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North American Caribou Workshop
Jasper, Alberta, Canada
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Editor: Rolf Egil Haugerud
Address: Centre for Sami Studies
University of Tromsø
N-9037 Tromsø
Norway

E-mail: nor.rangifer@sami.uit.no

Web address: www.rangifer.no

Telephone: +47 77 64 69 09
Telefax: +47 77 64 55 10
Mobile phone: +47 414 16 833

Bank: Sparebank1 Nord-Norge
N-9298 Tromsø, Norway
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To request a copy of *Rangifer* Special Issue No. 17:
Send your request to **Kirby Smith** at the Alberta Fish and Wildlife Division, Ste. 203, 111 – 54 Street, Provincial Bldg., Edson Alberta, Canada T7E 1TE, tele: 780-723-8248; fax: 780-723-7963, or email Kirby.Smith@gov.ab.ca

RANGIFER

Special Issue 2007 No. 17

Contents

Section 1: Status and recovery efforts

Section 2: Predator-prey interactions

Section 3: Habitat

Section 4: Population dynamics

Section 5: Research techniques

Section 6: Mitigation and management

Preface

Over 200 people attended the 11th North American Caribou Workshop which was held in Jasper, Alberta, Canada. Participants came from Canada, the United States, Sweden, Norway and Greenland. Almost 80 papers and posters were presented and over 30% are published in these proceedings.

The conference theme was "***Managing Caribou Populations that are at Risk***" and many of the presentations examined all aspects of this challenge including predator/prey dynamics, habitat, human interactions, mitigation, techniques, population dynamics, genetics and even enhancing survival through temporary captivity. One of the highlights of the workshop was a presentation by Dr. Tom Bergerud reflecting on his career-long synthesis of wolf/caribou interactions throughout their range in North America.

In addition to the poster and oral papers, there was a panel discussion on Canada's woodland caribou recovery plan and an information session on the Circumarctic *Rangifer* monitoring and assessment network.

One of the principle goals of the North American Caribou Workshop is to provide the opportunity for researchers, managers, First Nations peoples, students and the general public to interact, trade ideas and make or renew contacts with others interested in the conservation and management of *Rangifer*. The 11th North American Workshop provided this opportunity in the spectacular setting of Jasper National Park.

Kirby Smith, Conference Chairman

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Plenary Session: *National Woodland Caribou Recovery Plan.* – Dave Hervieux, Gerry Racey, Stan Boutin, Andrew deVries, Brian Horesji, Helene Walsh.

The Eleventh North American Caribou Workshop,
Jasper, Alberta, Canada,
24-27 April, 2006.

Abstract

National recovery strategy for woodland caribou (*Rangifer tarandus caribou*), boreal population, in Canada

Dave Hervieux

Alberta Fish and Wildlife Division, 1701 Provincial Building, 10320 - 99 Street, Grande Prairie, Alberta, T8V 6J4, Canada.

Recovery planning for the boreal population of woodland caribou is a complex task, spanning eight Canadian provinces and territories. To accommodate unique situations across the country, recovery planning for this Species at Risk Act-listed threatened species is occurring at both provincial/territorial and national levels. The national recovery strategy strives to identify nationally important issues and provide direction for provinces and territories as they plan and implement boreal caribou recovery within their jurisdictions. The national vision is to conserve and recover boreal caribou and their habitat across Canada. Specific goals are to: 1) Prevent extirpation of local boreal caribou populations from all existing caribou ranges; and 2) Maintain or enhance local boreal caribou populations at or to self-sustaining levels within all existing caribou ranges; and 3) Maintain or enhance boreal caribou habitat to support self-sustaining local populations. Nineteen broad national approaches are identified. These approaches include items relating to: habitat planning and management, caribou population monitoring and management, management of human-caused mortality, management of other wildlife species, consideration of government legislation and policy, promotion of stewardship and public outreach, and research. Specific outcomes are provided for each stated recovery approach. For more information on Canada's national recovery strategy for the boreal population of woodland caribou please see www.speciesatrisk.gc.ca/recovery/default_e.cfm

Key words: legislation, management, monitoring, species at risk, stewardship.

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Rethinking the basic conservation unit and associated protocol for augmentation of an 'endangered' caribou population: An opinion

Frank L. Miller[1*], Samuel J. Barry[1], Wendy A. Calvert[1] & Keri A. Zittlau[2]

[1] Canadian Wildlife Service, Environment Canada, Prairie & Northern Region, Room 200, 4999 – 98th Avenue, Edmonton, Alberta T6B 2X3, Canada (*corresponding author: frank.miller@ec.gc.ca).
[2] Division of Natural Sciences and Mathematics, Rocky Mountain College, 1511 Poly Drive, Billings, Montana, 59102, USA.

Abstract: Use of the subspecies as the basic unit in the conservation of endangered caribou (*Rangifer tarandus*) would produce a "melting pot" end-product that would mask important genotypic, phenotypic, ecological, and behavioral variations found below the level of the subspecies. Therefore, we examined options for establishing the basic conservation unit for an endangered caribou population: use of subspecies based on taxonomy, subspecies based solely on mtDNA, Evolutionarily Significant Units, and the geographic population. We reject the first three and conclude that the only feasible basic unit for biologically and ecologically sound conservation of endangered caribou in North America is the geographic population. Conservation of endangered caribou at the level of the geographic population is necessary to identify and maintain current biodiversity. As deliberations about endangered caribou conservation often involve consideration of population augmentation, we also discuss the appropriate augmentation protocol for conserving biodiversity. Management of a critically endangered caribou population by augmentation should only be initiated after adequate study and evaluation of the genotype, phenotype, ecology, and behavior for both the endangered caribou and the potential 'donor' caribou to prevent the possible 'contamination' of the endangered caribou. Translocation of caribou into an endangered population will have failed, even if the restocking efforts succeed, if the donor animals functionally alter the population's gene pool or phenotype, or alter the ecological and behavioral adaptations of individuals in the endangered population. Most importantly, a seriously flawed restocking would risk irreversibly altering those functional characteristics of caribou in an endangered population that make them distinct and possibly unique. It might even result in the loss of the endangered population, thus eliminating a uniquely evolved line from among the caribou species.

Key words: augmentation, behavior, ecology, genotype, geographic population, phenotype, *Rangifer tarandus*, translocations.

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Introduction

There is considerable public relations value in the perception of doing something for conservation by capturing large animals and moving them to different locations to increase or reestablish populations. Historically, there have been many reasons for translocating animals, including aesthetic, commercial, and mitigative. For example, Griffith *et al*. (1989) report several hundred translocations per year from 1973–1986 in Australia, Canada, and the United States of America, with the number of translocations doubling over that period. For endangered caribou, population augmentation (restocking) is a commonly considered management tool (e.g., Audet & Allen, 1996; Almack, 2000; Vanderstar & Keim, 2000). However, appropriate augmentation protocols for conserving biodiversity have not been implemented to date. Most likely, this is because management agencies have been forced by sociopolitical pressure to consider first retaining or increasing the number of caribou when a caribou population is at proximate risk of extirpation.

In this paper, we address the use of translocations for the purpose of augmenting geographic populations of critically endangered caribou for the sole purpose of conserving that population. Such augmentations would emphasize the long-term maintenance of the population's biodiversity, while allowing naturally occurring gene flow over time–and not just conserving the species' range of occupancy. To do this, we must first establish a basic conservation unit that will allow the identification and separation of biological and ecological groupings that represent variation in genetics, phenotypes, ecology and behavior, which we believe forges the functional characteristics that we wish to conserve.

The attributes of an ecosystem depend predominantly on its biodiversity in terms of the functional characteristics of organisms present in the ecosystem and the spatial and temporal distribution and abundance of those organisms (Hooper *et al*., 2005). We believe that the primary goal of all conservation efforts should be the maintenance of biodiversity. This can be addressed at the start by detailed examination of the available evidence, including pertinent publications and agency reports plus ongoing work. This will aid initially in determining what feasible level of animal grouping and the associated land unit best identifies the lowest, most refined, division of separation for maintenance of biodiversity within the species under consideration. In this paper, we first consider four possibilities for a basic unit of conservation for endangered caribou; we then present our views on selecting the basic unit of conservation that recognizes the most appropriate (i.e., refined) division for applying conservation measures to caribou; and then we develop our associated reasoning and the procedure that we believe is necessary for a biologically and ecologically sound augmentation protocol for endangered populations of North American caribou.

Definitions of terms

The biological literature is full of examples of imprecise terminology leading to misunderstanding and division among different natural science disciplines. As an example, Wells & Richmond (1995) offer a non-exhaustive list of 13 definitions of 'population' and present 20 terms for different kinds of populations. Failure to unambiguously define important terms has hampered both clear communication and comparative evaluation of studies. Important terms should be defined explicitly and then used discerningly in a way that makes us fully aware of their implications (Wells & Richmond, 1995). We recommend that any biologist interested in the conservation of endangered caribou populations and the use of *ex situ* conservation actions become familiar with the definitions of pertinent terms and their functional meanings (see Wells & Richmond, 1995; Stockwell *et al*., 2003; DeYoung & Honeycutt, 2005; Hooper *et al*., 2005 and the references therein). We describe below our understanding and use of the key terms that we apply specifically for caribou in this paper.

Basic conservation unit (BCU)

The BCU for caribou is the smallest feasible grouping that can be used consistently for all North American caribou as an identifying unit to recognize and maintain the differences in their existing biodiversity. Working at any less refined level above the BCU would mask much of the variation in existing functional biodiversity and would prevent obtaining the primary conservation goal–maintenance of the current level of existing biodiversity.

Geographic population

Wells & Richmond (1995:461) define a 'population' as "–a group of conspecific individuals that is demographically, genetically, or spatially disjunct from other groups of individuals," and they suggest that spatial disjunction is probably the most important because it is easiest to detect. Lane (1976:618) and Wilson (1980:8) define a 'population' in terms of the delimited land area (geographic region) occupied by a group of conspecific organisms. We place special emphasis on 'spatial separation' for a geographic population, whether physical (e.g., islands) or through the lack of intermixing as the result of learned behavior where no physical barriers exist (traditional seasonal and annual range occupancy). It is the known annual home range boundaries of a caribou population that define the fixed land unit of the geographic population. Thus, a geographic caribou population is all of the caribou found anywhere within the boundaries of a clearly defined fixed land unit during the 'caribou-year' (July to June).

Augmentation (also known as restocking, reinforcement, and supplementation)

Augmentation, as we use it, involves the addition of individual caribou from a viable free-ranging population to an existing remnant population of endangered caribou, with the intention of increasing the number of individuals in the endangered population in their original habitat, without meaningfully altering the functional characteristics of future individuals in the endangered population.

Four possibilities for the BCU for conservation of endangered caribou

We examine four possibilities for establishing a BCU for an endangered caribou population: subspecies based on taxonomy, subspecies based solely on mitochondrial DNA (mtDNA), the use of Evolutionarily Significant Units, and the geographic population.

Subspecies based on taxonomy

Banfield (1961:6) noted that 55 species and subspecies of caribou and reindeer have been described since Linnaeus' 10th edition of *Systema Natura* (Linnaeus, 1758). However, in his revision of the genus *Rangifer*, Banfield (1961) recognized only four extant forms of North American caribou and three extant forms of Eurasian reindeer. The four North American forms are the Canadian barren-ground caribou (*R. t. groenlandicus* Linnaeus, 1767), the Alaskan barren-ground caribou (*R. t. granti* Allen, 1902a), the Peary caribou (*R. t. pearyi* Allen, 1902b), and the woodland caribou (*R. t. caribou* Gmelin, 1788). The taxonomic nomenclature of North American caribou has indeed been fluid: scientific names of the currently recognized four extant forms were assigned 92 times between 1767 and 1961, resulting in 52 variations of those names (Table 1). If classification changes were debated on a taxonomic basis in the early 1900s, the debate would have had to start at the species level. Now, with only the single Holarctic species *tarandus* recognized in the genus *Rangifer*, the debate falls first to the subspecies level.

The transitional nature of the taxonomy for *Rangifer* was discerned early on: Banfield (1961:103) remarked that the single Holarctic species of *tarandus* and its several subspecific forms did not readily fit into the classical species or subspecies categories but that a precise fit should not be expected as evolution is a dynamic process. Banfield (1961:106) concluded in his revision of the genus *Rangifer* that "Many of the demes mentioned in the report will reach subspecific rank." Should his predictions materialize, a major regrouping of any BCU based on the current four subspecies would be required as it would confound or undo any earlier conservation efforts based upon the original four. Identification of new subspecies, as was predicted by Banfield (1961:106) for tundra reindeer (*R. t. groenlandicus* and *R. t. pearyi*) and woodland caribou (*R. t. caribou*) would make it obvious that the variation in their genetics, morphology, and ecology was ignored in the past when the new subspecies were ranked below the subspecific level.

