition was treated separately as "Alpine 1". Fecal fragments were identified to forage class (e.g. lichens, conifers) and major species (e.g. *Cladonia, Alectoria*) by the Wildlife Habitat Lab at the University of Washington.

Population Characteristics

Late winter aerial population surveys were conducted on the Wolverine Range in the Southern Area in February 1993, and the Chase and Butler Ranges in the Northern Area in March 1993. An inventory of the Wolverine Range was also conducted in 1989, prior to the initiation of this study. Alpine areas were searched and caribou were classified as adult male, adult female, and calves. Females were identified by the presence of a black vulval patch and males by the lack thereof. The proportion of radio-collared animals observed during the Northern Area survey was used as a sightability correction factor and applied to the total count using the Petersen mark-recapture estimator (Krebs, 1989, eqn 2.2, pg. 17), and variance from White & Garrott (1990, eqn 10.2, pg. 256). Densities were calculated for each of the Northern and Southern study areas by dividing the estimated total caribou population by the maximum area used by radio-collared caribou over the two year period.

The typical group size for each survey was calculated by summing the number of animals that each individual caribou was found with, and dividing by the total number seen on the survey. Typical group size is the size of group in which the average animal finds itself, and is a more accurate measure of the behaviour of individuals than is the frequency of groups as measured by the mean (Jarman, 1974; Heard, 1992). Typical group sizes of radio-collared caribou were calculated by summing the number of individuals in the group that each radio-collared caribou was located in (even if other radio-collared caribou were in the same group), and dividing by the total number of radio-collared animals seen.

Blood samples drawn from females captured in 1991 were analyzed for serum progesterone levels at the Department of Animal Science, University of British Columbia (UBC), Vancouver, B.C. Samples from females captured in 1992 were analyzed at the Endocrine Service Lab at the Western College of Veterinary Medicine, University of Saskatchewan. Measurements of progesterone in blood serum indi-

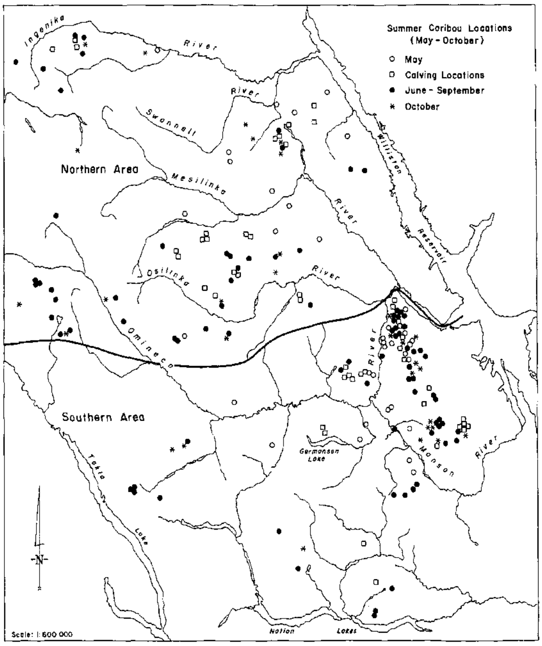

Fig. 2. Locations of radio-collared caribou in summer (May to October) 91/92 and 92/93 combined.

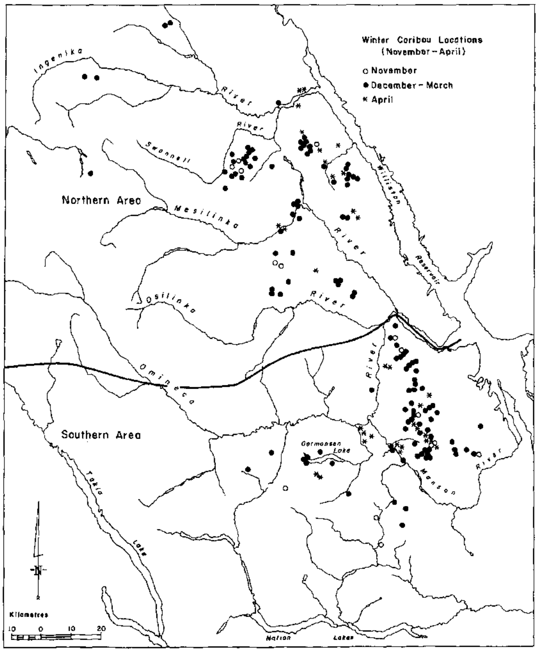

Fig. 3. Locations of radio-collared caribou in winter (November to April) 91/92 and 92/93 combined.

Table 1. Mean migration distances ±SD (km) of female radio-collared caribou between seasonal ranges. (n= number of collared caribou, r= range of distances).

	Northern Area		Southern Area	
Migration Period	91/92	92/93	91/92	92/93
SPRING (late winter range to calving area)	58.1 ±22.5 (n=7) (r=23-88)	25.0 ±15.0 (n=8) (r=8-45)	28.3 ±12.9 (n=6) (r=11-49)	16.2 ±10.4 (n=9) (r=4-31)
PRE-RUT (summer range to rut area)	19.2 ±16.9 (n=7) (r=1-48)	28.9 ±28.2 (n=7) (r=3-88)	12.6 ±9.0 (n=4) (r=4-25)	9.0 ±8.3 (n=9) (r=1-24)
POST-RUT (rut area to late winter range)	52.6 ±36.0 (n=7) (r=13-110)	30.1 ±31.1 (n=7) (r=3-98)	10.4 ±8.3 (n=4) (r=3-19)	8.5 ±7.0 (n=9) (r=4-26)

Table 2. The effects of year (91/92, 92/93) and location (Northern Area, Southern Area) on mean migration distances of collared females during spring, pre-rut and post-rut periods.

Source	D.f.	Sum of Squares	Mean Square	F Ratio	*P*
SPRING					
Among	3	7396.98	2465.66	10.09	.0001
Within	26	6353.89	244.38		
Year	1	3729.62	3729.62	15.26	.001
Location	1	2708.73	2708.73	11.08	.003
Yr x Loc	1	799.70	799.70	3.27	.082
PRE-RUT					
Among	3	1617.83	539.28	1.69	.196
Within	23	7320.29	318.27		
Year	1	50.29	50.29	0.16	.695
Location	1	1055.75	1055.75	3.32	.082
Yr x Loc	1	259.41	259.41	0.82	.376
POST-RUT					
Among	3	8794.32	2931.44	4.75	.010
Within	23	14202.76	617.51		
Year	1	913.17	913.17	1.48	.236
Location	1	6300.70	6300.70	10.20	.004
Yr x Loc	1	653.11	653.11	1.06	.314

cate pregnancy status (Rehbinder *et al.,* 1981). I concluded that values over two ng/ml indicated pregnancy as two caribou with low values of 2.1 and 2.39 were both observed with calves on telemetry flights. Values below 0.1 indicated nonpregnant females or males, based on the value of 0.1 for a tested male.

Collared caribou mortalities were located during radio-telemetry flights with the aid of the motion-sensing mortality collar. Three mortalities were investigated. Annual mortality rates were estimated by summing the number of collared caribou that died each year, and dividing by the number of caribou-years of monitoring.

Results

Seasonal Movements and Ranges

Spring Migration

Most collared caribou moved off winter ranges in April to low elevation forested areas, although some remained on their winter ranges, or moved to other high elevation ranges. Two-thirds (63%, n=35) of all locations of collared caribou during the two spring periods were found in low elevation ranges. All spring ranges used by Southern Area caribou were in the Omineca River valley bottom immediately west of the Wolverine Range (Fig. 1), with the exception of one collared male that used a low elevation spring range further west. Many different spring ranges were used in the Northern Area. A lack of fidelity to spring ranges for two consecutive years was shown by all collared caribou in the Northern Area (n=6), and by five of six collared caribou in the Southern Area.

Both year and location accounted for a significant amount of variation in mean distances moved during spring, with longer distances moved by collared caribou in 91/92 than in 92/93, and with longer distances moved by Northern Area caribou than Southern Area caribou (Tables 1 and 2).

Calving

Timing of calving is between late May and mid June with the peak of calving around the end of the first week in June. Calving areas in the Northern Area were widely dispersed and primarily in the west (Fig. 2). In the Southern Area, most females calved on the Wolverine Range, but some used other small mountain ranges to the south and west (Fig. 2).

In 91/92, all radio-collared female caribou in both Areas moved from winter ranges to different calving ranges. However, in 92/93, two of seven Northern Area females and four of eight Southern Area females used their winter ranges for calving. At least six of ten female collared caribou (three each in the Northern and Southern Areas) showed fidelity to their calving areas in the two years (some calving sites were not confirmed in consecutive years).

Only two of seven collared females in the Northern Area were located on the same range during the calving period in both 91/92 and 92/93. The other five all used different ranges from each other. Similarly in the Southern Area, only two of six collared females used the same range during calving, but only in 91/92. In 92/93, nine caribou were located in only four ranges during the calving period.

Summer

Summer ranges were in the vicinity of calving ranges to the west in the Northern Area (Fig. 2). The primary summer ranges used by Southern Area female caribou were in the east, on the Wolverine Range. In both the Northern and Southern Areas in 91/92, most collared females were located on their calving ranges throughout the summer. However, in 92/93, six of eight females in the Northern Area, and six of nine in the Southern Area moved to other ranges for the summer period. Few data on early calf survival are available, therefore no correlation between early calf loss and subsequent movement to other areas could be made. Collared males in both the Northern and Southern Areas summered on ranges in the west. Eight of ten collared females for which there is two years data (Northern and Southern caribou combined) returned to their same summer range each year, as did the two Southern Area males.