It is possible that groups of caribou that have both unique geographic ranges and recognizable appearance can be treated as different from each other (O'Brian & Mayr, 1991). However, the assumption that *only* recognizable appearance will allow meaningful separation among groups of caribou does not hold. The phenotypic expression of an animal that is supposedly inherited is not always clear-cut. Two or more groups of animals can share the same or similar phenotypic expression without having common ancestry (convergent evolution) while other animal groups can exhibit differences in appearance but have a common ancestry (divergent evolution). Apparently, this disconnect holds true for caribou, as mtDNA demes described by Dueck (1998), which are presumed to reflect ancestry, only partially support the demes described by Banfield (1961), upon which our current subspecies designations are based. Thus, although we seek to conserve natural patterns of diversity, when it is argued that distinctive appearance or behavior is a manifestation of diversity, we have to be careful that we do not assume that similarities or dissimilarities indicate something they do not.

For example, even though one woodland caribou assigns to the Southern mtDNA clade and a second from the same population assigns to the Northern mtDNA clade (Dueck 1998), their phenotypic appearance cannot be told apart. On the other hand, caribou from the Canadian Arctic Islands classified as *R. t. pearyi*, and *pearyi* x *groenlandicus*, Dolphin and Union caribou on southern and eastern Victoria Island, Canada, classified as *R. t. groenlandicus* (*groenlandicus* x *pearyi* below the subspecies), and Canadian mainland barren-ground caribou (*R. t. groenlandicus*) can be easily separated from each other on the basis of their respective appearance even though they all form part of the same mtDNA group (Dueck, 1998; Eger *et al.*, in press). Phenotypic and genetic traits do not evolve at equivalent rates, which therefore challenge the sole use of recognizable differences in appearance to indicate meaningful separations. The above examples emphasize the importance of differences among environmental settings in forging phenotypic diversity.

DNA evidence exists that allows separation of North American caribou well below the subspecific level (Zittlau, 2004). Thus, the subspecies level masks much, if not most, of the functional biological and

Table 1. Number of classification assignments and name changes in the taxonomic nomenclature for North American caribou between 1767 and 1961: derived from Banfield (1961).

North American Caribou	Time span (yr)	Number of changes			Classification assignments (name changes)
		Genera	Species	Subspecies	
R. t. groenlandicus	1767–1961	3	4	3	23 (9)
R. t. granti	1902–1961	2	5	2	9 (6)
R. t. pearyi	1902–1961	1	3	1	7 (3)
R. t. caribou	1788–1961	3	11	13	53 (34)

ecological differences that indicate biodiversity within, between, or among different populations. When both Manning (1960) and Banfield (1961) did the taxonomic classification of caribou at the subspecific level on the Canadian Arctic Islands, they recognized the considerable variation that existed below the subspecies level between and among caribou on the Canadian High Arctic Islands (north of 74ºN), collectively known as the Queen Elizabeth Islands, and those caribou on the Canadian Arctic Islands to the south of 74ºN latitude.

The melting-pot composition of *R. t. pearyi* is exemplified by the 'umbrella use' of the subspecies. *R. t. pearyi*, as described by Manning (1960) and Banfield (1961), was based on relatively few samples, without a complete examination of the entire range across which those caribou were believed to occur, thus resulting in a diversity of caribou lumped into the same taxonomic group. In his revision of the genus *Rangifer*, Banfield (1961) based his assessment of *R. t. pearyi* on 113 specimens (107 from Canada and 6 from northwest Greenland). Only 73 of the 107 Canadian specimens were identified as "Typical *pearyi*." Those 73 were all from the Queen Elizabeth Islands, with the exception of 7 specimens from Prince of Wales Island. Those last seven caribou were all large adult males collected and used by Manning & Macpherson (1961) to describe the 'ultra *pearyi*' of Prince of Wales Island. Banfield (1961) then used the same seven caribou, drew the same conclusions as Manning & Macpherson (1961), and called them a 'super deme of *pearyi*.' Neither Manning & Macpherson (1961) nor Banfield (1961) examined any of the smaller caribou on Prince of Wales Island (or any caribou from Somerset Island or Boothia Peninsula) and they assumed that the smaller caribou type on Prince of Wales Island was the same type as those on Banks Island (i.e., "Intergrades *pearyi* x *groenlandicus*"). Thirty-three of the 34 remaining specimens representing caribou from the Canadian Arctic Islands south of 74ºN latitude were actually all from Banks Island and the remaining one was a migrant collected on Cape Dalhousie, Mackenzie District, on the Canadian mainland. All 34 were identified as "Intergrades *pearyi* x *groenlandicus*." To lump all of these sampled caribou at the subspecies level for the purpose of their conservation prevents an adequate evaluation of the biodiversity found among these caribou below the subspecific level.

mtDNA genetics

Dueck (1998) showed that there were two mtDNA clades of North American *R. tarandus.* These groups represent northern and southern refugial origins during the Wisconsin Glaciation. It has generally been thought that phenotypic, ecological, and behavioral differences that form the basis of current subspecies designations were derived from isolated northern (barren-ground) and southern (woodland) refugia (Banfield, 1961:41). Therefore, the subspecies designations should coincide with mtDNA differences. However, the mtDNA clades do not always separate according to present-day designations of subspecies. Phenotypic differences evolve at a faster rate than mtDNA if selection pressure is strong, and thus degrees of similarity based on each measure are not equivalent. MtDNA is most useful for examining genetic differences at or above the subspecies level and would not detect a relatively recent difference below subspecies that had been established within the past few thousand years. We should reconcile this lack of agreement between the four extant North American caribou subspecies determined taxonomically and the two "subspecies" demonstrated by mtDNA before we get into *ex situ* conservation efforts that involve the mixing of caribou from two or more populations.

Although usually only one genetic line exists within a geographic population, the genetic situation can be complex in many instances. In Arctic Canada, for example, the Prince of Wales-Somerset-Russell islands-Boothia Peninsula geographic caribou population is (or was: see Gunn *et al.*, 2006; Miller *et al.*, 2007) represented by four ecotypes: the arctic-island ecotype, the 'ultra *pearyi*' ecotype, the Boothia Peninsula ecotype, and the mainland ecotype (Banfield, 1961; Manning & Macpherson, 1961; Miller *et al.*, 2005; 2007). The most complicated geographic populations solely in terms of their genetics exist among populations identified as woodland caribou. Within such populations, some individuals assign to the Southern mtDNA clade, and represent caribou with a southern refugial origin, while other individuals assign to the Northern mtDNA clade, representing caribou with a northern refugial origin, indicating that caribou from different genetic ancestry can occur in a single geographic population (Dueck, 1998).

Many of the caribou sampled by Dueck (1998) and currently identified as woodland caribou from Yukon to Labrador were found to belong to the Northern mtDNA clade. That is, if there were a genetic basis for the woodland caribou subspecies, they all would have been assigned to only the Southern mtDNA clade and vice versa for barren-ground caribou. However, proportionately many individuals were assigned to the Northern mtDNA clade in 12 of 15 woodland caribou populations sampled while 3 of 7 barren-ground caribou populations contained individuals that were assignable to the Southern mtDNA clade. All four of the woodland caribou populations sampled in Yukon were assigned 100% to the Northern mtDNA clade and only the critically endangered Pukaskwa National Park woodland caribou population north of Lake

Superior in Ontario and the Humber and Middle Ridge woodland caribou populations in Newfoundland were assigned 100% to the Southern mtDNA clade. Although it is possible that larger samples from those populations could change the proportional representation of the two mtDNA clades, it does not lessen the importance of the fact that those populations contained individuals belonging to both mtDNA clades.

Therefore, if conservation measures are based solely on mtDNA genetics, the Canadian and Alaskan forms of barren-ground caribou, all caribou on the Canadian Arctic Archipelago, and many of the caribou in populations currently recognized as woodland caribou, would not be considered as separate. Obviously, this would be illogical–but it could happen under strong socio-political support for using transplants from essentially any source to reestablish harvestable populations, despite the lack of biological or ecological support for such actions.

Most importantly, the mtDNA differences reported here reflect subspecies-level genetic differences and may not represent any recent (~ <10 kybp) phenotypic, ecological, or behavioral adaptations that form the basis for the functionally meaningful differences among caribou populations. Thus, when we wish to conserve the existing biodiversity of caribou and to protect the natural pathways for continued gene flow between and among populations, we must work below the subspecific level based on mtDNA (or on taxonomy).

Evolutionarily significant units

The concept of the 'Evolutionarily Significant Unit' (ESU) was first developed by Ryder (1986). Crandall *et al.* (2000) noted that as a new concept, the definition of an ESU has received considerable alteration, emphasizing reproductive isolation rather than the maintenance of adaptive differences. Ryder (1986) first suggested that any population that actually exhibited significant adaptive variation as demonstrated by sets of data obtained by different techniques qualified as an ESU. Waples (1991) added a further restriction and focused on populations that are reproductively separate from other populations as well as having unique or different adaptations as the standard for an ESU. Then Moritz (1994) made the definition even more restrictive by suggesting the populations had to be 'reciprocally monophyletic' for mtDNA and show significant divergence of allele frequencies at microsatellite loci. The reciprocal monophyly standard presents an obstacle for evaluating populations with paraphyletic histories (Crandall *et al.*, 2000).

When Moritz's (1994) definition is accepted for establishing ESUs, it seems to negate or at the very least seriously confound the possible application of the ESU to the North American caribou that have been reported to have a polyphyletic origin. Gravlund *et al.* (1998) concluded from mtDNA sequence analysis that the three forms of small-bodied high-arctic *tarandus* (Peary caribou, *R. t. pearyi;* the now extinct East Greenland caribou, *R. t. eogroenlandicus*; and the Svalbard reindeer, *R. t. platyrhynchus*) had a polyphyletic origin. Those authors suggested that the three forms were ecotypes of relatively recent diphyletic origin (*pearyi* and *eogroenlandicus*, versus *platyrhynchus*) that likely evolved convergently as a result of exposure to similar climatic conditions and levels of nutrition.

Also, based on mtDNA analyses, none of the North American caribou subspecies have a monophyletic origin (Dueck, 1998; Eger *et al.*, in press). Eger *et al.* (in press) show that Peary caribou from Bathurst Island within the Queen Elizabeth Islands are genetically different from caribou populations on Eglinton Island to the west, on the more southerly Arctic Islands of Prince of Wales, Victoria, and Banks islands, and also at Coppermine (Kugluktuk) and Spence Bay (Taloyoak) on the mainland. In fact, they indicate that monophyly does not hold true even for individuals from a single Arctic Island. The range in environmental conditions across the Canadian Arctic Islands varies from "extreme" north of 74°N to more "benign" south of 74°N latitude, with much diversity between. Presumably, this environmental range has led to ecological and morphological divergence that is not reflected by mtDNA diversity. These findings suggest that the role of environmental variables is great in forging successful individuals and bring concerns for variations in phenotype, ecology, and behavior to the forefront, especially when both mtDNA clades described by Dueck (1998) are present in the same populations. That is, the genome would set the limits for adaptability but the environment would mold the successful adaptations and the variations in those adaptations among different populations in different environmental settings.

Crandall *et al.* (2000) point out that the conceptual framework of the ESU demands a decision–ESU or not–that is based on a continuum of genetic diversity, variation in habitat types, and differences in selective pressures across populations. Thus, the application of ESUs to polyphyletic populations would be highly questionable, especially if there were more than two possible origins. Vogler & DeSalle (1994) concluded that no generally accepted definition existed for an ESU that would serve as a basis for its use in practical conservation situations.

Geographic population

Fixed land boundaries for a geographic caribou population should first be determined by the known history of the population's annual range occupation (including seasonal migrations) compiled over a series of years and with further study where necessary. All caribou found within an annual home range boundary should be considered as a single geographic population. This condition holds even if some caribou subunits within the geographic population exhibit different demographic performances, with more than one calving ground and rutting area possibly occurring in the same year. It should be expected that as evidence is accumulated over time, the need for changing at least some boundaries of some geographic populations will become evident.

Although fidelity to calving grounds is a criterion for defining many populations (Thomas, 1969; Gunn & Miller, 1986; Nagy *et al.*, 1999), there are many exceptions, especially among caribou on the Canadian Arctic Archipelago and also among woodland caribou populations. Thus, while relying on calving grounds serves well as the focus for identifying some geographic populations (mostly for mainland Canadian and Alaskan barren-ground caribou) it is not always useful for determining other geographic populations.

The most conservative and easiest approach to the conservation of endangered North American caribou is to initially treat all populations as unique from each other and worthy of being conserved as discrete entities regardless of their relative complexities or lack of complexity and known fidelities to different calving areas, until proven otherwise. We would do this by first identifying the annual land boundaries of each population and then treat all caribou that occur within each of those fixed areas as a single geographic population. These geographic populations are the potential BCUs. Then, we can begin a 'lumping and splitting process' only after a satisfactory amount of supporting data allows us to objectively conclude that it is or is not justifiable to combine or further divide those geographical populations.

Selecting the best BCU for endangered caribou

The most satisfactory BCU for caribou should be a naturally occurring one, such as a free-ranging population. Miller & Gunn (2003) concluded in their discussion about caribou on the Canadian Arctic Archipelago that the most basic and consistently workable caribou conservation unit is the geographic population. We agree and apply the geographic population as the best choice for endangered caribou throughout North America. We believe that while a BCU should rely on genetics and morphology, it also should rely heavily on ecology, which includes behavioral adaptations. As has already been shown (Zittlau, 2004), it is most likely that further study will reveal a high degree of complexity among caribou populations below the subspecies that now is obscured by the subspecies classification. Therefore, recognition of the geographic caribou population as the BCU would provide a much more meaningful biological and ecological approach to the management and conservation of endangered caribou than could be realized by any approach based on the subspecies or the ESU.

Many geographic populations have been functioning as distinct units for numerous generations according to comparisons of microsatellite DNA (Zittlau, 2004). This forms the basis for adaptations within the populations, leading to meaningfully functional differences. By recognizing geographic populations as functionally distinct in their respective contribution to the evolutionary lines of caribou within a region, the need for affording protection to the natural pathways for the flow of genes between populations should also be appreciated. This protection strategy should promote and preserve adaptive diversity among caribou. However, access to movement corridors can have a down side, including the possible spread of disease, and much more investigation and evaluation of associated pros and cons is needed (Simberloff *et al.*, 1992; Hogg *et al.*, 2006).

Working at the subspecific level would produce a "melting pot" end-product that would mask important variations in genotype, phenotype, and in ecological and behavioral differences found well below the level of the subspecies. This could lead to the unwitting loss of functional biological and ecological differences that indicate ongoing contributions of biodiversity between or among different populations. Thus, relying solely on the subspecific level of taxonomic classification is unsuitable for the conservation of endangered caribou populations. In addition, the use of an ESU for a polyphyletic species like caribou is questionable and should not be used as a BCU because of the extremely low likelihood of collecting adequate data within a reasonable time for all of the caribou populations that we can already recognize by other standards. We believe this limitation in the use of subspecies and ESUs applies equally to all caribou throughout North America.

The three possibilities rejected above are all markedly less discriminating and well above the level of the geographic population. If any one of these three that we reject was accepted, it would allow the corruption of thousands of years of evolution through human-induced manipulations of caribou populations. Such a superficial standard would permit the capture and release of caribou from any location within the subspecies' range into other populations, with total disregard for the variation in genetics, morphology, ecology, and behavior that exists among those populations. Such actions would obviously defeat any attempt to maintain current biodiversity through the distinctive and unique evolutionary lines of these endangered populations of caribou.

We recommend that the geographic population be used as the standard for the BCU in the conservation of endangered North American caribou. The only possible shortcoming that we currently can discern for the use of the geographic population as the BCU for endangered caribou is in not adequately collecting the necessary information for each geographic population to accurately describe its geographical land base. However, we view this as much less of a problem to deal with than the shortcomings that we have described above for working at the level of the subspecies or the use of the ESU.

Augmentation of endangered caribou populations

We have considered the four possibilities for a basic unit of conservation for endangered caribou and have reviewed our reasoning for the selection of the BCU that recognizes the most appropriate (i.e., refined) division for applying conservation measures to caribou. We now develop our associated reasoning and procedure that we believe is necessary for a biologically and ecologically sound augmentation protocol for endangered populations of North American caribou.

What needs to be considered

Our position is that we do not currently have enough detailed information on genetics, phenotypes, ecology, or behavior of critically endangered caribou populations or on candidate donor caribou populations to proceed with translocations at a satisfactory level of biological confidence. Our primary aspiration is that no human-induced actions are taken that risk causing detrimental outcomes, especially irreversible ones, for the endangered caribou. Among all the probable management and conservation prescriptions, translocation of caribou has the greatest potential for causing negative results, and the greatest potential for contamination of a critically endangered caribou population would come from augmentation with incompatible donor caribou from a viable population.

The dichotomy between management-orientated wildlife biologists and conservation biologists is real: it starts with each having differing basic philosophies, leading to the divergence of their respective objectives and goals. Therefore, it is extremely important when evaluating the use of translocations to keep in mind the difference between introductions, reintroductions, and restocking solely for management purposes versus augmenting critically endangered caribou populations solely for conservation efforts. The primary aim for management purposes is to retain or expand a species' range of occupancy and population size, and to avert further population declines by preventing populations from occurring in isolated habitat patches (Storfer, 1999). These management-orientated translocations are not based on the preservation of biodiversity created by distinct evolutionary lines. Rather, they are often driven by hunter incentives for game animals (Bergerud & Mercer, 1989) or by eco-tourists for non-consumptive viewing opportunities (e.g., aesthetics and photography). They also often occur as last-ditch efforts without concern about genetic dissimilarity.

We are proposing guidelines that are concerned with the conservation of biodiversity through augmentation for the sole purpose of sustaining a genetic line of endangered caribou that are more naturally adapted to their surroundings than are caribou from elsewhere. Even if human-induced manipulation that alters functional characteristics of an endangered caribou population results in more animals or an "improved animal," it would defeat the stated purpose of the conservation of a distinct group of endangered caribou and cause the loss of any unique contribution that the group previously made to the biodiversity of North American caribou.

The augmentation of the Selkirk Mountains woodland caribou population in northern Idaho between 1987 and 1992 with 60 caribou from British Columbia serves as an example of the need to reconcile differences in what is judged an acceptable protocol for conservation efforts with the stated purpose of preserving an endangered caribou population. This is also a good example of what we consider a geographic population. The Selkirk caribou population was listed as endangered in 1984 under the U.S. Endangered Species Act. Although the stated purpose of the translocations was "to assist in the recovery of the endangered Selkirk population" (Compton *et al.*, 1995:490); the augmentations were carried out without knowledge of the possible differences between the genetics of the endangered caribou and the donor caribou. There was no mention of concern about possible phenotypic differences or the known differences among ecotypes and their respective ecology and behavior. Some of the donor caribou came from the 'Interior Plateau region' of west-central British Columbia and represented 'northern ecotype' caribou that rely primarily on terrestrial lichens in winter, while the other donor animals came from the 'Interior Wet Belt region' of southeastern British Columbia and represented 'mountain ecotype' caribou that rely primarily on arboreal lichens in winter, as do the Selkirk caribou. It was known that the "Mountain ecotype caribou exhibit different habitat use patterns, seasonal migrations, and winter diet selections than northern ecotype animals…" (*in* Compton *et al*., 1995:494). As they knew they were mixing caribou ecotypes, and as they did not know the genetics of the caribou they were working with, it is likely that there was little concern for retaining the functional characteristics of the caribou in the endangered Selkirk population to truly aid in the recovery and maintenance of the Selkirk population *per se*.

From a purely management position, these augmentations could be viewed as justifiable efforts. The augmentation program would have been judged successful if the translocated animals survived and established a stable population within the Selkirk range–this did not happen. However, from a conservation position where maintenance of the functional characteristics of the caribou already in the Selkirk population is the primary goal, the augmentation efforts cannot be considered valid, regardless of the outcome. Later augmentation efforts were made between 1996 and 1998, translocating northern and southern ecotype caribou from four regions in British Columbia into the Selkirk Mountains of Washington (Audet & Allen, 1996). These later augmentations attempted to use donor animals that were likely to be as genetically similar as possible to the original Selkirk population, where the degree of genetic similarity was assumed–but neither measured nor proven at that time–to correspond with geographic proximity of the potential donor populations, which is not supported by subsequent limited microsatellite DNA analysis (Zittlau, unpublished data).

The consideration of genetic similarity may be most difficult for management biologists to accept or appreciate as a primary concern. That is, the potential benefits of improvements in reproduction, survival, and fitness-related traits in maximally outbred individuals in small isolated populations could make it appealing to overlook the potential negative aspects of introductions (Hedrick, 2005)–if one ignores the need to keep human intervention from unnaturally altering contributions from different evolved lines of caribou. The conundrum created by these alternative outcomes serves to emphasize the need for establishing and clearly stating the primary long-term goal of any human-induced manipulation.

Unless management-orientated efforts are not allowed to interfere in any way with the biologically and ecologically sound conservation of an endangered caribou population, 'optimal strategies' will not be kept within the bounds of 'natural change'. We must determine what degree of genetic deviation, if any, is acceptable between an endangered caribou population and the donor caribou population, or what is the latitude for causing genetic change before we are "playing God." We must also pay more attention to the importance of the environment in shaping variation in phenotypic, ecological, and behavioral adaptations of caribou. These questions cannot be answered with complete confidence until considerably more studies are made.

We must keep in mind that the current lack of detailed information about the various endangered caribou populations makes augmentation of endangered caribou populations extremely risky. Working with critically endangered caribou populations does not allow us the luxury of initial 'trial-and-error' efforts. Until we increase the necessary data for the populations under consideration, our efforts should be directed first at obtaining adequate information that will allow us to make objective decisions about moving caribou from one population to another without disrupting or corrupting the endangered population or the natural system within which that population lives. We must remember that what works in one case will not necessarily work in another. We should consider first exhausting *in situ* conservation efforts (e.g., habitat protection, harvest restriction, and predator maintenance) before turning to *ex situ* actions (e.g., augmentation, reintroduction; and or captive breeding, rearing, and release into the wild).

The exception

We believe the one exception to our considerations above is the preventive measure of capturing caribou from an endangered caribou population while the population still has enough animals to spare them (Caughley & Gunn, 1996), and then raising them in captivity for potential release back into that endangered population when conditions are favorable. However, using captive-raised animals after long periods in captivity has its own set of problems that need to be clarified and resolved.

The apparently large number of captive caribou needed to promote a successful release back into the wild seriously limits the use of captive rearing. When deciding to augment a population, consideration must then be given to the 'effective population size' for caribou and how the effective size may vary among different caribou populations due to differences in their biotic and abiotic environments. Genetic considerations must be combined with many other factors that could or would influence the effective population size (Franklin, 1980; Lande, 1988; Caughley & Gunn, 1996; Franklin & Frankham, 1998a, b; Lynch & Lande, 1998), and thus the conservation of endangered North American caribou. Proposed effective population sizes currently range from as few as 50 individuals up to 5000 (Franklin & Frankham, 1998a).

Extremely endangered caribou populations that have been augmented or that are being considered for augmentation are each already below 100 individuals (Compton *et al.*, 1995; Audet & Allen, 1996; Almack, 2000; Vanderstar & Keim, 2000).

However, captive-rearing could be of value in special cases where *in situ* efforts have failed. Even if the animals raised in captivity are not released back into the wild, there is considerable public relations value in displaying endangered animals in a pleasant setting where they can be viewed by the public with educational materials provided; thereby, keeping the endangered animals' plight before the public. Free-release introduction of endangered caribou to areas beyond their known past range should not be considered as a valid *ex situ* conservation effort.

What needs to be done

Prescriptions for conservation should focus on the long-term goal of conserving caribou populations by maintaining biodiversity that results from naturally occurring evolutionary lines. We recommend a precautionary approach for the conservation of caribou, where investigators should step back and carefully assess their knowledge to avoid implementing actions that may lead to irreversible results. Our intent is to take only those actions that will allow evolutionary development to continue along natural pathways and to prevent any corruption of endangered caribou populations by human manipulations (Fig. 1).

Although the logic of first controlling or reversing the original cause(s) of a population decline before initiating an augmentation effort is abundantly clear, in reality it is seldom possible for caribou populations. In many cases, the cause of a decline is not even known. Even if the cause is known, it may be beyond our ability to reverse or even mitigate. Often our inability to do so is governed by socio-political pressures: e.g., hunters disbelieving population survey results, public objection to the control of predators, on-going pressure from nonrenewable and renewable resource development companies on caribou range, et cetera. In reality, the complexity and uncertainty of an unfavorable socio-political atmosphere can make all aspects of what would normally be a relatively simple planning and implementation recovery effort from a technical standpoint into a task burdened with unnecessary challenges and delays or even abandonment.

We must first determine what we can justifiably do and what we must avoid before human-induced manipulations become commonplace and especially before augmentation becomes the prominent part of any conservation effort. Otherwise, we run the risk of committing detrimental and possibly even irreversible acts. Many actions that might now be seen as beneficial and not intrusive based on our current limited knowledge may subsequently prove not only to have been unbeneficial but also seriously intrusive in the natural process of change. In addition, an all-important initial procedure for all translocations is to make every effort to determine that the donor animals are disease-free before being used.