Fall/Rut

Most collared females in the Northern Area spent the fall rutting period on or near their summer ranges in the west. Mean post-rut movements were longer than mean pre-rut movements in 91/92 ($t=2.23$, $p<0.05$), but were similar in 92/93 when two females moved to winter ranges for the rut ($t=0.08$, $p>0.05$) (Table 1). In the Southern Area almost all collared females were located during the rut on the Wolverine Range, usually on or adjacent to their summer ranges. There were no significant differences between mean pre-rut and post-rut distances moved in the Southern Area in 91/92 ($t=0.36$, $p>0.05$) or 92/93 ($t=0.14$, $p>0.05$) (Table 1).

In the Northern Area, most collared female caribou were located on different ranges from each other during the rut in both years, and three of five females returned to their same rutting ranges each year. In contrast, four of five collared females were located on one range during the rut in the Southern Area in 91/92, while two different ranges were used by five and three collared females respectively in 92/93, accounting for all but one collared female ($n=9$). Three of five females in the Southern Area showed fidelity to rutting ranges in the two years. The only collared male in the Northern Area was not located; one of the two collared Southern Area males (not located in 91/92) used a range on the Wolverine Range in 92/93, while the other used a range in the western part of the study area in both years. No collared females were ever located in this area during the rut.

There were no significant differences in the pre-rut migration distances between years or Areas, or between years for post-rut migration distances (Table 2). However, location accounted for a significant amount of the variation in mean post-rut movements, with longer distances moved in the Northern Area than in the Southern Area.

Early Winter

Early winter ranges in the Northern Area in 92/93 were primarily in the east (only two caribou locations were documented in 91/92) (Fig. 3). The only female caribou for which there is two years early winter data used different ranges each year. Collared caribou in the Southern Area in 92/93 (no data for 91/92) were found primarily on or near the Wolverine Range, or in low elevation ranges to the southwest. Almost half the collared caribou remained on their rutting ranges during the early winter period.

Late Winter

Most collared caribou in the Omineca Mountains wintered in the eastern part of the study area (Fig. 3). In the Southern Area, the Wolverine Range was the most highly used mountain range during the late winter period, while the Butler, Chase and Prospector Ranges were the most heavily used in the Northern Area (Fig. 1). During the late winter period of 91/92, 77% ($n=22$) of all radio-collared caribou remained within their winter ranges, however, in 92/93, only 50% ($n=20$) of the collared caribou remained within their late winter ranges.

Most collared individuals wintered on different ranges each year. Of five collared females monitored in the Northern Area over three late winter periods (includes initial capture period), four were located on different ranges each winter. The same lack of fidelity to winter ranges was exhibited by the five collared caribou in the Northern Area which were monitored over two consecutive winter periods. However, over three winter periods in the Southern Area, only two of seven collared caribou were located on different ranges. One of the remaining five caribou was even found to return to the same range each winter. Of the collared caribou monitored over two winter periods, two of four were located in different ranges each year.

Seasonal Habitat Use

Over 60% (n=93) of the caribou locations in spring (Apr/May) of both years were in forested areas, primarily in low elevation lodgepole pine and pine/spruce forests. Use of those habitats was greater in spring than at any other time of the year (Figs. 4 & 5). Use of early seral stages was also more common in spring than at any other time, and included use of immature lodgepole pine, pine/aspen, non-commercial brush and meadow sites. Females moved to upper elevation calving areas in mid to late May, while all collared males remained in lower elevation forested habitats.

Almost all collared females were located in upper elevation balsam/spruce forests or in alpine/subalpine areas during calving in late May/early June. Those were the primary habitats used throughout the summer as well (Figs. 4 & 5). During the calving period of 1993, most collared females were located in rocky outcrops near treeline (Wood, unpubl. data).

Use of low elevation forests decreased from April to October, while use of alpine/subalpine areas increased. By the fall period (September/October) only 8% (n=40) and 11% (n=18) of all collared caribou in 91/92 and 92/93 respectively, were located in forests below 1300 metres.

In early winter (November to January) of 92/93, 56% (n=34) of the locations of collared caribou were in forested habitats, primarily in the upper elevation balsam/spruce and lower elevation mixed pine/spruce forests (Fig. 5). No data are available for the early winter period of 91/92. In late winter (February/March) of 91/92, all live radio-collared caribou in the Omineca Mountains were located in alpine and subalpine habitats. One dead female radio-collared caribou was located in a low elevation spruce stand (Fig. 4). The pattern of habitat use in the late winter of 92/93 contrasts markedly with the previous year, with only 55% (n=40) of collared caribou locations in alpine and subalpine habitats (Figs. 4 & 5). The use of forested areas during that late winter period, 45% of locations (n=40), reflects only a slight decrease in use from the early winter period when 56% (n=34) of caribou locations were in forested areas. Use of low elevation pine and/or spruce dominated forests remained consistent from early winter (26%, n=34) through late winter (27%, n=40), use of upper

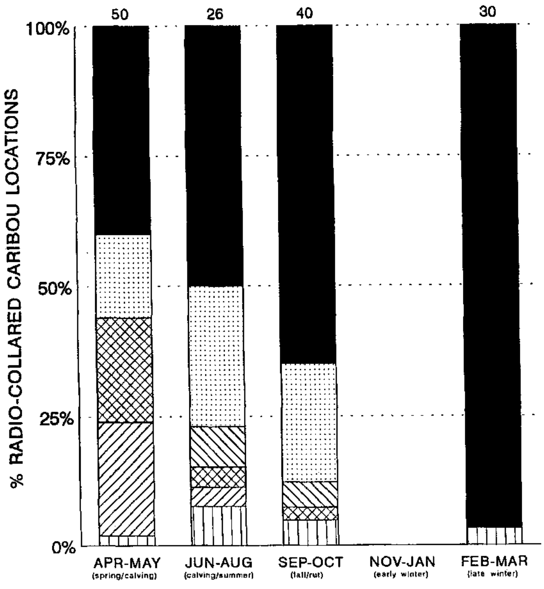

Fig. 4. Proportion of radio-collared caribou locations in different habitat types from April 1991 to March 1992. (Number of locations given above each bar.)

■ ALPINE/SUBALPINE
░ BALSAM/SPRUCE (≥1300m)
▧ PINE (>1300m)
⊠ PINE/SPRUCE (≤1400m)
▨ PINE (≤1300m)
▥ SPRUCE (<1300m)

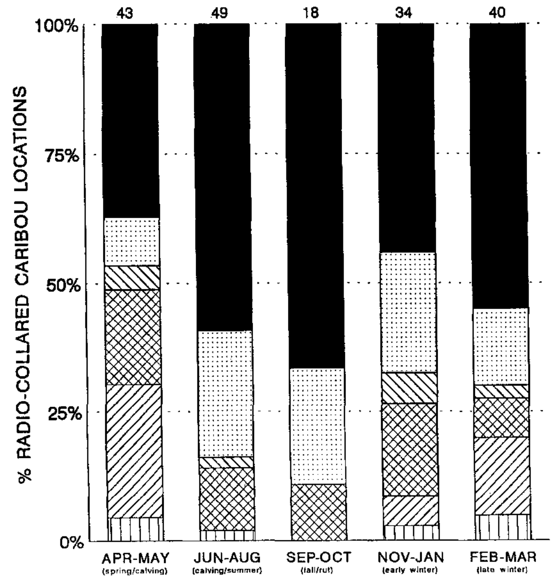

Fig. 5. Proportion of radio-collared caribou locations in different habitat types from April 1992 to March 1993. (Number of locations given above each bar.)

elevation forests decreased from 29% to 18%, and use of alpine/subalpine areas increased.

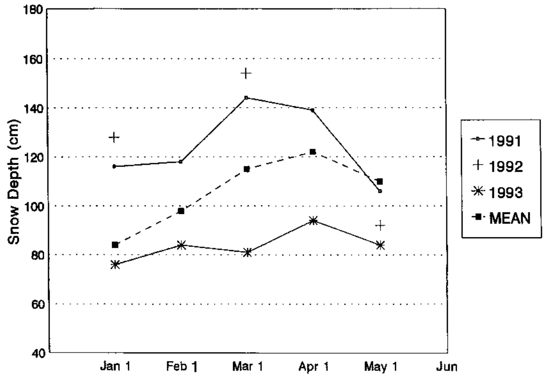

Fig. 6. Snow depths measured at Germansen Snow Station (1500 metres). Mean snow depths based on 31 years data with exception of January (10 years) and February (24 years).

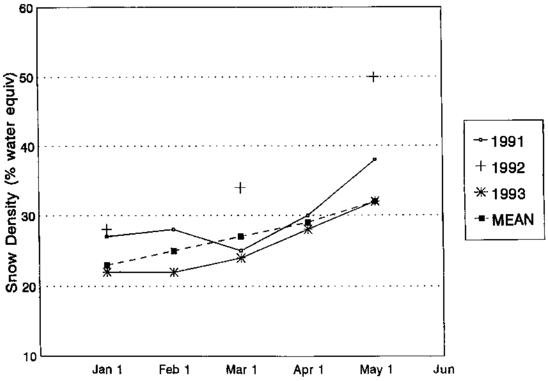

Fig. 7. Snow densities measured at Germansen Snow Station (1500 metres). Mean densities based on 31 years data, with exception of January (10 years) and February (24 years).

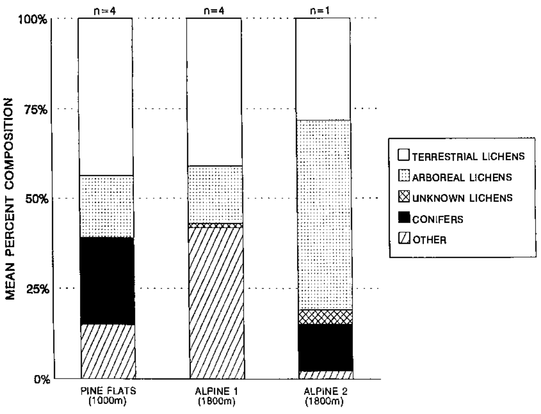

Fig. 8. Mean vegetation composition (%dry matter) of late winter composite fecal samples. (n=# of composite samples.)