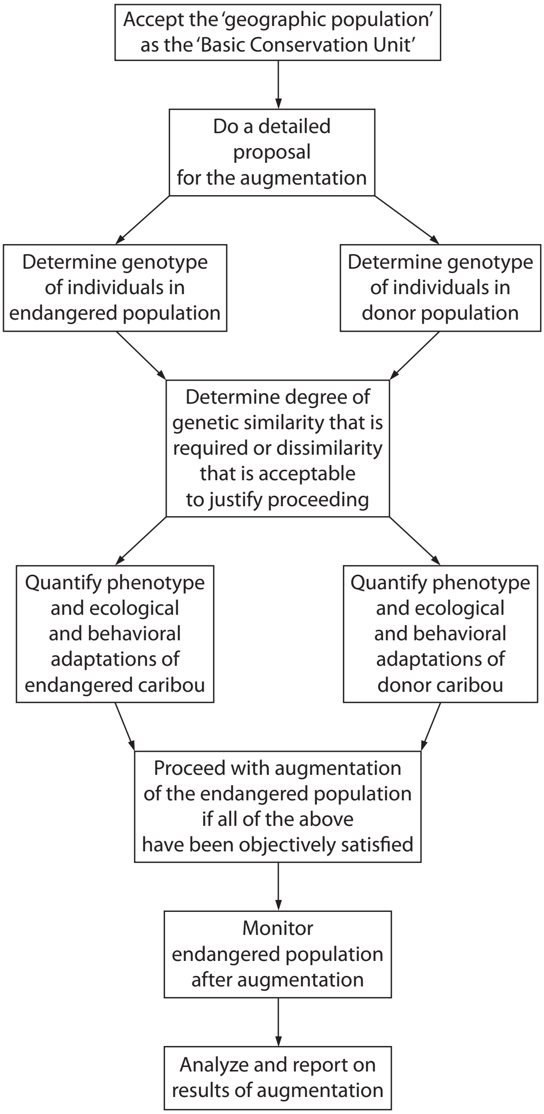

Fig. 1. Protocol for augmentation of an endangered caribou population with caribou from a viable wild population.

There are many problem areas in conservation biology that need more work before augmentation becomes commonplace (Frankham, 1995:306; 1999:238; Stockwell *et al.*, 2003). We need to learn much more about individual variation within a population and between or among populations (Hayes &

Jenkins, 1997; Holmes, 1997; Lacy, 1997). We need to learn much more about 'contemporary evolution' where evolutionary changes take place within a few hundred years and often even within decades (Stockwell *et al.*, 2003). To the best of our knowledge, no one has considered the effects of translocation on the historical phylogeographic structure of caribou (Stephen *et al.*, 2005).

We must develop consensus as to what actions must be taken before, during, and after the transplanting of caribou into an endangered population. Specific augmentation guidelines will have to be developed on a case-by-case basis. Then, specific detailed augmentation plans will have to be developed, each starting with an unambiguous statement of purpose. The proposal should consider the potentially negative as well as the potentially positive outcomes, as well as an adequate accounting of the original cause(s) of the decline or at least an objective acknowledgement that the root cause(s) of the decline is not known.

Augmentation of an endangered caribou population demands strict adherence to the accepted protocol and uncompromising attention to the predetermination of all four areas of concern: genetics, phenotypic expression, ecological (physiological and morphological) adaptations, and behavioral repertoires. We must give detailed consideration to the above in terms of their respective inheritable linkages that were forged by the respective group's environmental setting–both biotic and abiotic (Vogler & DeSalle, 1994; Craven *et al.*, 1998; Miller *et al.*, 1999; Fischer & Lindenmayer, 2000). We believe this approach will deal with the important biological and ecological distinctions between or among caribou populations. Each case must include a complete work-up for both the endangered caribou and the potential donor candidates (Fig. 1) to prevent 'contamination' of endangered caribou by incompatible donor animals, to avoid the risk of potentially irreversibly altering functional characteristics of resident endangered caribou, and to avoid corrupting and thereby removing a distinctly evolved line from among the region's caribou–forever.

Conclusions

The geographic population is the most refined and consistently workable BCU for the conservation of endangered populations of North American caribou, as it is spatially disjunct and thus relatively easily recognized. Therefore, it is not reasonable to lump caribou in a large and biologically or ecologically meaningless BCU at the level of the subspecies, as such an action would ignore the considerable biodiversity that exists among groupings of caribou in geographic populations well below the subspecfic level.

The conservation of endangered caribou requires attention to the biology and ecology of the caribou under consideration at the smallest possible scale. It is reasonable to assume from marked biotic and abiotic differences in their respective environments that physical adaptations and behavioral repertoires acquired by caribou are important to their long-term survival and that these differences further separate the geographic populations into their particular niches on a meaningful ecological basis. Therefore, conservation efforts should identify the fundamental interdependency of genetic and non-genetic processes affecting viability among geographic populations.

It is our position that before any augmentation of an endangered caribou population occurs, there is a great need to review our knowledge base to prevent actions that could result in negative outcomes and, most importantly, could create irreversible results. It should be a prerequisite in any conservation program that there be prior determination that both the endangered and donor caribou are indeed genetically, phenotypically, and ecologically the same. In the absence of a match, even out of desperation or even if highly similar caribou exist, no augmentation should proceed until we know with a high level of biological confidence that the functional characteristics of the caribou being augmented will not be lost. We recommend that this subject be given in-depth consideration–at the level of the geographic population.

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Special communication

Defining subspecies, invalid taxonomic tools, and the fate of the woodland caribou

Valerius Geist

Faculty of Environmental Design, University of Calgary, Canada.
(e-mail: kendulf@shaw.ca, postal address: P. O. Box 1294, St. A, Port Alberni, BC, V9Y 7M2, Canada).

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My concern pertains to the true woodland caribou, the uniformly dark, small-manned type with the frontally emphasized, flat-beamed antlers. Judging from the low complexity of its nuptial characteristics, it is probably the oldest and most primitive *Rangifer* alive. Whether the taxonomic name *Rangifer tarandus caribou* Gmelin 1788 is applicable to this form is uncertain as the type locality given is Quebec City and a true geographic location for the type specimen is thus lacking. The true woodland caribou is scattered thinly along the southern rim of North American caribou distribution. It needs urgent attention, but the urgency is compromised by a flawed taxonomy. This flawed taxonomy, using - in this case misusing - the authority of science, suggests that there are far more "woodland caribou" than there really are. A re-examination of caribou subspecies is urgently required.

Frank Banfield (1961) made the subspecies *Rangifer tarandus caribou* Gmelin 1788 a catchall for larger caribou. He lumped into this subspecies not only the (a) true woodland caribou, but also (b) the totally different Newfoundland caribou (*R. t. terreanovae* Bangs 1896), the (c) form closest related to true woodland caribou, but nevertheless biologically distinct barren-ground form, the Labrador caribou (*R. t. caboti* Allen 1914), as well as the (d) totally different western Osborn's caribou (*R. t. osborni* Allen 1902) from British Columbia. The latter is so different from the dark woodland form (called the Mountain caribou in British Columbia and found to the south of the Osborn's caribou's distribution) that even bush pilots I flew with noted the difference, let alone a competent taxonomist such as Dr. Ian McTaggart-Cowan who segregated the two forms in his and Charlie Guiguet's (1965) *Mammals of British Columbia*. All of the above forms can be identified or differentiated visually at a glance by differences in the mature bull's coat and antler characteristics. Even cave artists from the Upper Paleolithic sketched the coat and antler characteristics of European tundra reindeer correctly. That's how distinct nuptial characteristics are!

In addition there is talk of "mountain" and "woodland caribou" north of 60. However, we appear to be dealing here with splinter populations of barren ground caribou, which have adapted to a more sessile life style, increased in body size and assumed some "woodland mannerisms". This needs close scrutiny and clarification!

Consequently, on the face of it we have "woodland caribou" roaming Canada from Newfoundland and Labrador right through British Columbia and well into the Yukon Territory, North West Territories, and Nunavut. And that is an artifact of a taxonomy based on an inappropriate methodology. Therefore, the populations unjustly labeled woodland caribou or subspecies *caribou* obscure the fact that the true woodland caribou is very rare, in very great difficulties and requires the most urgent of attention.

Banfield did spend time with barren ground caribou, but I do not know if he even saw Labrador or

Newfoundland caribou, let alone the difficult to reach western Osborn caribou (which I observed frequently during 1961-65 on my Stone's sheep study area in the Spazisi, about 130 km south of Telegraph Creek, BC). Secondly, he may not have had an "eye" for details in a picture-plane. I am aware of this difficulty in individuals with minimal artistic talent or training, because, having sketched different subspecies of big game for court or publication purposes, I have asked colleagues how the sketches differed. Some said that, yes, they do look different, but they could not detail why they were different. To such a person, all caribou might look much the same. Nevertheless, even in 1961 when Banfield's monograph came out, my then mentor Ian McTaggart Cowan, who wrote two major taxonomic monographs (on mule and black-tailed deer [*Odocoileus hemionus* Rafinesque 1817] and American sheep [*Ovis dalli* Nelson 1884, *O. canadensis* Shaw 1804]) considered that monograph unacceptable! So, my concerns with Banfield's inadequacies in his taxonomy of caribou are not new.

Banfield (1961) fell victim to an error, which is, unfortunately, not uncommon in taxonomy: he used comparative morphometrics to distinguish subspecies. That is, while descriptions of color, hair and antler patterns appear to be "subjective", skull measurements appear to be "hard" and amenable to "objective" analysis. A statistical analysis of measurements appears to be "scientific". Unfortunately, that assumption is false! A comparison of skull measurements between populations, no matter how voluminous the data set or how refined and sophisticated the statistical tools, cannot be used taxonomically, because such an analysis confounds and confuses genetic variance, epistatic variance, the compounded, multiple environmental variances as well as true statistical variance. And there is no way to disentangle and pronounce on such.

Comparative morphometrics cannot - in principle - be used in taxonomy. However, because of its great precision it can be used forensically, or it can be used to illustrate growth trends, etc. It's a fine tool, but not to identify *genetic* differences. It cannot do that on principle. Unfortunately, this fundamental error has been done frequently in the taxonomy of various mammals (Geist, 1991, a; b; c). Moreover, taxonomy is now contained in legislation and subject to court action. Having been cross-examined in one case for six days for some 24 hours on red deer taxonomy, I speak from experience (Geist, 1992). Because of far-reaching legal consequences, it is vital to clarify terminology and concepts used in taxonomy (Cronin, 2006), distance oneself from flawed methodology, and seek robust, workable criteria for classification.

Consequently, let me please elaborate a little about morphometrics. As skulls are plastic in their growth, the same genetic system - depending on nutrition and stresses during ontogeny - can generate infinite varieties of skull forms and sizes. In addition, skull size and shape are linked by allometry. Size and proportions are, therefore, linked, and differences in proportions have nothing to do with differences in genetics. Nor do differences in size, which are primarily driven by net-nutrition. Within a subspecies, such as the Central European red deer (*Cervus elaphus hippelaphus* Kerr 1792), body size due to differences in habitat quality can differ five fold (from 70 kg adult stags from very poor industrial habitats to 350 kg stags from the Carpathian mountains). These types of growth differences have been long explored experimentally by the agricultural discipline of Animal Science, and they are nothing new. Also, nutrition experiments have been done that more than doubled "normal" body size of red deer within five generations. This splendid work by Franz Vogt is virtually unknown as it was published in German (Vogt, 1936; 1946; 1951). Nor is the taxonomic thinking based on such known here for the same reason (I have integrated such, among others, in my 1998 book *Deer of the World*. See references there).

It is not fair to single out Banfield for criticism. Others also committed the far-reaching error, namely, to apply straightforward comparative morphometrics to taxonomy (i.e in bison or sheep see Geist 1991b; 1991c). Only under rare circumstances can one draw on comparative morphometrics to argue for probable, but unproven, genetic differences and neither Banfield nor zoologists in general are aware of these. One of the first taxonomists to pioneer comparative morphometrics was the Norwegian Ingebrigtsen (1923) who used such to demonstrated paedomorphism in red deer. Ironically, that happens to be a correct use of that methodology! I hunted down Ingebrigtsen's 1923 monograph in Memorial University in the 1970s - and had to use a razor to cut open the pages. It had never been read in all its 50 year of existence in North America!