Snow depths were above average in the winter of 90/91 when the first caribou were captured and radio-collared (Fig. 6). Snow depths in the winter of 91/92 were even greater, setting a new record over 31 years for the maximum depth recorded at the weather station in March. Snow densities were also the highest ever recorded for that station (Fig. 7). Snowfall over the winter of 92/93 was below average. Snow depths measured each month were lower than the mean, especially during the latter part of the winter, and approached that of the lowest snow depths on record set in 1980.

Winter Diet

Terrestrial lichens, arboreal lichens and conifers were the primary forage types found in winter fecal samples (Fig. 8). Over 60% (n=4) of the "Pine Flats" samples were comprised of terrestrial and arboreal lichens in a 72:28 ratio. Conifers accounted for an additional 24% of the fecal pellet samples. Lichens made up 58% (n=4) of the "Alpine 1" samples with an identical proportion of terrestrial to arboreal lichens as in the "Pine Flat" samples. Conifers were absent in the Alpine 1 samples, while the remaining 42% included mosses, grasses, shrubs, sedges and forbs in declining order of prominence. Lichens comprised 85% of the only "Alpine 2" fecal sample, with a ratio of 35:65 for terrestrial to arboreal types.

Population Characteristics

Sightability of collared caribou was greater during summer, fall and late winter when more caribou used open alpine and subalpine habitats. Group sizes varied among seasons, with the largest groups observed in October and in late winter (Table 3). In both years, typical group sizes of collared caribou more than doubled from February to March. This trend was also observed during aerial population surveys (Table 4). Lowest typical group sizes were recorded during calving and summer periods.

During a survey of alpine areas on the Wolverine Range in the Southern Area in February 1993, we counted 66 caribou, of which 12% were calves (Table 4). Weather conditions limited access to many alpine areas and none of the twelve radio-collared caribou in the Southern Area were observed on the survey. A winter inventory of the Wolverine Range was also conducted prior to the initiation of this study, in February 1989 (Hatler, 1989), during an average snowdepth winter. On that survey 214 caribou were located, with calves comprising 16% of the caribou observed. Although no collared animals were available to provide a sightability correction, it is likely that some members of the population were missed. Based on the minimum count by Hatler (1989), and assuming a relatively stable population since that time, I estimate the minimum population in the Southern Area at approximately 200 animals. The maximum area that collared caribou used during the two years of this study was 3780 km^2. Assuming that only caribou that wintered in the census area used that 3780 km^2 area, the minimum density estimate is 0.053 caribou/km^2.

In March 1993, we surveyed the Chase and Butler alpine winter ranges in the eastern part of the Northern Area (Fig. 1), and counted 396 caribou, 90% of which were located on the Chase Range. Calves accounted for 17% of the caribou observed. Three of six collared caribou were observed during the survey, resulting in a population estimate of 690 ± 202 (SD) caribou in the Northern Area. Thus, using the 95% confidence limits, and the minimum number observed on the survey, the population in the Northern Area is estimated to be between 396 and 1085 animals. Collared caribou used a maximum area of 10,700 km^2 during the two years of the study, resulting in a density estimate of between 0.037 and 0.10 caribou/km^2. Based on presently available information, my minimum estimate for the caribou population in the Omineca Mountains (Northern and Southern Areas combined) is approx- imately 600-700 animals, while the actual total could be up to 1200 or more. Both bulls per 100 cows, and calves per 100 cows were lower in the sample from the Southern area than that from the Northern area (Table 4). Serum progesterone levels were greater than two ng/ml for 17 of 20 female caribou at capture indicating that they were pregnant at the time. Serum progesterone levels ranged from 0.04 to 0.1 for non-pregnant caribou, and 2.1 to 9.4 for pregnant females. Of the three caribou with very low values, one was estimated at 21 months of age, while the ages of the other two were not estimated at the time of capture. The pregnancy rate of suspected adult females was 89% (17/19).

To date, eight radio-collared caribou (six captured in 1991, and two in 1992) have died (Table 5). Three mortality sites were investigated; evidence remaining at the sites was scarce but pointed to wolf predation as the primary cause of death. One of the eight, a young male captured in March 1992, died prior to the first telemetry follow-up flight, and capture myopathy is suspected. Five of the remaining

Table 3. Typical group sizes of radio-collared caribou observed during radio-telemetry flights. (n = number of radio-collared animals located, even if in same group; TGS = typical group size ± SD).

	91/92		92/93		Total	
Month	n	TGS	n	TGS	n	TGS
April	2	20.5 ± 16.3	-	-	2	20.5 ± 16.3
May	2	4.5 ± 0.7	12	5.0 ± 4.2	14	4.9 ± 3.9
June	4	2.8 ± 1.5	3	3.3 ± 2.3	7	3.0 ± 1.7
July	3	2.3 ± 0.6	5	2.8 ± 2.7	8	2.6 ± 2.1
Aug	-	-	3	3.3 ± 1.5	3	3.3 ± 1.5
Sep	13	6.6 ± 4.5	-	-	13	6.6 ± 4.5
Oct	11	15.9 ± 9.4	11	10.4 ± 5.7	22	13.1 ± 8.1
Nov	-	-	7	8.9 ± 7.5	7	8.9 ± 7.5
Dec	2	14.5 ± 12.0	-	-	2	14.5 ± 12.0
Jan	-	-	8	5.1 ± 3.4	8	5.0 ± 3.4
Feb	12	7.8 ± 3.8	7	7.3 ± 4.5	19	7.6 ± 3.9
Mar	6	18.5 ± 9.7	14	17.6 ± 12.6	30	18.1 ± 10.9

Table 4. Sex and age composition, and typical group size of caribou observed during late winter surveys of alpine mountain ranges in the Northern and Southern Areas.

Area	Bulls	Cows	Calves	Total Count	Bulls/ 100 Cows	Calves/ 100 Cows	Calves/ 100 Adults	Typical Grp. size
SOUTHERN AREA (Wolverine) 1989	46	133	35	214	35	26	20	14.3 (Feb) (range 2-27)
SOUTHERN AREA (Wolverine) 1993	15	43	8	66	35	19	14	11.2 (Feb) (range 1-16)
NORTHERN AREA (Chase/Butler) 1993	107	222	67	396	48	30	20	42.0 (Mar) (range 3-89)

Table 5. Season, elevation and habitat of collared caribou mortalities during 91/92 and 92/93. M= male, F = female.

Caribou	Month/Year	Season	Elev	Habitat	Area
083* M	Mar-May 92	Spring	1850	Alpine	S
493 F	Apr-May 91	Spring	850	Spruce forest	S
466 F	Apr-Jun 91	Spring	775	Pine/Aspen forest	S
412 F	June 91	Summer	1700	Alpine	N
322 F	Jun-Jul 92	Summer	1250	Pine/Spruce forest	N
332 M	Oct-Dec 91	Early Winter	1850	Alpine	N
392 F	Feb-Mar 92	Lt. Winter	1200	Spruce forest	N
494 F	Feb-Mar 93	Lt. Winter	1200	Pine/Spruce forest	N

* Suspected cause of death: capture myopathy.

seven caribou died while in low elevation forested habitats. In the Northern Area, three of nine collared caribou died in 91/92, and two of ten in 92/93 for an average annual mortality rate of 27% ± 6.6 (SE). In the Southern Area, two of nine (91/92) and none of eleven (92/93) collared caribou died, for an average annual mortality rate of 11% ± 11.1 (SE). However, there was no significant difference between the two mortality rates ($t=1.19$, $p>0.10$). Combined, the average annual mortality rate for the Omineca Mountains caribou between 1991 and 1993 was 19% ± 6.9 (SE).

Discussion

Seasonal Habitat Use and Movements

Telemetry data suggest that at least two populations of caribou reside on the west side of the Williston Reservoir. The term "herd" has been applied to those caribou that congregate in a particular rutting area (Bergerud & Elliott, 1986), while a "population" is defined as a collection of herds sharing a common winter range (Hatler, 1986) or that rut on adjacent ranges removed from other herds by at least 60 km in the fall (Bergerud & Elliott, 1986). To date, no seasonal ranges of collared caribou in the Northern and Southern Areas have overlapped. In addition, one male in the western part of the Southern Area used different seasonal ranges from all other collared Southern Area caribou. He was usually accompanied by other caribou however, and may belong to a third population that inhabits the Takla Lake area.

In the spring (April/May), about two-thirds of all collared caribou moved from winter ranges to low elevation forested areas; primarily lodgepole pine and lodgepole pine/white spruce dominated stands. Use of habitats such as southfacing deciduous hillsides, aspen stands and meadows that become snowfree earlier than heavily timbered areas, was also more common in spring than at any other time. Many Northern Area females moved from winter blocks to lower elevation spring blocks in a direction opposite from their calving areas, and many Southern Area females used low elevation forested areas adjacent to their alpine winter blocks, which they then returned to for calving. These data suggest that caribou were using low elevation forested habitats in spring primarily for foraging, although low elevations were also used during migration to calving areas. Most collared caribou used different spring blocks each year. Unpredictable use of spring ranges may be an effective predator avoidance strategy (Simpson & Woods, 1987).

The mean distance moved from winter blocks to calving blocks (spring migration) was longer in 91/92 than in 92/93. The shorter mean migration distance in 92/93 (after the heavy snowfall winter) may reflect use of some winter blocks that were closer to calving areas than in the previous year. This suggests that caribou did not travel as far to winter ranges during the more severe winter, however, no data are available on the pre-rut or post-rut movements prior to the average snowfall winter of 90/91 for comparison.

Collared caribou calved below treeline, in rocky outcrops at treeline and in alpine areas. Cichowski (1989) and Hatler (1986) also documented use of calving areas below treeline for collared caribou in Tweedsmuir Park and Spatsizi Park respectively, while observations by Bergerud *et al.* (1984) implied use of calving sites in Spatsizi that were mostly rock.

The peak of calving occurred in the first week of June. By that time, most collared females were dispersed in mountainous areas and calved alone, while males remained in low elevation habitats until mid to late June. Dispersion in mountains for calving is considered to be an antipredator strategy of woodland caribou in B.C. (Bergerud *et al.*, 1984). While males remain in areas of higher forage quality, females reduce predation risk by dispersing to mountainous areas to separate themselves from moose and predators in valley bottoms (Bergerud & Page, 1987; Seip, 1992). Collared caribou in the Northern Area dispersed more widely, moving greater distances from winter ranges to calving areas than did caribou in the Southern Area. This appears to reflect the large expanse of mountainous terrain and dispersed calving habitat in the Northern Area relative to the Southern Area. Calving areas for caribou in the Southern Area were primarily on the Wolverine Range and on two small adjacent mountain ranges. The use of only four ranges by nine caribou during the calving period in 92/93, may be a reflection of the lack of suitable calving habitat in the Southern Area. However, it could also be a reflection of the larger proportion of collared caribou in the Southern Area population, relative to the Northern Area population.

Most summer and rutting ranges used by collared caribou were in the upper elevation balsam/spruce and alpine/subalpine habitats, and were in the vicinity of their calving areas: on mountains in the west for Northern Area caribou, and on the Wolverine Range for those in the Southern Area. Many collared caribou showed fidelity to both calving and summer ranges. Fidelity to calving areas has also been reported in other woodland caribou populations (Shoesmith & Storey, 1977; Hatler, 1986; Edmonds, 1988; Cichowski, 1989). About two-thirds of all radio-collared caribou showed fidelity to rutting ranges too. In the Northern Area, no two collared animals used the same rutting ranges, while in the Southern Area, many ranges were used by two or more collared individuals. Again, this may reflect the larger relative sample size of caribou in the Southern Area, however, it is also likely a result of the lack of mountain ranges in that area. Longer post-rut movements were observed in the Northern Area as summer and rutting areas were much further away from winter ranges than in the Southern Area, where some caribou remained on summer ranges through the winter, or moved only to an immediately adjacent range.

Collared caribou wintered on high elevation alpine or low elevation forested areas in the eastern foothills of the Omineca Mountains. Most collared individuals used different winter ranges each year. Range rotation is thought to occur to reduce grazing pressure on slow growing lichens (Bloomfield, 1980). Snow depths appear to influence movements and habitat use of the Omineca caribou in the early and late winter periods, which has also been documented in northern B.C. (Hatler, 1986) and west-central Alberta (Edmonds & Bloomfield, 1984). In the record heavy snowfall year, deep snows apparently forced caribou onto windswept slopes to crater for terrestrial lichens. Deep snows impede caribou movement and reduce forage availability thus increasing energy expenditures required to obtain the forage (Fancy & White, 1985; Thing, 1977). In the winter of below average snow depths when movement and forage availability were not as restricted, more than half of the early winter collared caribou locations were in low elevation forest. Because many caribou remained there through the late winter period suggests that caribou prefer to winter in forested areas, and are forced onto alpine ridgetops by deep snows.

Although dispersal to other ranges for the calving and early winter periods exists, overlapping use of seasonal ranges by collared caribou in the Southern Area reflects the relative compactness and apparent importance as caribou habitat of the Wolverine Range and its surrounding lower elevation forested areas. On the other hand, lack of fidelity to winter and spring ranges suggests that caribou continue to explore new areas throughout their lives (Simpson & Woods, 1987), and additional areas will probably be documented as more data is collected.

Winter Fecal Analyses

Fecal fragment data suggest that terrestrial and arboreal lichens were the primary food types used in the winters when samples were collected. Samples collected in lodgepole pine habitats not only indicated cratering for terrestrial lichens, but also foraging on arboreal lichens and conifers. The high proportion of terrestrial lichens, mosses, shrubs and grasses in most of the alpine samples reflected use of open treeless habitats, while one alpine sample comprised of high proportions of arboreal lichens and conifers reflected use of upper elevation Engelmann Spruce Subalpine Fir (ESSF) forests in winter. Analyses of plant fragments in fecal pellets usually overestimate proportions of mosses and shrubs, resulting in incorrect proportions of the remaining forages such as lichen (Boertje *et al.*, 1985). Thus, lichens were likely an even more important component of these caribou's diet.

Population Characteristics

The largest typical group sizes were found in October when caribou congregated in rutting areas, and in late winter when caribou were concentrated on winter ranges. Typical group sizes of collared caribou more than doubled from February to March in both years. Increased snow depths and densities through late winter may force caribou to concentrate in smaller areas where forage is accessible, or to increase foraging efficiency. Russell & Martell (1984) report that groups of caribou can crater through deeper snow (80-90 cm) than solitary animals (50-60 cm). Increased group size in March could also be a defence against predation. Snow density increases through late winter, making it easier for wolves to move across the snowpack and access high elevation winter ranges. Caribou already concentrated on alpine winter ranges may form larger aggregations thus reducing the risk to each individual through increased numbers (risk is shared among more individuals) and increased vigilance.

At least 600-700 caribou reside in the Omineca Mountains in two populations, with a high observed pregnancy rate of 89% indicating that the populations are not nutritionally stressed (Skogland, 1985). If the observed indicators of recruitment and mortality rates are representative, then the moderate calf recruitment and low mortality rate in the Southern Area would suggest a stable or increasing population, and the high calf recruitment but even higher mortality rate in the Northern Area would suggest a decreasing population. However, the survival and mortality rates are based on extremely limited data, and these results should be interpreted very cautiously.

Predation was suspected to be the primary cause of death for collared adult caribou that died at low elevations in the Omineca Mountains area. Although no data are available on wolf densities in the study area, the higher observed adult mortality rate in the Northern Area cautiously suggests that wolves may be more abundant there than in the Southern Area. However, observed bull/cow ratios were much lower in the Southern Area (35/100) than in the Northern Area (48/100), suggesting greater mortality from predation in the Southern Area. Adult males are thought to die at greater rates than adult females when predation is high (Bergerud & Elliott, 1986). The proportion of males in the population was 22% in the Southern Area, and 27% in the Northern Area, which are comparable with other populations in northern B.C., but below the mean of 36% for North America (Bergerud, 1980).

Based on data gathered to date, caribou were present at densities of 0.056 caribou/km^2 in the Southern Area, and between 0.037 and 0.10 caribou/km^2 in the Northern Area. These figures compare to the mean density of 0.06 ± 0.022/km^2 calculated for 24 caribou populations in North America where wolves are unexploited (Bergerud, 1992).

Forest harvesting activities have been extensive in the Northern Area. A large proportion of the major river valley bottoms have been clearcut harvested, and harvesting continues. Little timber extraction has occurred in the Southern Area: harvesting there has primarily occurred on the eastern side of the Wolverine Range and very few collared caribou have ever been located in that area. The continuation of this study of the woodland caribou in the Omineca Mountains aims to explore the relationship between forest harvesting and these two caribou populations.

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Brief communication

Generic preference and *in-vivo* digestibility of alectorioid arboreal lichens by woodland caribou

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Key words: digestion trials, intake rate, *Alectoria sarmentosa*, *Bryoria*

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Introduction

Lichens are eaten by most ungulate species in North America (Bergerud, 1972; Stevenson, 1978; Jenkins & Wright, 1987; Fox & Smith, 1988; Klein & Bay, 1990). However, none of these species are more obligate lichen feeders than woodland caribou (*Rangifer tarandus caribou*) in ecosystems of western North America where deep snowpacks preclude cratering. The digestibility of lichens is reported to vary substantially (21% to 85%; Hanley & McKendrick, 1983; Robbins, 1987) depending on technique and, in the case of *in-vitro* analyses, inoculum source (Person *et al.,* 1980; Thomas *et al.,* 1984; Antifeau, 1987). The objective of this experiment was to determine the *in-vivo* digestibility and generic preference of the 2 primary arboreal lichens found in late-winter woodland caribou habitat in southeastern British Columbia, northern Idaho and northeastern Washington.

Methods

Three bottle-raised woodland caribou calves were used in a winter field experiment for 12-37 days prior to the initiation of digestion trials. Caribou weights on day 1 were: #1=64kg, #2=69kg, and #=60kg. Daily diets were composed primarily of lichen and were then shifted to solely lichen 3 days immediately preceding 7-day total collection trials. Trials were conducted March 15-22, 1993. Hand-cleaned arboreal lichen, separated by genus (*Alectoria* and *Bryoria*), was offered *ad. lib.* throughout the 7-day trial. Lichen orts were collected daily and air-dried for 72 hours and then corrected for dry matter by oven-drying subsamples for 24 hours at 100° C. All feces were collected and a daily subsample freeze-dried for chemical/microhistological analyses. The remaining feces were oven-dried for 24 hours at 100° C and weighed.

Preference was measured as the percent of each genus consumed during the course of the trial. Contents of feeders containing each genus of lichen were switched daily to minimize any potential feeder placement bias. Caribou had access to water ad-libitum during the trial. Daily intake was corrected for dry-matter. Caribou were weighed on alternate days throughout the trial.