That gets us back to square one: what is a subspecies? Mayr (1963) defined a subspecies as an aggregate of populations in a geographic subdivision of the species' range that differs taxonomically from other populations. If one can distinguish the individuals from different populations by *taxonomically valid criteria*, then each population so distinguished is a subspecies. The populations may differ greatly by *taxonomically invalid criteria*, in which case they are not subspecies, but *ecotypes*. This applies, for instance, to populations of the phylogenetically most advanced of the elk (*Cervus canadensis canadensis* Erxleben 1777). All elk in North America have exactly the same coat pattern, antler characteristics and rutting voice as well as the same genetics (see Geist, 1998). The one gene difference between Olympic elk and Rocky Mountain elk is taxonomically trivial. That's why there is only *one* subspecies of elk in North America and the regional differences, primarily in body size and environmentally affected growth-patterns of the antlers are *ecotypic.* Moreover, elk with exactly the same *nuptial* characteristics as North American elk are found in Mongolia and Siberia. Ergo, the subspecies *C. c. canadensis* Erxleben 1777 inhabits two continents. Genetic studies have born this out (Ludt *et al*., 2004).

One possible way to characterize subspecies is to segregate populations by their nuptial or rutting dress, or "uniform". These characteristics vary with the age of the males, are minimally affected by environment and are best expressed in old males at breeding time. Biologically, this suggests that selection for nuptial characteristics is done through female sexual selection. Genetic studies on deer, in which specimen were selected rigorously by nuptial characteristics, generated very clean segregations (Ludt *et al*., 2004), suggesting minimal gene flow between subspecies. This matches field observations, as subspecies of the "red deer" complex appear to differ ecologically, while narrow or missing hybrid zones speak of hybrid disadvantage. Such subspecies are thus biologically real. The non-abstract reality of the subspecies makes it, ironically, the old *Linnean species*. Social adaptations thus reflect common descent and segregated gene pools, and are thus useful characters for taxonomy. Note: using the criterion, nuptial characteristics, drastically reduces the number of subspecies as listed; for instance, in O'Gara (2002), because it eliminates the confusion of subspecies and ecotypes.

Subspecies cluster naturally into species, whose unifying feature is an identical *adaptive syndrome.* Again, please let me illustrate with the latest in "red deer": the cluster of wapiti/maral deer are six-pronged *cursors* (runners), the Himalayan cluster are 5-pronged *saltors* (jumpers). These two clusters represent two different adaptive syndromes, and, therefore, two different *species* of "red deer" as they differ entirely in their anti-predator adaptations and require very different landforms (level, open sub-alpine/sub-arctic steppe versus steep, long, shrub-covered mountain slopes). While both are close in mtDNA, they are in morphology farther apart, than either is from the more distantly related third species, the European red deer (saltatorial/cursorial body form). Genetic data reveals here three long-segregated genetic clusters (Ludt *et al.* 2004), morphology indicates greatly different adaptations, and field observations confirm clean segregation. Here the *criterion* for the taxonomic *species* classification is *adaptation*, while the genetic data (phylogenetic lineages) is in a support position, confirming a long-standing genetic segregation. Consequently, there are three species of "red deer". In zoos one can interbreed deer across genera, making *potential interbreeding in captivity* an irrelevant taxonomic consideration. The *Biological Species* of Ernst Mayr, falls out as a necessary consequence of evolving different adaptive syndromes and is applicable only to animals living under natural conditions that include predation.

The nuptial dress criterion works well with the subspecies of red deer and mule deer. And I - tentatively - think it works with *Rangifer* as well. Consequently, I applied it in my 1998 *Deer of the World* (pp. 324-328). However, it was presented there as a challenge. I suspect that it will work with caribou, but I would sleep easier if it could be based not on a few dozen, but on thousands, of individuals compared.

I emphasized the above because the subspecies criterion - *nuptial characteristics* - does not apply to white-tailed deer (or cougars, grizzly & black bears, wolves, etc.). For white-tails, we need to draw up separate subspecies criteria, though I do not currently know which. White-tails show huge regional genetic differences that do not reflect themselves either in their minimal external differences nor in the taxonomy based on skull morphometrics. White-tails from South America differ genetically more from white-tails in Georgia, than do Georgian white-tails from California coastal black-tails. The genetic differences within a species are here greater than between species (see Geist, 1998).

I was excited by Matt Cronin's *et al.* (2005) caribou paper. It basically fits the *Rangifer* taxonomy I suggested. However, it is necessary to study thoroughly the nuptial coat and antlers in *Rangifer* to see if integration between purported subspecies as I defined them does or does not exist. The Newfoundland caribou is by nuptial characteristics a subspecies. I think that true woodland and Labrador caribou segregate cleanly as their differences relate to radically different breeding biology. I think that the southern caribou in BC, the mountain caribou, has the same pelage and antler characteristic as the true (or very dark) woodland caribou and thus may be the same subspecies. Osborn's caribou are quite different from true woodland or BC mountain caribou, a conclusion supported also by Cowan and Guiguet in *Mammals of British Columbia.* I think the mountain caribou of the Yukon and NWT are non-migratory barren ground caribou.

Clearly, we need a thorough review of caribou taxonomy.

In short, if my argument is valid, then true woodland caribou are only the very few, dark, small-manned caribou scattered across the south of caribou distribution. They need the most urgent of attention.

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In search of a critical habitat concept for woodland caribou, boreal population

Gerald D. Racey[1] & **A. Alan Arsenault**[2]

[1] Ontario Ministry of Natural Resources, Northwest Science and Information, RR#1 25th Sideroad, Thunder Bay, Ontario, Canada P7C 4T9 (corresponding author: gerry.racey@ontario.ca).
[2] Saskatchewan Environment, Fish and Wildlife Branch, 112 Research Drive, Saskatoon, Saskatchewan, Canada S7K 2H6.

Abstract: A hierarchical approach to critical habitat identification has been proposed in the draft *National Recovery Strategy for the Woodland Caribou (Rangifer tarandus caribou), Boreal Population*. This approach proposes that critical habitat for boreal caribou be identified as equivalent with caribou ranges and their composite range components, and that it be consistent with the biological needs of a wild, self-sustaining local population of woodland caribou. These components include seasonal ranges, high use areas and calving sites, each of which provide for important ecological functions and are subject to specific risks from human development activities. Protection of critical habitat is accomplished through management of the amount and type of human developments and potential natural disturbances, not by prohibiting all activity. This approach to critical habitat sets the stage for management and monitoring of habitat at spatial and temporal scales appropriate for conservation of a wide ranging species such as woodland caribou.

Key words: boreal forest, management, population, range, recovery, species at risk.

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Introduction

The Committee on the Status of Endangered Wildlife in Canada first assessed the Boreal Population of Woodland Caribou as a Threatened species in May 2000, confirmed in May 2002 (COSEWIC, 2002). Five provinces have listed the boreal population of woodland caribou as a Threatened (or Vulnerable, in Quebec) species under their respective wildlife legislation and the federal government has listed it as Threatened under the Species at Risk Act (SARA) (Statutes of Canada, 2003).

A coordinated national approach for the conservation of species at risk among federal, provincial and territorial governments was committed to in the 1996 *Accord for the Protection of Species at Risk*. Under the auspices of the Accord as well as SARA, a multi-jurisdictional National Boreal Caribou Technical Steering Committee (TSC) was established in February 2002 to develop the national recovery strategy and action plan for 'boreal caribou' consistent with the requirements of SARA, to provide collective advice to the 10 jurisdictions responsible for boreal caribou recovery, and to coordinate recovery planning and implementation among the jurisdictions. In recognition of the broad distribution of boreal caribou in Canada and regional variability in ecology, issues and threats, recovery planning is being undertaken at both provincial/territorial and national scales. It is in this collective context that issues surrounding recovery planning such as goals, objectives, and higher-level consideration of threats and critical habitat are proposed and discussed.

The national Recovery Handbook (National Recovery Working Group, 2005) defines recovery as the process by which the decline of an endangered, threatened or extirpated species is arrested or reversed, and threats removed or reduced to improve the likelihood of the species' persistence in the wild. The recovery goal in the recovery strategy sets out what can realistically be achieved for a particular species. Not all species can be recovered to a level where long-term persistence in the wild is secured.

In the case of boreal caribou, the proposed national recovery goal encompasses the notion of achieving both national and local population levels that are self-sustaining or capable of long-term persistence in the wild. The draft strategy links this goal to the sustained availability of quality habitat at a scale and over a time period consistent with a desirable population-level response. SARA defines habitat as "the area or type of site where an individual or wildlife species naturally occurs or depends on directly or indirectly in order to carry out its life processes, or formerly occurred and has the potential to be reintroduced".

SARA requires that the 'critical habitat' of endangered, threatened, and extirpated species be identified to the extent possible in the recovery strategy and/or action plan(s), and includes provisions to protect such habitat. Critical habitat is defined in SARA as: "the habitat that is necessary for the survival or recovery of a listed wildlife species and that is identified as the species' critical habitat in the recovery strategy or in an action plan for the species". Critical habitat is legally identified when the final recovery strategy or action plan containing the critical habitat description is posted on the SARA public registry. This triggers a process to ensure that the critical habitat is effectively protected. Identification of the critical habitat should be consistent with the recovery goal for the species. For a widespread species such as boreal caribou, identification of critical habitat is an ambitious undertaking made more difficult by lack of experience with the new Act and with application of the concept of critical habitat.

This paper describes a proposed approach to critical habitat for boreal population woodland caribou that meets SARA requirements, is biologically sound, and is consistent with recovery planning underway in the provinces and territories. It elaborates on the approach to identification of critical habitat within the draft National Recovery Strategy for the Woodland Caribou *(Rangifer tarandus caribou)*, Boreal Population, in Canada (Environment Canada, 2006). Much of the science-based rationale for boreal caribou recovery is referenced in that document. However, the proposed approach to identification and conservation of critical habitat is predicated upon the hypothesis that habitat selection is inherently hierarchical and that caribou have distinct habitat requirements at different spatial and temporal scales (O'Brien *et al.*, 2006; Johnson *et al.*, 2001; Rettie & Messier, 2000). They tend to select habitat to avoid predation at coarser scales (Bergerud, 1988; Johnson *et al.*, 2001) and then select habitat to meet forage requirements at finer scales (Schafer & Pruitt, 1991; Rettie & Messier, 2000). Within most of their national range, predation is the major proximal factor affecting boreal caribou populations (Bergerud, 1988; Stuart-Smith *et al.*, 1997; Rettie and Messier,1998; Schaefer *et al.*, 1999; James and Stuart-Smith, 2000; Wittmer *et al.*, 2005). Land use practices resulting in habitat degradation and that increase predator numbers or facilitate higher rates of predation and legal and illegal hunting are ultimate factors influencing caribou populations. Enhanced predation risk through increased predator numbers may significantly reduce or even eliminate local boreal caribou populations (Seip, 1991; 1992). Human developments such as industrial infrastructure and timber harvest blocks may reduce effectiveness of habitat adjacent to these developments (Chubbs *et al.*, 1993; Smith *et al.*, 2000; Dyer *et al.*, 2001). Factors that influence the predator-prey system anywhere in the range can affect the caribou population and must be addressed at that scale and be consistent with the natural background dynamics of the boreal forest.

Methods

Organizational involvement

Eight provinces and territories (Newfoundland and Labrador, Quebec, Ontario, Manitoba, Saskatchewan, Alberta, British Columbia and the Northwest Territories), the Canadian Wildlife Service, and the Parks Canada Agency participate in recovery planning for the boreal population of woodland caribou. Each jurisdiction has one or more representatives on the TSC, which has developed a draft National Recovery Strategy meeting the requirements of SARA (Environment Canada, 2006). This strategy will evolve in response to comments received during targeted consultation and peer review.

The draft National Recovery Strategy includes sections dealing with threats, recovery goals and objectives, and recommended approaches for achieving the objectives. However, the TSC struggled with the concept of critical habitat as it would apply to a wide-ranging species such as woodland caribou. Thus the group initiated a process to examine regional variations in woodland caribou biology and threats, seek over-arching conservation concepts, and reach consensus on a national approach that would support conservation and allow for implementation in all jurisdictions.

Analysis

In October 2004, the TSC reviewed the concept of critical habitat for applicability to boreal caribou across Canada. Agreement was reached on a biologically-based, spatial and temporal hierarchical approach to describing critical habitat, in order to address both the wide-ranging behavior of the species and the complex nature of conservation issues expressed at various spatial and temporal scales. A broad approach to critical habitat would be described in the draft National Recovery Strategy but specific delineation and identification would occur within each provincial/territorial jurisdiction. The agreement on a hierarchical approach was complicated by different individual interpretations of the nature of the hierarchy. It could be nested, with smaller spatial units contextually arranged within larger spatial units. It could reflect progressively increasing levels of protective measures. It could reflect temporal consideration of immediate and future habitat needs to be satisfied for caribou conservation. It could reflect an incremental approach or gradual refinement of definition and delineation. All these variants of a hierarchical approach were important and needed to be rationalized within a consistent framework.