Results and discussion

Mean apparent dry matter digestibility (ADMD) was 82% (range=77-86%). All caribou exhibited a strong preference (92%) for lichen in the multi-species *Bryoria* complex (range=87-99%) versus *A. sarmentosa* (8%). Mean daily dry matter intake was 43 g/kg $BW^{0.75}$ (range=25-61 g/kg $BW^{0.75}$). These data include 2 days when animal #2 became nearly anorectic, eating only 292 g and 57 g. The 2 calves that spent only 12 days adjusting to a 100% alectorioid lichen diet did not eat as much and lost 1.8 and 4.6 kg during the trial. In addition, these animals did not produce solid feces during the trial indicating less than optimal adjustment to this diet. The calf that had 37 days to adjust to a lichen diet ate substantially more, continued to produce solid feces, and gained 3.2 kg during the trial.

This high ADMD value is in agreement with the only other in-vivo study on arboreal lichens (Robbins, 1987) and suggests that lichen digestibility is inadequately measured using in-vitro analyses with non-lichen fed inoculum donors. Preference for *Bryoria* may be a function of higher protein content (Antifeau, 1987; this study), lower tensile strength (pers. obs.), or differences in concentrations of secondary plant constituents.

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Brief communication

Population dynamics of the Taimyr reindeer population

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Abstract: The Taimyr herd of wild reindeer (*Rangifer tarandus tarandus* L.) is one of the three largest herds of wild *Rangifer* in the world, and numbered about 600,000 in 1993. The herd grew continuously from 1959 to 1990, and is now stable due primarily to intensive commercial harvesting along the Khatanga River. Meat from the commercial harvest is processed and sold in population centers in the northern Krasnoyarsk region, particularly Norilsk. The herd has expanded its range to about 1.5 million km^2, but movements to the southwestern portion of the winter range may have been impeded by pipeline, road and railroad construction, and winter shipping of ore on the lower Yenisey River.

Key words: commercial harvest, density, hunting, industrial development, movements, Russia

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Introduction

The Taimyr population of wild reindeer, the largest in Eurasia, has been studied for about 30 years. Since 1959, 18 censuses have been conducted by the same specialists. The age structure, sex ratio, spatial distribution, migrations, fecundity and rate of population increase have also been studied. In contrast to most herds of caribou in North America, the Taimyr herd is intensively managed for meat production and is commercially harvested. In this paper, we review the population dynamics and movements of the herd in relation to intensive harvest and industrial development.

Population size and harvest

Population size of the Taimyr herd was estimated from aerial surveys flown with fixed-wing aircraft (Antonov AN-2 biplane) during the July period of maximum aggregation from 1959 to 1993. When groups were suitably aggregated, whole groups were photographed in black and white and the entire group was counted. If aggregations were dispersed, group sizes were estimated without photography by extrapolation from line transects flown over the areas covered by the loose aggregations. Sizes of the loose aggregations were estimated independently from two aircraft which flew transects at right angles to each other.

From 1959 to 1993 the Taimyr herd grew from about 100,000 to about 600,000 (Table 1). From 1959 to 1972 the herd was lightly hunted and grew at a mean annual rate of about 11%. Subsequently, intensive commercial harvest reduced the rate of population growth and eventually stabilized the herd by 1993 (Table 1). Most harvest occurred along the Khatanga River in August and September by commercial hunting cooperatives. Most of the meat was flown to Norilsk by helicopter to be sold or processed into meat products. Despite the annual harvest of 50,000-100,000 wild reindeer from the Taimyr herd, and up to 20,000 domestic reindeer, the Norilsk area is a net importer of meat and meat products. Meat continues to be relatively expensive. Antlers and skins of harvested reindeer have also been sold. Klein & Kolpashchikov (1991) previously discussed aspects of commercial harvesting.

Movements and herd distribution 1959-1993

Movements and distribution of reindeer were documented from aerial surveys in spring, summer and autumn, and from reports of hunters, reindeer herders and others. Some colored visual collars have been deployed at lake and river crossings, but radio-collar technology has not been available.

During the 1950s and 1960s, the herd primarily wintered in the mountain tundra of the central Putorana region south of the Taimyr Peninsula (Fig. 1). As the herd increased it also expanded its range. Beginning in 1970 Taimyr reindeer began to invade the northern portion of Evenkia and reached as far south as 65° N latitude by the late 1980s. The

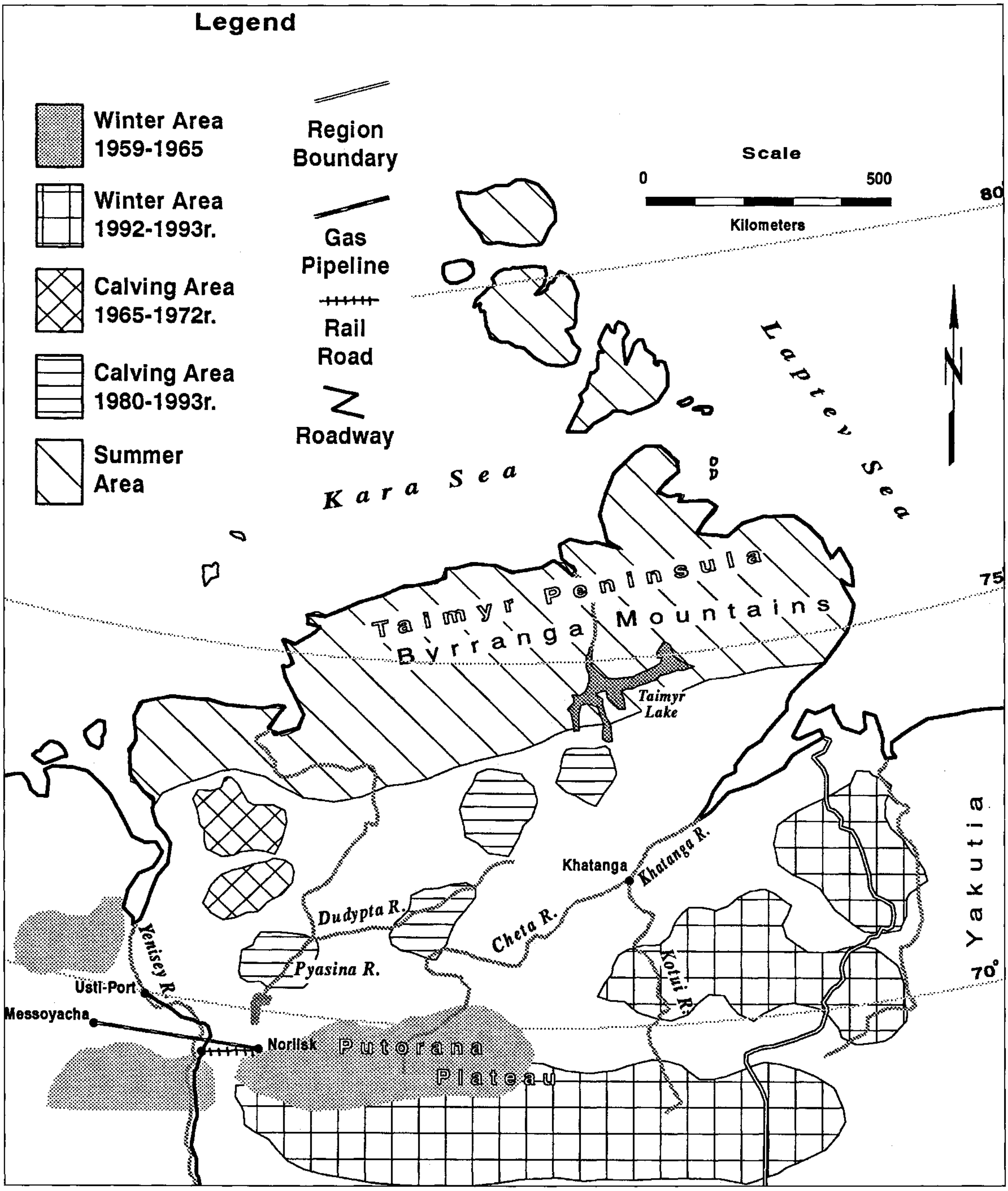

Fig 1. Seasonal ranges of the Taimyr herd.

herd also began to use wintering areas to the southeast, south and southwest of the Putorana Plateau, including northwestern Yakutia and areas along the Yenisey River. However, winter distribution of reindeer may have been influenced during the 1970s by construction of the Messoyacha-Norilsk gas pipeline and other associated pipelines, and roads near Norilsk. In addition, in 1980, winter shipping of ore from Norilsk began on the lower Yenisey River. Pipelines and roads were constructed without allowance for reindeer passage, and the shipping left open channels in the river ice which resulted in deflection of reindeer movements and direct mortality. As a result, the southwest portion of the winter range may be largely unavailable to the herd. Presently the largest migrations occur in a

Table 1. Population size, rate of increase and harvest of Taimyr wild reindeer, 1959-1993.

Year	Estimated population size[a] (thousands)	Mean annual finite rate of increase (λ)[b]	% Harvested[c]
1959	100	–	–
1966	250	1.14	–
1969	300	1.063	2.8
1972	386	1.088	5.0
1975	449	1.052	8.9
1978	475	1.019	12.3
1980	485	1.01	–
1981	510	1.054	14.5
1982	525	1.03	–
1983	540	1.029	–
1984	575	1.065	15.6
1985	590	1.026	–
1986	595	1.009	15.0
1988	570	0.979	–
1990	625	1.047	15.9
1993	600	0.987	–

[a] Data from aerial censuses.

[b] Mean annual rate of increase from previous census.

[c] Data from harvest estimates primarily during commercial harvesting along Khatanga and Cheta Rivers.

Table 2. Age structure and sex ratio of the Taimyr wild reindeer, 1972-1993.

Year	July[a] % calves	Aug-Sep[b] % yearlings	Aug-Sep[b] males:100 females > 3 yrs
1972	21	20	42
1975	23	23	53
1978	23	20	43
1980	23	22	53
1981	26	15	50
1982	21	21	56
1983	26	17	63
1984	24	23	53
1985	24	26	45
1986	22	29	53
1988	25	27	45
1990	23	30	56
1993	26	22	40

[a] From July census.

[b] From age structure of harvest.

Table 3. Fecundity in female wild reindeer harvested from the Taimyr herd in March and April.

Age group	Percent fecund 1981-1983 (n = 1,491)	 1987-1990 (n = 1,149)
2	46	19
3-6	82	89
7-9	70	87
10+	69	80
mean	75	83

southeast-northwest direction across the Khatanga River basin.

During the 1990s the Taimyr herd was ranging over approximately 1.5 million km², but range size has not expanded as fast as population size, so density has increased. In addition, as herd size increased the calving area has expanded and shifted to the east and southeast (Fig. 1). The shift in calving areas may also have been influenced by acid rain fallout from Norilsk, although in recent years a new calving concentration has occurred along the lower Pyasina River near Norilsk (Fig. 1).

Age and sex structure of the population

Recruitment into the Taimyr herd has remained relatively stable (Table 2) although the mean age of the population became younger in response to the intensive harvesting that began in the early-mid 1970s. Based on cementum age, during 1981-1983 the oldest females were 16-19 years old, but during 1987-1990 the oldest female was 14. After intensive hunting began in the early 1970s, it was rare to find males older than 10 years, although the sex ratio of adults has not changed appreciably (Table 2). The primary sex ratio slightly favors males, but sometime during the first two years of life it begins to favor females.

Fecundity

Fecundity rates in the Taimyr herd were studied by examining harvested females in March and April during 1981-1983 and in 1987-1990. Females usually begin producing calves at age 3, but fecundity in this age class was quite variable (Table 3). The productivity of individual generations of females varies, and many females fail to reproduce each year. Overall, an average female produces about 4-5 calves during her reproductive period, but some produce 10-11. As the population has increased fewer 2-year-olds have been fecund, possibly indicating that nutrition has been suboptimal in recent years (Table 3).

Because the Taimyr herd is very large in relation to numbers of wolves, bears and other predators, the size of the calf cohort in fall is primarily related to variations in the annual fecundity rate particularly among 3-year-olds.

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Brief communication

Wild reindeer of the Kamchatka Peninsula - past, present, and future

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Abstract: A unique subspecies of wild reindeer (*Rangifer tarandus phylarchus* Hollister) that is endemic to the Kamchatka Peninsula has been declining in number since the 1950s due to commercial hunting, increasing industrial development and competition with domestic reindeer. The largest remaining herd of wild reindeer occurs in the Kronotsky Reserve in northeastern Kamchatka, and the reserve is now critical to the preservation of this subspecies of reindeer.

Key words: commercial hunting, industrial development, Kronotsky Reserve, *Rangifer*

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Introduction

The Kamchatka Peninsula of the Russian Far East is inhabited by a subspecies of wild reindeer (*Rangifer tarandus phylarchus* Hollister) which is unique to the area. These animals are the largest subspecies of *Rangifer*, and are adapted to local climatic conditions. The area is dominated by volcanoes, and summer pastures are moist and highly productive. Snow is often very deep in winter and lingers late into summer. The wild reindeer population of the peninsula has been declining since the 1950s, and biologists are concerned about its continued well-being.

Population size

During the 1960s there were an estimated 12,000 wild reindeer on the peninsula and the ranges of individual herds overlapped (Vershinin, 1972; Vershinin *et al.*, 1975). By 1970 the population had declined considerably, and occurred primarily in 3 non-overlapping herds (Fig. 1). Range size continued to become more restricted until 1980, but has not changed appreciably since then (Fig. 1). The total population declined through 1990 and has now stabilized as the Eastern herd increases and the other 2 herds continue to decline (Table 1).

Prior to the mid-1970s, the Southern herd prospered, and contained about 3,000 reindeer (Phili, 1973). During the early 1970s the herd was reduced by heavy commercial hunting. In 1985 commercial hunting was prohibited, but exploration, highway construction, and construction of geothermal stations for electricity production began and made the winter ranges of the herd more accessible. The herd continued to decline, and is in danger of being eliminated.

Until 1980, the range of the Northeastern herd was largely unaffected by human activity, but the winter ranges of the herd were also used for reindeer husbandry. A population decline began during the 1970s, and has continued to the present, although the rate of decline has slowed.

The Eastern herd is the healthiest of the 3 herds in Kamchatka because all of its summer range and some of its winter range is in the Kronotsky Reserve, which is closed to hunting and the grazing of domestic reindeer. However, particularly when snow is deep, the Eastern herd moves out of the reserve onto adjacent ranges where domestic reindeer herding occurs. Herders are intolerant of the wild reindeer because they compete for winter range with domestic reindeer and their animals may be led away by the wild ones.

Table 1. Number of wild reindeer in Kamchatka, 1975-1992.

	Number of animals[a]						
Herd	1975	1980	1983	1985	1987	1990	1992
Southern	3,300	1,450	800	550	300	220	150
Eastern	2,000	880	1,000	1,360	1,700	1,900	2,500
North-eastern	3,000	2,100	1,700	1,150	900	650	450
Total	8,300	4,430	3,500	3,060	2,900	2,770	3,100

[a] Estimated through aerial surveys.

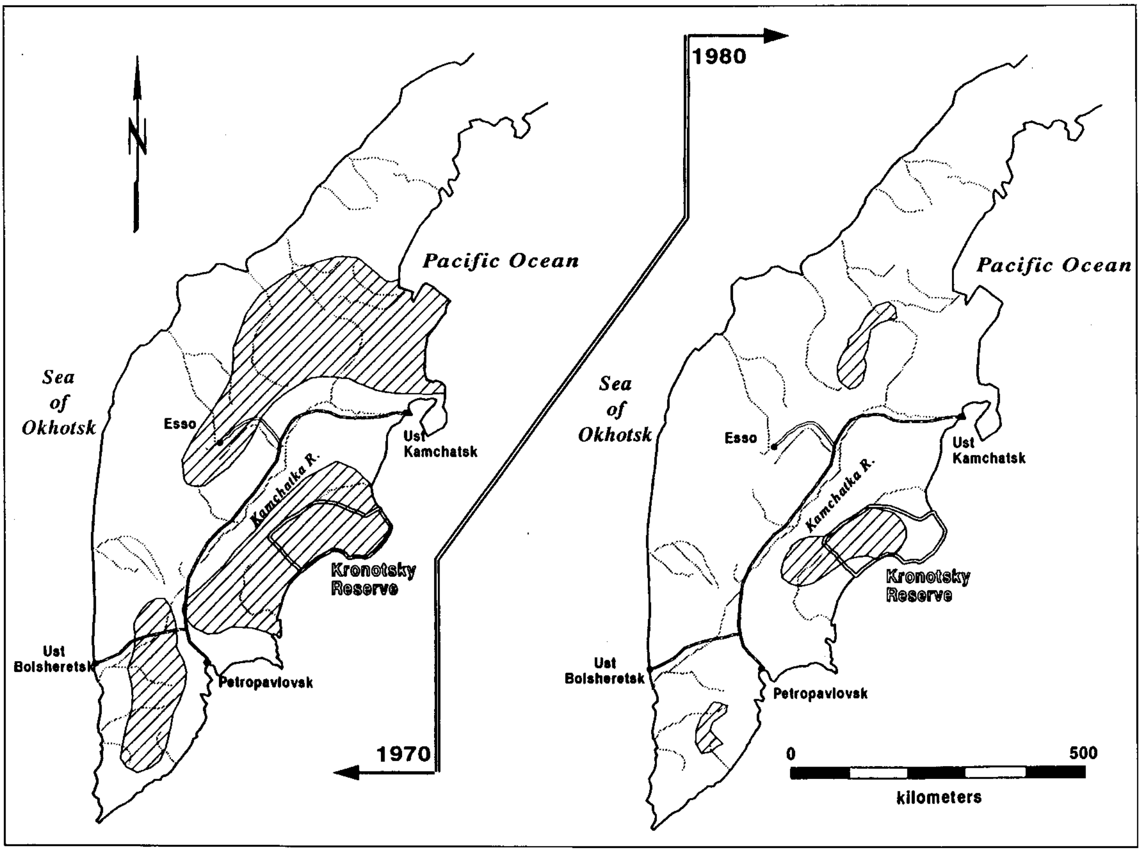

Fig. 1. Distribution of Kamchatka wild reindeer in 1970 and 1980.

Population conservation

The Kronotsky Reserve plays a critical role in the conservation of this subspecies of wild reindeer. However, even the relatively large reserve does not contain sufficient winter range and cooperative agreements, monitoring of herd movements and increased communication with adjacent reindeer herders is necessary.

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Brief communication

Wild reindeer of Yakutia

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Abstract: Three major herds of wild reindeer (*Rangifer tarandus tarandus* L.), totaling over 200,000 animals, occur in the tundra and taiga of northern Yakutia. These herds have been expanding since the late 1950s and now occupy most of their historic range. In addition, several thousand wild reindeer occupy the New Siberian Islands and adjacent coastal mainland tundra, and there are about 60,000 largely sedentary forest reindeer in mountainous areas of the southern two-thirds of the province. Wild reindeer are commercially hunted throughout the mainland, and the production of wild meat is an important part of the economy of the province and of individual reindeer enterprises which produce both wild and domestic meat.