Two workshops in 2005 provided opportunities to refine the approach to critical habitat. The first was a workshop hosted by the Manitoba Model Forest on April 26-27 in Winnipeg Manitoba, in which 38 invited participants from across Canada conducted an analysis of over-arching principles in caribou ecology reflected in conservation strategies from all jurisdictions. The second was a TSC workshop held on October 24-26 in Saskatoon, during which the TSC and invited supporting experts examined and refined a critical habitat approach suitable for the National Recovery Strategy. The concept was evaluated and explained by describing delineation and definitional criteria, critical habitat functions, factors that "destroy" or compromise critical habitat functions, and examples of measures that provide for effective protection. These are all criteria consistent with Environment Canada guidelines (2005a, 2005b).

Proposed approach

The TSC has determined that critical habitat for boreal caribou should be equivalent to caribou ranges and their components. In this paper, range refers to historic and current distribution of boreal woodland caribou and is defined as a geographical area partially or fully occupied by a defined local population of caribou. This definition is essential to acknowledge the spatial and temporal complexities of conserving a wide-ranging species on a naturally dynamic forested landscape. It also recognizes an appropriate functional role for specific habitat components, at different spatial and temporal scales, that are required to assure persistence of boreal caribou populations in the wild (consistent with the recovery goal). The primary ecological function that allows caribou to survive in a range is the provision of effective refuge from predation, although other risk factors are recognized. Each of the components of caribou range, including winter, summer and calving habitat, contributes to this refuge value and collectively allow caribou recruitment (births and immigration) to equal or exceed deaths and emigration. Persistent populations meet this criterion.

A range capable of supporting a self-sustaining population of boreal caribou is invariably composed of a number of components, each satisfying the life requirements for boreal caribou at specific times (diurnally, seasonally, inter-generationally and perpetually), such that collectively, overall range occupancy is continuous and uninterrupted. Thus there is recognition that these habitat components are also treated as critical habitat within the context of a range and long-term habitat and population dynamics. These range components are referred to as seasonal ranges, high-use areas and calving sites and may require progressively increasing levels of protection for more geographically localized habitat components.

Range

Delineation/definitional criteria:

Large landscape unit encompassing the known or inferred current local population, or the portion of the boreal forest landscape within which a local population is to be sustained (diffuse and/or wide ranging populations on highly dynamic landscapes). Delineation and size is consistent with local population sustainability objectives.

Critical habitat functions provided at this scale:

Sustainable habitat supply to satisfy all life requirements of local populations over multiple generations, including provision of present suitable habitat, future habitat and alternate habitat; adequate space for predator avoidance strategies to operate.

Activities likely to result in destruction of critical habitat:

Resource management actions that fail to provide for future habitat or alternate habitats which allow caribou to account for temporal and spatial dynamics of the landscape (fire, logging, succession); large human "footprint" contributing to increased predator numbers or hunting efficiency; landscape arrangement that reduces ability of caribou to evade or avoid predator encounters.

Example measures contributing to effective protection:

Manage present and future forest cover and composition to ensure an adequate and sustainable supply of seasonal and year-round habitat. Strategically plan access and linear feature development to avoid present and anticipated high use areas or seasonal ranges. Define and manage towards a habitat planning target across the range that allows for achievement of desired local population response. Ensure number, spatial arrangement and timing of resource development, extraction and human activities are appropriate to manage risk at pre-defined levels.

Special notes:

A range represents critical habitat for a local population, and a portion of critical habitat for the boreal population of woodland caribou. It includes land and water area providing for present and future local population objectives. Range-specific evaluation of threats and conservation opportunities is required to determine acceptable level and extent of industrial activities. Caribou habitat values are met within a managed and dynamic forest condition where present and future seasonal ranges and high use areas are sustained. It may include dedicated protected areas, commercial forest or some combination of the two.

Seasonal ranges

Delineation/definitional criteria:

Component of a range typically described as winter range or summer range but may also include specific travel linkages or spring/fall transition habitats. Usually associated with predictable landform, topographic, or hydrological landscape features and forest cover or compositional criteria.

Critical habitat functions provided at this scale:

Provides for predator avoidance and forage availability best suited for specific seasonal life requirements. Large enough to provide for alternate habitat selection attributable to different levels of seasonal stress such as severe seasonal weather patterns (precipitation, snow depth, crusting, etc) or direct human or predator harassment.

Activities likely to result in destruction of critical habitat:

Resource development activities that result in reduction of area in suitable vegetative condition (age class, patch size, spatial arrangement and species composition) required to provide effective refuge or forage required for the number/density of animals using the range or the number of animals that must use this range in order to have a self-sustaining population.

Example measures contributing to effective protection:

Promote seasonal range conservation through protective measures such as fire suppression; precautionary allocation (forest management/mineral exploration) and avoidance of adjacent development activities that may encourage habitat for alternate prey species or otherwise increase the relative abundance, distribution or mobility of predators within or near seasonal ranges. Manage density and rehabilitation of linear features that may increase predator mobility.

Special notes:

Seasonal ranges may or may not exist for some local populations or within some ranges. Where they do exist, they tend to be more dynamic in space and time than the overall range depending on the specific biological functions being met. These areas are generally suitable for current use and typically receive more rigorous prescriptions for conservation or management than the portion of a range between seasonal habitats.

High use areas

Delineation/definitional criteria: Component of a range or seasonal range regularly exhibiting higher than expected use, likely associated with especially desirable or effective habitat features such as forage or the absence of human, insect or predator harassment.

Critical habitat functions provided at this scale:

Nursery or calving areas facilitate summer calf survival by providing refuge from predation in the vicinity of forage resources during this high risk period. Reduction in calf mortality or improvement in body condition prior to winter will increase probability of recruitment into the local population. High use winter areas may provide high abundance or quality of forage, or efficient access to refuge or forage during extreme weather conditions. They may be associated with forest conditions that provide abundant lichen availability, lower snow depths or high visibility.

Activities likely to result in destruction of critical habitat:

Human disturbance that forces caribou cows and calves to become separated, forces cows with calves into unnecessary movement (increases potential for predator encounters), or displaces cows with calves into higher risk environments. Habitat alteration that increases actual or potential predator activity in the vicinity of winter or summer high use areas including food subsidies; forest management practices that create and maintain high diversity, browse-rich or early seral stage forests. Reduction or elimination of forage values due to changes in forest stand composition, structure or spatial arrangement. These changes may result from forest harvesting, natural disturbance (fire, blow-down, insects and disease), or from forest plant succession. Infrastructure or human activity that displaces caribou away from resources or into areas of greater risk of predation. Any infrastructure development (roads/trails) that encourages or increases efficiency of predator activity in or around high use areas.

Example measures contributing to effective protection:

Encourage direct or indirect forest management or access management practices in and around nursery areas to ensure appropriate balance between forest conditions that discourage predator numbers or hunting efficiency, enhance the ability of caribou to detect and escape from predators or enhance forage abundance and availability. Avoid factors that accelerate decline, deterioration, reduction of the habitat attributes that make high use area desirable. Avoid linear corridor development into or adjacent to present and potential high use areas. Manage human activities, including research activities, to minimize displacement of caribou.

Special notes:

Degree of use may vary with extent or intensity of weather, disturbance or other events. Use may be related to quality of neighboring habitats or range components. High use areas warrant management prescriptions with a high degree of protection/conservation consistent with the expected or planned dynamics of the range and the type and magnitude of threats to the local population.

Calving sites

Delineation/definitional criteria:

Typically very small, localized and discrete geographic units with demonstrated evidence of repeat successful calving activity. May represent islands, peninsulas or other specific topographic features.

Critical habitat functions provided at this scale:

Provide for effective predator avoidance during parturition and vulnerable early calf development period. Significant until calf is fully mobile and can travel freely with cow.

Activities likely to result in destruction of critical habitat:

Human infrastructure or activity that could displace cows before or during calving or cows with calves in early parturition period. Campsites, shore lunch fish cleaning locations or recreational activity that create an increased food supply that could attract predators; or alteration of vegetative cover (succession, harvest, fire) that might cause cows to select a higher risk environment for calving.

Example measures contributing to effective protection:

Prohibit alteration of forest cover, human disturbance/activities during high risk period, or human infrastructure development within a functionally effective radius.

Special notes:

Very high level of precautionary principle applied at this scale. If a functioning and repeat use calving site, then prohibitions to development and human use may be appropriate.

Discussion and rationale

The relationship between the local population, its range and critical habitat implies that critical habitat must be delineated based on the known or inferred distribution of caribou. This may include land and water that is currently unoccupied but has the capacity to provide for caribou life requirements in the future as part of a dynamic natural or managed landscape for the existing population size, or for a larger future population that might be deemed self-sustaining. Various components of a range may exist in some jurisdictions but not in others, and may or may not be explicitly defined as part of the overall critical habitat identification and delineation within the jurisdictional recovery strategy or action plan.

This range-based concept of critical habitat is biologically defensible and could perhaps apply to other wide-ranging species in addition to boreal population woodland caribou. The progressively increasing levels of management and protection at finer scales have a high likelihood of success and are capable of supporting a desirable population response only if broader, range-wide habitat outcomes are achieved. Therefore, more geographically localized components of a caribou range are inadequate as critical habitats by themselves, because full protection of any or all of these has a low expectation of caribou conservation at the population level unless higher-level range-wide threats are also addressed. In seeking an approach to critical habitat it is prudent to ask the question "critical for what"? Ultimately the only answer is, critical for achieving the recovery goal set out in the recovery strategy: of achieving long-term persistent populations in the wild.

Traditional thinking about the concept of critical habitat for species at risk often revolves around specific habitat components essential to the provision of a specific life requirement such as a nest, den or spawning area. To a large degree these very specific and often discrete habitat components may be adequately addressed through the residence provision under SARA. Traditional caribou calving sites may warrant very specific protection measures, but specific protection of the calving sites does not necessarily ensure calf recruitment if calf mortality is due to high endemic predation rates on the landscape (Seip, 1991; 1992). The proposed critical habitat approach also promotes rigorous protection for traditional calving sites but only within the context of the larger range.

Boreal forest landscapes across Canada are inherently dynamic within parameters determined by many natural bio-physical processes such as wildfire, forest succession, insects, disease, and climate. In large portions of caribou range, populations are also influenced by human developments such as agriculture, forestry, mining, roads, recreation and urbanization. Natural and human-caused disturbances vary over time, and vary in magnitude, periodicity and extent of influence. Consequently, the boreal forest landscape is a mosaic of patches representing different ages and conditions, only some of which are suitable for occupancy at a given time. The patchiness and temporal nature of caribou ranges and range components results in the need for caribou to occupy large boreal forest landscapes to ensure sufficient amounts of quality habitat and free movement amongst suitable habitat patches. These are sound reasons for critical habitat to be broadly delineated with consideration of specific habitat requirements at multiple spatial and temporal scales (Environment Canada, 2006). The spatial distribution of habitat components changes through time, although the overall critical habitat requirements of a given caribou population may remain static (Environment Canada, 2006). Habitat components in an earlier successional stage may become important contributors to the range and critical habitat in the future. Critical habitat must provide enough space and mix of appropriate habitat components to accommodate seasonal variation in habitat use, movement (connectivity), predator avoidance, and dispersal of self-sustaining populations existing at naturally occurring low population density levels.

Caribou are well adapted to cope with a dynamic landscape but only within the intrinsic limits of their biology. The TSC promotes the range as critical habitat because of the wide-ranging effects of local activities that might influence the biological functions of predation, predator avoidance, migration, genetic exchange, reproduction and growth. Ultimately it is the population that is the measure of recovery effort success, and it is the ecological functions at the scale of the range that are either supported or compromised by the cumulative effects of human activities. The temporal scales envisioned exceed the longevity of individual animals, forest stands and temporary human infrastructure, to ensure the long-term persistence of caribou populations in the wild. This suggests that it is as important to plan for renewal of habitat components, as it is to preserve or protect existing habitat components. It is as important to maintain alternate, unused but suitable habitats as it is to maintain currently used habitats. It is also as important to consider cumulative impacts from human activities many years in the future, as it is to consider human activities or developments that may be established this decade and abandoned the next. The range concept, applied as intended, is large enough to accommodate the management of habitat components within a dynamic landscape while accepting the uncertainties of a background natural disturbance regime.