Key words: commercial harvest, density, economic importance, industrial development, Lena-Olenek, movements, Russia, Sundrun, Yana-Indigirka

Rangifer, Special Issue No. 9, 387-390

Introduction

Three major herds of wild reindeer (*Rangifer tarandus*) occur on the continental tundras of the autonomous province of Yakutia. These herds are the Yana-Indigirka, Sundrun (Indigirka-Kolyma) and Lena-Olenek (Bulun) (Fig. 1; Table 1). A separate herd also inhabits the New Siberian Islands in summer but winters extensively on the adjacent mainland tundras (Fig. 1). In addition, there are about 60,000 sedentary wild forest reindeer distributed primarily in the mountains of the southern two-thirds of Yakutia, but these have not been extensively studied. Syroechkovskii (1984) believed that about 600,000-800,000 wild reindeer were present in northern Yakutia during the 1800s. These wild herds were drastically reduced at the beginning of this century by overhunting in connection with the expanding domestic reindeer industry. Domestic reindeer were raised throughout the province. This decline continued until the 1950s. Subsequently, herds began to rebuild, and the present herd distributions were recognized. The recovery of the wild populations occurred because domestic reindeer herding and distribution of the human population became more centralized around towns. Northern Yakutia remains largely roadless and undeveloped except for some mining development in the Yana River basin, and habitat for wild herds remains intact. It is the purpose of this paper to briefly review the distribution and movements of these herds and describe their population dynamics, economic importance, and conservation.

Yana-Indigirka herd

Movements and distribution

The current range of the Yana-Indigirka herd covers about 400,000 km^2 (Fig. 1) and is similar to the range of this herd at the turn of the century (Mikhel, 1938). In summer, the herd spreads out over the Yana-Indigirka lowland, except the extreme northwestern part adjacent to Yana Bay and the Yana River. Males and females are generally separated during summer, but use the seacoast for insect relief. About 1,000-

Table 1. Estimated[a] size (thousands of animals) of the 3 major herds of wild reindeer in north Yakutia.

Year	Yana-Indigirka	Sundrun	Lena-Olenek
1963-64	50	10	20
1975	109	22	50
1978	87	28	53
1981-82	113	27	61
1985	121	–	55
1987-88	130	29	73
1989-90	116	–	77
1991	101	–	–
1992-93	85	40	80

[a] Estimated by extrapolation from line transect surveys and aerial photography during July.

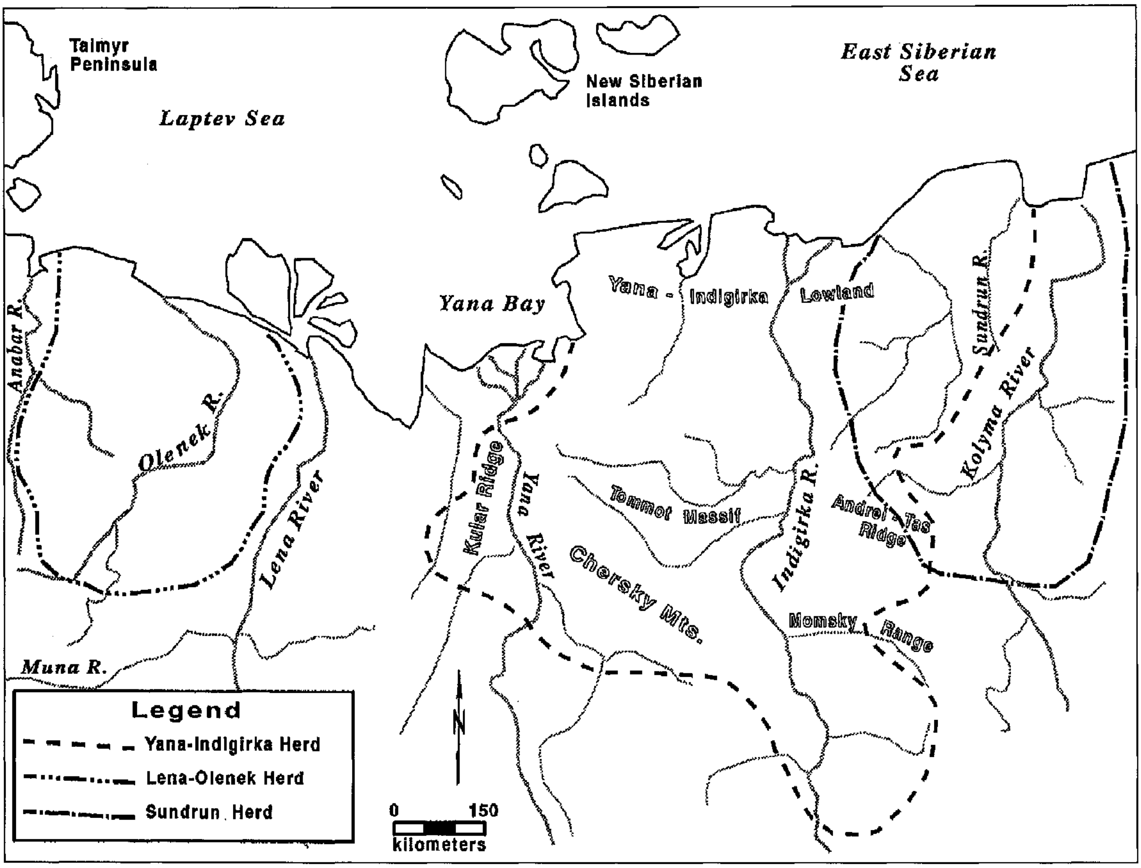

Fig. 1. Map of northern Yakutia with approximate ranges of Lena-Olenek, Yana-Indigirka and Sundrun herds.

2,000 wild reindeer from this herd also use adjacent mountain areas for insect relief. Aggregations occur until late July when the animals disperse widely over the tundra. Group sizes increase in mid-September but migration to winter ranges does not begin until early October. Four main migration routes leading to separate winter ranges are used: Andrei-Tas Ridge and Momsky Range, Tammot Massif, right bank of the Yana River basin, and Kular Ridge (Fig. 1). Timing of migration seems to depend on weather, and the rut often occurs during migration, and does not necessarily occur in the same place each year. The direction of movement may be altered in areas of the upper Yana River basin because of mining development and associated intensive hunting.

From north to south, migration routes extend for about 1,000 km, and reach far into the taiga zone. In years of early migration, the rut occurs far into the forest, but there is no evidence that the Yana-Indigirka reindeer reach the rutting areas of wild forest reindeer or domestic reindeer in time to interbreed. Yana-Indigirka reindeer mix with both wild forest reindeer and domestic reindeer in winter. Their preferred foods during winter are terrestrial lichens which make up about 44% of rumen contents.

In spring, migration begins in March or April, and females leave males and many yearlings behind as they move north. Calving begins in late May or early June when snowcover is usually still complete. The peak of calving (date by which 50% of calves have been born) occurred during 11-15 June in 1989. During the snow-free period the preferred food of the Yana-Indigirka wild reindeer is sedges and leaves of shrubs (43% of stomach contents).

Sex and age structure, and harvest

The age structure of the Yana-Indigirka herd has probably changed over time, as the herd has become more productive. In 1975, the male:female ratio was high and calves and yearlings composed only 31% of the population (Table 2). Subsequently, after heavy hunting occurred, herd numbers stabilized or decreased and the proportion of calves and yearlings increased (Table 2). Selective hunting of males during spring migration in May and June has been proposed as a method of reducing the male:female ratio and the effect of hunting on herd growth.

Wild reindeer of the Yana-Indigirka herd (and other herds) have been commercially harvested in the past with helicopters, drive fences and corrals, and snowmobiles. Hunting has been more difficult to control than in the Taimyr herd because the harvest is dispersed. Meat, hides and antlers were previously sold. In order to control harvest more closely and conserve wild reindeer, helicopter hunting was eliminated in 1980, and sale of antlers was prohibited in the early 1990s. Presently, the main methods of harvest are hunting during migration and on winter ranges from snowmobiles. There are no major water crossings as there are in the range of the Taimyr herd. Because of the expansion of wild reindeer, they now occur on most of the domestic reindeer farms in Yakutia, and are commercially harvested. In 1988-89 about 44,000 wild reindeer were harvested in Yakutia. On some farms, the production of wild meat makes up about 45% of the total production of meat. In the province as a whole, wild reindeer meat makes up 70-85% of the reindeer meat sold. Because herders are able to profit from the sale of wild reindeer, they are presently much more tolerant of the presence of wild reindeer among domestic reindeer than previously. The production of wild meat is much cheaper than the production of domestic reindeer meat.

Sundrun, Lena-Olenek and New Siberian Island herds

In general, ecology of the Sundrun and Lena-Olenek herds is similar to that of the Yana-Indigirka, but migratory movements are shorter (Fig. 1). These herds are more lightly harvested than the Yana-Indigirka, and their numbers have continued to increase slowly during the 1980s and early 1990s (Table 1). Wild reindeer on the New Siberian Islands have not been surveyed thoroughly since 1981, and biologists are concerned about their status. This population is interesting because it spends summer on the islands but then many animals move to the adjacent coastal mainland tundra to winter on a part of the summer range of the Yana-Indigirka herd.

Research direction

At present, research on wild reindeer in Yakutia is concentrated on monitoring numbers and population dynamics through aerial surveys, and determining how to maintain stable, productive populations as industrial development increases in the north.

Acknowledgements

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Section 5.

Other brief communications and abstracts

The Sixth North American Caribou Workshop,
Prince George, British Columbia, Canada,
1-4 March, 1994.

Brief communication

Growth and body composition of arctic caribou

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Nutrition and growth have been considered inseparable prior to puberty in mammals, and first summer growth is an important determinant of adult body size, likelihood of overwinter survival, and potential reproductive success. Knowledge of growth and its regulators is therefore critical to understanding and predicting changes in herd productivity. In addition, the relative importance of milk intake to growth rate changes with age (White, 1992), and the timing of nutritional independence may be affected by both regulatory (endogenous) and ecological components.