The proposed hierarchical approach is consistent with the need to address cumulative effects at a scale relevant to caribou biology. Ecosystems are inherently hierarchical with processes at one scale interacting with processes at other scales to influence landscape structure, composition and function (Ecological Stratification Working Group, 1995; Wiken, 1986). Caribou habitat selection is hierarchical (Rettie & Messier, 2000) with predation avoidance being addressed at coarser spatial scales (Bergerud, 1988; Stuart-Smith *et al.*, 1997) and foraging being addressed at finer spatial scales (Schaefer & Pruitt, 1991; Rettie & Messier, 2000). Threats that seem local, such as roads or linear corridors, can have far-reaching effects at the landscape or population level (Dyer *et al.*, 2001, 2002; Smith *et al.*, 2000), while forest harvesting or forest fire patterns at the landscape scale may alter the distribution and abundance of prey species over broad areas (Telfer, 1978; Schwartz & Franzmann, 1989), the effects of which may not be demonstrated by the local population for a period of many years or even decades (Vors, 2006).

The proposed hierarchical approach is also consistent with caribou population responses to biotic and abiotic factors at different scales. At the landscape scale, natural and human-caused disturbance influence the spatial and temporal distribution and connectivity of local caribou populations, by affecting the amounts, size and configuration of preferred habitat types. The effect on the landscape is a function of the frequency, magnitude and duration of disturbance factors (Haufler *et al.*, 2002). At the landscape level, the quality, quantity, structure, juxtaposition, connectivity and function of habitats influence home range size, productivity and survival. At a more local scale, the spatial distribution of forage and microclimate influences movements, foraging behavior, calving site choice, and resting site locations.

Critical habitat has been biologically defined as a perpetual supply of large, contiguous areas of suitable summer and winter habitat, allowing self-sustaining viable population(s) to disperse at low densities over a large area to avoid predators (Arsenault, 2003; Bergerud, 1992; Environment Canada, 2006; Seip & Cichowski, 1996). This biological definition includes calving habitat, and acknowledges the implications of human access and disturbance. Arsenault *et al.* (2006) concluded that the range, described as critical habitat, may be the land base required through time to effectively conserve boreal caribou, and which may require special management considerations or protection.

By biologically defining the critical habitat as the range, we recognize that local mitigation of threats is only effective if the cumulative mitigation effort reduces the risk of extirpation at the local population or range level. Using a biologically derived hierarchical approach to critical habitat allows us to consider those physical and biological features that are essential to boreal caribou conservation, and that may require special management considerations or protection within a spatial and temporal hierarchical context.

Management implications

The proposed approach to critical habitat is well suited to envisioning a practical and effective management regime to satisfy recovery goals. It is robust and flexible. As a general approach, it can be readily adapted to accommodate new knowledge to support caribou conservation. Of particular significance is new knowledge on cumulative effects, effective scales of habitat selection, quantitative analysis of threats and resulting population level consequences, and the interaction between human development and natural disturbances. This might be particularly relevant when other factors such as climate change add uncertainty (Racey, 2005) to our understanding of natural processes and caribou. Future growth of caribou biology and management knowledge should allow for progressively more certainty in setting criteria for range delineation or for describing effective resource management practices consistent with conservation of boreal caribou populations.

There is jurisdictional flexibility, while working within this approach, to develop local procedures in support of critical habitat identification and delineation that suit the specific biophysical environment within which their caribou populations live. Managers believe that the relative importance of different habitat components across the country varies with the specific climate, geology, forest growth patterns, disturbance regimes, and human development pressures. Thus, the resulting range delineations and the specific treatment of habitat components may differ between areas with relatively continuous range as opposed to areas with smaller, relatively discrete populations near the southern edge of caribou distribution.

Protection of the range as critical habitat may be achieved through formalized management or conservation agreements setting out the amount and type of human development and potential natural disturbances; rarely would all commercial activity be prohibited. Thoughtful and targeted management actions that influence forest composition or structure (i.e., logging) may prove useful for the renewal of some range components and ultimately for the provision of alternate habitats within the range, to provide insurance against loss of existing habitat components from wildfire. This approach has been acknowledged for piping plovers (*Charadrius melodus circumcinctus*) (Martens & Goosen, 2005), where water level manipulation in reservoirs might be used to maintain or enhance critical habitat, or for Canada lynx (*Lynx canadensis*) in the United States (Department of the Interior, 2005), where special forest management practices may be used to ensure boreal forest landscapes provide a mosaic of forest stands of various ages to maintain critical habitat.

A very important management implication of the proposed approach is that effective protection for the range may be achieved through the combined contributions of parks, protected areas, reserves and managed lands. There is a certain amount of risk and uncertainty in using landscape management approaches and we recommend this risk be addressed by applying the precautionary principle (Cooney, 2004). There is a very clear obligation assigned to the resource management community to apply measures that ensure the biological processes are achieved at the range level and realized in a persistent caribou population. This means:

- select and apply harvest and silviculture practices that do not just maintain current habitat values, but renew and enhance habitat components for the future,
- develop management strategies in protected areas that contain caribou that recognize the role of natural processes in sustaining range values and functions,
- develop range delineations for some local populations that exceed the documented area of occupancy in order to provide for a larger population, alternate areas for natural disturbance contingency, or renewal of currently unused potential habitats,
- rehabilitate temporary human infrastructure such as roads and seismic lines,
- mitigate direct human disturbance and food subsidies for predators caused by industrial and recreational human activities and dumps.

As ranges are shared across jurisdictional or corporate license boundaries, it is essential that there be cross-boundary cooperation in delineating critical habitat and applying effective protection measures. This may only happen if governments create policies and guidance that encourage such cooperation.

Caribou conservation requires management strategies across large areas and long time periods. The proposed hierarchical approach to critical habitat not only facilitates management actions, it facilitates effectiveness evaluation of management strategies by providing a framework for setting and monitoring numerical objectives. It discourages decisions made about individual habitat components such as high use areas, or seasonal ranges independent of their context within the larger range and the total local population. It helps prevent a piecemeal approach to caribou habitat management that will ultimately lead to continued recession of caribou range as described by Racey & Armstrong (2000). Finally, it facilitates the use of range-wide management approaches that meet the needs of the species while avoiding conflicting management direction caused by inconsistent reference conditions at specific temporal or spatial scales (Haufler *et al.*, 2002).

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Special communication

The need for the management of wolves — an open letter

Arthur T. Bergerud

1233 Isabella Road, Salt Spring Island, British Columbia, Canada.

Abstract: The Southern Mountain and Boreal Woodland Caribou are facing extinction from increased predation, predominantly wolves (*Canis lupus*) and coyotes (*Canis latrans*). These predators are increasing as moose (*Alces alces*) and deer (*Odocoileus* spp). expand their range north with climate change. Mitigation endeavors will not be sufficient; there are too many predators. The critical habitat for caribou is the low predation risk habitat they select at calving: It is not old growth forests and climax lichens. The southern boundary of caribou in North America is not based on the presence of lichens but on reduced mammalian diversity. Caribou are just as adaptable as other cervids in their use of broadleaf seed plant as forage. Without predator management these woodland caribou will go extinct in our life time.

Key words: adaptive management, balance of nature, critical habitat, caribou extinction, density dependent, population regulation, wolf predation.

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Introduction

A major ecological question that has been debated for 50 years is: are ecosystems structured from top-down (predator driven) or bottom-up (food limited) processes (Hairston *et al*., 1960; Hunter & Price, 1992)? Top-down systems can vary widely from sea mammals such as sea otters (*Enhydra lutris*) to ground nesting birds. The sea otter causes an elegantly documented trophic cascade through sea urchins (*Strongylocentrotus* spp.) down to kelp beds (Estes & Duggins, 1995). Ground nesting waterfowl and gallinaceous birds are not limited by food resources but are regulated by top-down nest predation caused by a suite of predators, mainly skunks (*Mephitis mephitis*), red foxes (*Vulpes vulpes*) and crows (*Corvus brachyrhynchos*) (Bergerud, 1988; 1990; Sargeant *et al*., 1993). Management decisions depend on understanding which structure is operational.

Discussions on top-down or bottom-up have been recently been rekindled with the introduction of wolves (*Canis lupus*) to Yellowstone National Park and Idaho in 1995 (Estes, 1995; Kay, 1995; 1998). The elk/wapiti (*Cervus elaphus*) population in Yellowstone prior to introduction were basically limited by a density-dependent shortage of food (Singer *et al*., 1997) but now is declining from wolf predation (Crête, 1999; White & Garrott, 2005). All three states, Wyoming, Idaho, and Montana, are litigating the federal government to get the wolf delisted so they can start wolf management to maintain their stocks of big-game.

We conducted a 30 year study (1974 to 2004) of two caribou (*Rangifer tarandus*) populations, one in Pukaskwa National Park (PNP) and the other on the Slate Islands in Ontario, relative to these two paradigms of top-down or bottom-up. (Bergerud *et al*., this conference). In Pukaskwa National Park, there was an intact predator-prey system including caribou, moose (*Alces alces*), wolves, bears (*Ursus americanus*), and lynx (*Lynx canadensis*). On the Slate Islands, our experimental area, there were no major predators of caribou. The PNP populated was regulated top-down by predation and existed at an extremely low density of 0.06 caribou per km^2 whereas the population on the Slate Islands averaged 7-8 animals/km^2 over the

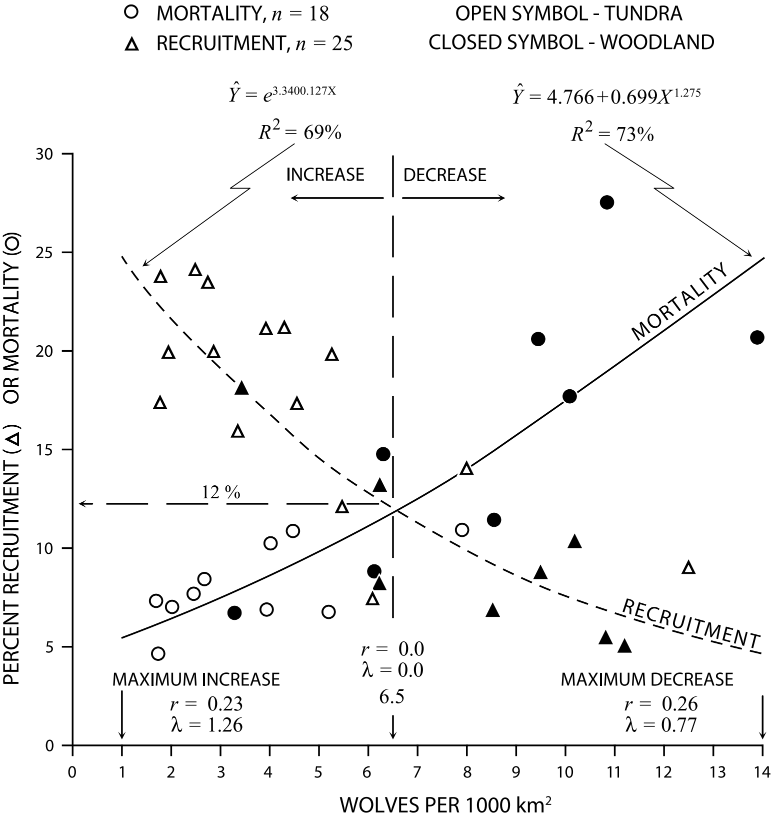

Fig. 1. The recruitment of caribou based mostly on the percentage of calves at 6 or 10-12 months-of-age, and adult mortality, both parameters regressed against the density of wolves. This figure is a modification of a figure in Bergerud & Elliott, 1986. The figure included all the studies in North America as of 1986 that had provided data on all three parameters, recruitment, adult mortality (mostly females) and wolf densities.

30 years (100X greater than in PNP). In the absence of predators, these island caribou were regulated from the bottom-up by a shortage of summer foods and the flora was impacted, resulting in some floral extinctions. The extremely low density of only 0.06 caribou per km^2 in PNP is normal for caribou populations coexisting with wolves (Bergerud, 1992a: Fig. 1, p. 1011). The top-down predator driven ecosystem of caribou in PNP also applies in Canada to moose, elk, and black-tailed deer (*Odocoileus hemionus*) that are in ecosystems with normal complements of wolves and bears (Bergerud, 1974; Bergerud *et al.*, 1983; Bergerud *et al.*, 1984; Messier & Crete, 1985; Farnell & McDonald, 1986; Seip, 1992; Messier 1994; Hatter & Janz 1994; Bergerud & Elliott, 1998; Hayes *et al.*, 2003).