We characterized growth and body composition of free-ranging arctic caribou from two herds. Calves of the Central Arctic herd were collected at birth, and at 24, 44 and 130 days after peak calving, while adult females were collected 30 days prior to calving, and 24 and 130 days post-calving. Porcupine Herd calves were collected at 0, 24, and 100 days after peak calving. Animals were weighed, eviscerated and skinned, and selected organs and muscles were dissected and weighed. Left halves were frozen, and were minced 3 times in a meat grinder (calves), or sliced into sections with a bandsaw (adults; Huot & Picard, 1988). The homogenate or sawdust was collected for chemical analysis.

No differences in first-summer growth were found between herds. Body weight and skeletal size increased with age to approximately 100 days, but growth was greatly reduced or absent between 100 and 130 d. The proportion of water, protein, and ash in the ingesta-free body was relatively constant from birth to autumn, but fat varied through nearly the annual range observed in adult females. Calves were leanest (1.9% body fat) 6 weeks after calving, during the period of insect harassment and increasing nutritional independence, defined by declining milk intake (White & Luick, 1984; Parker *et al.*, 1990) and suckling rate (Parker *et al.*, 1990; Lavigueur & Barrette, 1992). They were fattest (6.1% fat) in autumn. Percent fat in autumn calves was more similar to that of George River Herd caribou (Huot, 1989) than that of captive reindeer (Ringberg *et al.*, 1982) or Coat's island caribou (Adamczewski *et al.*, 1987). Calves were approximately 8 times heavier in autumn than when born, and the increase was accounted for as water (53.0%), protein (18.5%), fat (5.7%), ash (4.8%), and alimentary fill (18.9%). Adult females were approximately 1.6 times heavier than calves in autumn, and the difference was accounted for by water (45.8%), protein (23.0%), fat (7.7%), ash (6.5%), and alimentary fill (17.1%).

Body weight was a good predictor of ingesta-free body weight ($r = 0.99$), because variation in alimentary fill at a particular body weight was relatively small. However, variance in the relation between body weight and ingesta-free body weight increased with age and body size. In juvenile caribou only, both body weight and skeletal dimensions were good predictors of body composition. The inverse relation between percent body fat and percent body water was similar to that described previously for reindeer, and for other mammal species. However, arctic caribou gained or lost 1.05 units of fat per unit water, a much smaller change in fatness than the 1.5 units reported in Svalbard reindeer (Reimers *et al.*, 1982).

Acknowledgements

This research was part of a collaborative study with the USFWS (Dr. Brad Griffith). Funding was provided by the Canadian Wildlife Service, the Anuvialik Game Council, the Northern Oil and Gas Action Program, the Alaska Dept. of Fish and Game, the Institute of Arctic Biology, and a National Science Foundation Graduate Research Fellowship to KLG.

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A retrospective review of disease diagnoses in caribou from Canada

Trent K. Bollinger & Dwight Welch

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Abstract: We compiled reports on 418 caribou specimens submitted to veterinary diagnostic laboratories and wildlife agencies from across Canada. The earliest record was from 1969; however, the majority were from 1987 to the present. Most submissions were tissues from huntershot animals. *Brucella suis* and *Brucella* sp. (untyped) were the most common bacterial pathogens isolated, accounting for 69 and 16 cases respectively. Parasitic conditions were also common. Besnoitiosis was diagnosed in 40 cases from various locations in the Northwest Territories, northern British Columbia, Alberta, Saskatchewan and Manitoba. Cysticercosis was diagnosed in 49 cases. Fibropapillomas, likely of viral origin, were present in 5 cases. Individual cases of chondrosarcoma, pulmonary carcinoma and renal adenoma were also reported. Deficiencies in data collection were also noted; in 43% of cases the age of animal was not reported and in 42% of submissions the sex of the animal was not indicated. The Canadian Cooperative Wildlife Health Centre has established a central repository for disease diagnostic reports which will be useful in identifying disease problems and geographic occurrence of disease in caribou. A standardized reporting format which includes accurate information on location, age, and sex of animal is required.

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Caribou calf weight gain in relation to habitat use on summer range

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Abstract: We estimated the relationship between daily weight gain of caribou calves and their proportional use of 5 habitats on the Arctic National Wildlife Refuge coastal plain during 1992 and 1993. Calves (1992, n=80; 1993, n=72) were captured, weighed and equipped with radio-collars when approximately 1 day old. These calves were recaptured with netguns and reweighed at approximate ages of 3 weeks (1992, n=62; 1993, n=61), and 6 weeks (1992, n=12; 1993, n=15). Proportional habitat use between weighings was estimated from aerial relocations of the collared calves. Daily gain was higher during the first 3 week period (1992, $\bar{x}$ = 0.380 kg/D, SE = 0.051; 1993, $\bar{x}$ = 0.441 kg/D, SE = 0.064) than during the second 3 week period (1992, $\bar{x}$ = 0.344 kg/D, SE = 0.056; 1993, $\bar{x}$ = 0.193 kg/D, SE = 0.091) in each year. Daily gain in each 3 week period differed between years. Habitat use differed between the first and second 3 week periods and between years. Weight gain was associated with proportional habitat use in each 3 week period and in each year, but the relationships between daily gain and habitat use varied between the two 3 week periods and between years. Positive, neutral, or negative relationships between daily gain and proportional habitat use may be used to rank habitats as having high, medium, or ow value, respectively. Our results suggest that the value of a habitat can change within and between years.

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The Sixth North American Caribou Workshop,
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Abstracts

Genetic relationships between Woodland and Barren ground caribou

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Abstract: The genetic relationships between woodland and barren ground caribou herds are being investigated using both mitochondrial and nuclear DNA. DNA sequence variation in the most variable region (the D-loop region) of mitochondrial DNA indicate the woodland caribou from Newfoundland, Ontario, Alberta, and British Columbia are closely related and form a monophyletic clade although introgression of barren ground mitochondrial genotypes occur in some herds. In addition, micro-satellites, which are highly variable nuclear loci used for DNA finger printing, are being developed which can distinguish individuals within and between herds.

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Importance of summer weight gain to the reproductive success of caribou in Arctic Alaska

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Abstract: In early July and again in early October 1988-91, 36 different adult female caribou (*Rangifer tarandus granti*) of the Central Arctic Herd were captured and weighed 92 times (i.e., 46 pairs of weights). For nonlactating females, July-October weight gain (y_i, kg) varied inversely with July body weight (x_i, kg): $y_i = -0.51\ x_i + 54.71$ ($r = 0.75$; $P < 0.001$); the hypothetical autumn "target" body weight (i.e., x-intercept) of 107 kg yields a 99% probability that a female will ovulate, conceive, and carry a fetus to term. For lactating females, however, that relationship was not significant ($P > 0.1$), and mean body weight by autumn was significantly lower than that of nonlactating females (85 vs. 94 kg, respectively; $P < 0.001$). The 9-kg difference in weight gain represents the net or "ecological" cost of mid- and late lactation, which would theoretically depress the parturition rate of the herd by 28%. Reduced fecundity probably results from repeated failure to compensate for the metabolic demands of lactation, thereby increasing the likelihood of breeding pauses.

Key words: body weight, fecundity, *Rangifer*, reproduction

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The Sixth North American Caribou Workshop,
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Abstract

Ecological Aspects of Woodland Caribou in the Pedigree Area of Northwestern Alberta, 1991 to 1994

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Abstract: Nine woodland caribou were radio-collared in the Pedigree oil and gas exploration area of northwestern Alberta during December 1991. Movements and habitat use were analyzed for a three-year (36 month) period, December 1991 to November 1994. Population status was investigated from mortality of radio-collared individuals, and the available estimate of late-winter recruitment of calves. Spatial habitat requirements, range fidelity, and habitat use were also investigated. Habitat use was compared to availability based on a habitat map developed for the "core" Pedigree caribou range. Recruitment and adult mortality appear to be closely balanced; indicating that the population has been approximately stable. Causes of calf and adult mortality were not determined, although predation by wolves was identified as an important factor. Individual movement patterns of Pedigree caribou did not appear to be synchronous; there was no strong seasonality to movement patterns. Individual caribou exhibited different patterns of movement, and spatial habitat requirements varied year to year and season to season. Some caribou made seasonal shifts between winter and summer range, but not during every year. Some caribou showed fidelity to winter ranges, while others did not. There are no calving grounds in the Pedigree area used collectively by parturient caribou. Available evidence, however, suggests that some caribou return annually to familiar areas during calving. Similarly, there is no common rutting grounds for caribou in the Pedigree, although some caribou tended to be in the same part of their annual range during each rutting season. Spatial habitat needs among caribou varied greatly between years and among seasons. Overall, spatial needs shown by Pedigree caribou appear to be larger than reported for other non-migratory caribou herds in Alberta. The significance of this large variation in spatial requirements is not known, although it may reflect adaptive behavior both in response to predation, and including response to industrial activities. This monitoring program has not established a link between industrial activity and caribou behavior. A link would require closer integration of industrial developments with the caribou relocation database. On an annual basis, treed muskeg and scrub conifer forest were key caribou habitat components. Other habitat types that were selected for by caribou on an annual basis included treed muskeg complexed with upland pine, and herbaceous wetland areas. Habitat types by caribou changed on a seasonal basis; caribou during winter frequented less treed muskeg and scrub conifer habitat, while showing increased use of mixedwood, upland pine and spruce habitats. Weakness in the current database are acknowleged, and further information needs are discussed. On-going monitoring for conservation of Pedigree caribou is recommended. Integration of industrial activities and developments with the ecological database is also recommended.

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