Of all the predator driven ecosystems of cervids, the threat of extinction is most eminent for the southern mountain and boreal woodland caribou ecotypes, both classified as threatened (COSEWIC 2002, Table 11). These herds are declining primarily from predation by wolves plus some mortality from bears. From west to east the equations for continued persistence are not encouraging -- in British Columbia the total of the southern mountain ecotype is down from 2145 (1992-97) to 1540 caribou (2002-04) and four herds number only 3, 4, 6, and 14 individuals (Wittmer *et al.*, 2005). In Alberta, the range has become fragmented and average recruitment recently was 17 calves/100 females, despite high pregnancy rates (McLoughlin *et al.*, 2003). That low calf survival is less than the needed to maintain numbers - 12-15% calves or 22-25 calves per 100 females at 10-12 months-of-age to replace the natural mortality of females (Bergerud, 1992a; Bergerud & Elliott 1998). In Saskatchewan, populations are going down, $\lambda = 0.95$ (Rettie *et al.*, 1998). The range is retreating in Ontario (Schaefer, 2003) as southern groups disappear; in Labrador the Red Wine herd is now less than 100 animals (Schmelzer *et al.*, 2004); in southern Quebec, there may be only 3000 caribou left (Courtois *et al.*, 2003), and in Newfoundland, herds are in rapid decline from coyotes (*Canis latrans*) and bear predation (G. Mercer and R. Otto, pers. comm.). In Gaspé, the problem for the endangered relic herd is also coyotes and bear predation (Crête & Desrosiers, 1995). In Gaspé, these predators have been reduced and there is a plan in place to continue adaptive management (Crête *et al.*, 1994). Do we have to wait until the herds are listed as endangered to manage predators?

Woodland herds can be expected to decline when wolf densities exceed 6.5 wolves/1000 km^2 (Fig. 1). Thomas (1995) reported a similar estimate of only 5 to 8 wolves/1000 km^2 that seriously impacted woodland herds. Wolf populations are increasing because moose are spreading north with climate change with wolves on their heels - now some woodland caribou populations face wolf numbers greater than 7-8/1000 km^2. These wolves commonly switch from moose to caribou in the winter especially when deep snow increases the difficulties of killing moose (Mech *et al.*, 1998).

I do not agree with one option expressed at this conference that we not try and save these southern vulnerable herds. Not only can extinction be avoided but with pulsed reductions of predators, both predator and prey can prosper. In the Muskwa region of British Columbia, both elk and moose were decreasing from 1982 to 1985. 505 wolves were removed in 1984, 1985, and 1987; by 1988-89, the total elk plus moose populations in the region had increased from 23 000 to 33 000 animals. Further five cohorts of caribou and Stone's Sheep during and just after the removal had recruitment > than 25 young per 100 females; hence these populations also increased. Wolves then emigrated into the vacant wolf territories and reached densities of 20 woves/1000 km^2 by 1990 (Bergerud & Elliott, 1998). Because these ungulate systems are not food limited, **with management we could have it all - densities of caribou of 1 per km^2 and more wolves;** without management, we will have extinctions and fewer wolves. We know the problem, yet continue to spend large sums on research that could be used for adaptive management (*sensu* Walters & Hilborn, 1978). We should be counting and radio tracking wolf populations. The problem is not the habitat, it is predation; habitat per se does not kill caribou. The Slate Island study documented the wide tolerance levels of caribou for disturbed habitats and meager lichen supplies, but also showed their wide use of herbaceous and deciduous forage; they are a very tolerant adaptable species (see also Cringan, 1956 and Bergerud, 1977).

The northward march of extinction

The northern demise of woodland caribou in the Lake States started in the middle of the 1800s (Fig. 2) (Cringan, 1956; 1957; Fashingbauer, 1965). The common cliché is that this decline resulted from habitat disturbance (fire and logging and human disturbance); the altered deciduous forest that lacked lichens were not suitable and coupled with disturbance, the animals shifted further north. These ideas are in error. The animals did not move north. The animals remained and declined because of increased mortality. Cow caribou show philopatry to their calving habitat and do not shift, **when they can't be found they have died**.

There was a rise in temperatures when the "The Little-Ice-Age" ended in the 1850s. This warming trend coincided with the opening of the coniferous canopy by logging, facilitating deciduous succession. The range of both moose and later white-tailed deer (*O. virginianus)* expanded north. Riis (1938) stated that there were no deer in the caribou range in Minnesota in 1860. By 1900, the deer were common north to the Canadian border and the Minnesota caribou were gone. The deer brought the brain worm disease fatal to caribou (i.e., *Paraelaphostrongylus tenuis*; Bergerud & Mercer, 1989; Bergerud, 1992b) and both the deer and the moose provided an increase in prey biomass that supported a larger wolf population. It was increased mortality that caused the caribou extinction, and warming temperatures were a factor in the expansion north of the two other cervid species.

Baker (1983) argued that caribou in the 1800s may have only populated northern Michigan and Wisconsin during the autumn, winter, and early spring. The latest spring record for Michigan is March 2 and April 18 in Wisconsin. Caribou in northern Minnesota were also seen only in the fall and winter (Fashingbauer, 1965). The last stronghold of the herd in Minnesota was on the muskeg north of Red Lake. The old leads from that muskeg went directly north to the shore of Lake-of-the-Woods (Bergerud, 1992b), where the caribou had previously calved on the islands. In Wisconsin, the caribou probably calved on the Apostle Islands. In Michigan, Isle Royale was a strong hold but the animals were gone by 1926 (Dustin, 1946 in Cringan, 1956). Other islands in Michigan occupied included High, Beaver and Drummond (Burt, 1946; Cringan, 1956). Hence, the caribou decline during this period resulted from increased mortality from hunting, predation, and disease that took place in the period when water safety was not available. The spring and summer strategy of remaining near water escape habitat remained successful.

In our study, the PNP population had adequate summer survival because of its proximity to water safety in Lake Superior. It also resided in an undisturbed wilderness park with abundant winter lichen food, but the caribou were susceptible to winter wolf predation when land fast ice formed on Lake Superior in the winter. This undisturbed wilderness (balance

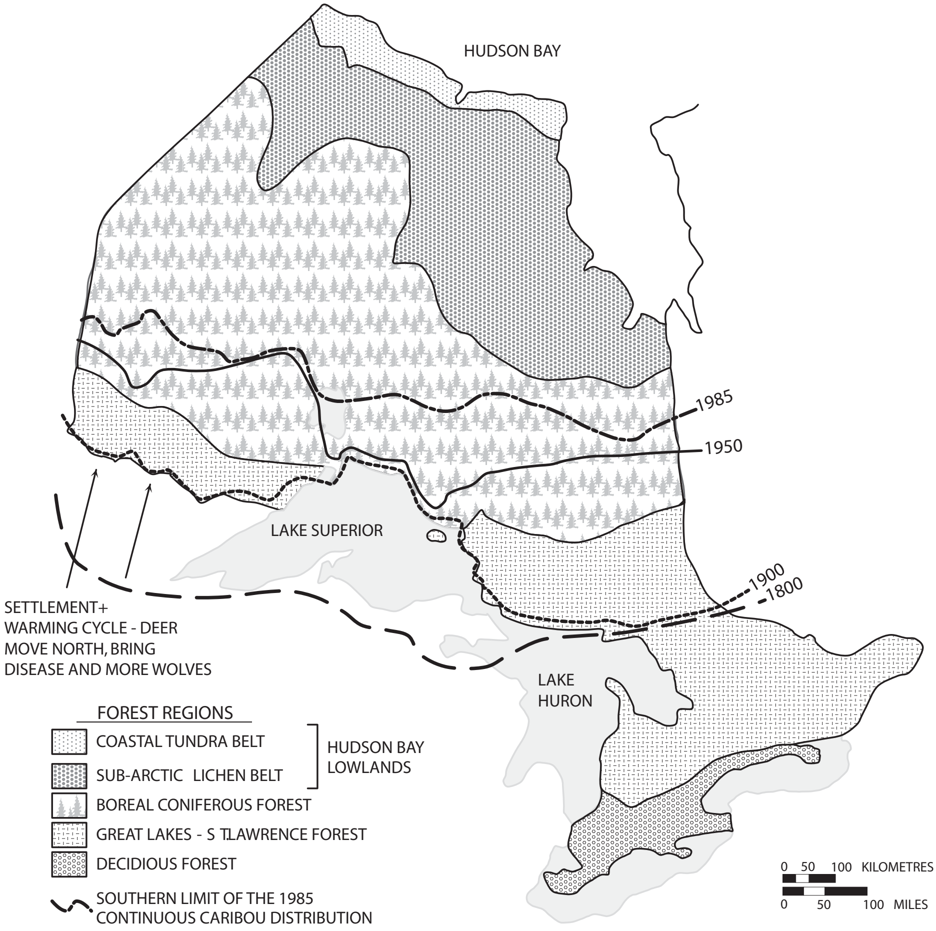

Fig. 2. The line of continuous distribution has moved northward since the end of the Little Ice Age as moose and deer moved north increasing the mortality of caribou through predation and disease. Hunting also contributed to the decline of caribou.

of nature view) and the abundant lichens were not sufficient to maintain numbers. The Slate Island population has persisted for 50+ years on an island archipelago in the absence of predators by foraging primarily on deciduous/herbaceous forage and ground hemlock; the presence of extensive lichens was not necessary for their persistence. In recent years these caribou have persisted despite considerable disturbance from power boats, canoeists, and kayakers.

But the late 1800s scenario is here again, as logging is hastening secondary succession. Temperatures are rising, accelerating the growth of deciduous species more favorable to moose and deer. The density of wolves is increasing and leading to predation rates greater than the equilibrium needed for recruitment to balance mortality for caribou (Fig. 1). The southern mountain and boreal woodland caribou will go extinct south of 60°N in our time unless we are prepared to manage wolf populations and find a solution to the *P. tenuis* disease.

Fragmentation of the Ontario caribou distribution

"Because of forest fires, timber operations and spruce budworm infestations much of the climax forest was removed and replaced by forests ... favourable to moose and deer. Consequently moose and deer increased, while caribou become confined to islands of suitable habitat, each island being surround by newly- created moose and deer range... the higher population of wolves now supported by moose and deer in the peripheral range may have an adverse effect on the caribou populations" (Simkin, 1965, p. 46). Everything that goes around comes around.

Fragmentation of the southern distribution of woodland caribou commenced in the mid 1800s in northern-central Minnesota, Wisconsin and Michigan, and has now reached midway across Ontario (Fig. 2). This range loss has repeatly been attributed to forest harvest, wildfires, and settlement. This over simplification explains little. For the population to disappear, mortality has to exceed recruitment. The problem is not the summer critical range; the fidelity of calving near water bodies results in satisfactory recruitment (>15%, Bergerud, 1974; 1992a). Simkin (1965) documented 40 years ago in his research on the islands at Irregular Lakes that 86% of the cows were accompanied by calves in three summers; that calf survival was better than the exclosure study of pregnant females in the Yukon discussed at this conference (Farnell *et al.*, this conference). Islands are exclosures in the growing season but become predator traps when ice forms. Cumming & Beange (1987) reported a recruitment of 21 per cent calves in the Lake Nipigon herd where males also used the islands. But when lakes freeze and the animals aggregate, this survival advantage disappears. The mortality sequence is complex: initially, the forest canopy is opened (logging + land-clearing + fires), summer temperatures can increase (end of The Little Ice Age-1850), deciduous forage increases, white-tail deer and moose expand their range and, then the wolf population increases; the mortality of caribou from disease, predation and hunting exceeds the high summer calf increments. Gradually, all the females and their female progeny that recognize a safe calving location and show philopatry are gone, and a summer critical range is left vacant. Vors *et al.* (in press) calculated that in central Ontario, the time sequence from the time an area is logged until the caribou disappear is now about 20 years. With global warming it may be sooner.

When a tradition is lost the range is fragmented. It is the "burned-out" marsh theory of Albert Hochbaum (1955): when all the locally reared ducks that first saw their natal marsh from the air are killed by local hunters before they disperse, the breeding homing tradition to that marsh is lost. When the last females are killed that calve on the shore and islands of Lake Nipigon, Ontario, the tradition will be lost and the line of continuous occupation will be retreat further north. Lost traditions are near-impossible to rebuild.

Critical habitat

The Federal Species At Risk Act requires that critical habitat be identified. It is generally accepted that the calving grounds of the migratory barren-ground herds are the critical habitat (review Russell *et al.*, 2002). However some still do not recognized that the key value of that habitat is reduced predation risk rather than optimal foraging. The critical habitat of the montane (southern mountain) and boreal woodland populations (the sedentary ecotype) is also the habitat used for calving to reduce predation risk for their neonates. The calving locations for this ecotype are the anchors to their annual ranges and philopatry is strong (Shoesmith & Storey, 1977; Hatler, 1986; Brown *et al.*, 1986; Edmonds, 1988; Cummings & Beange, 1987; Schaefer *et al.*, 2000). The spacing of the females at calving represents the maximum spread of each "herd" and the concept of being rare (Bergerud, 1990). This distribution represents the key density-dependent component in the regulation of the herd by predation. Herds with densities above D_s (the stabilizing density) should decline from predation until the surviving females are sufficiently spaced due to philopatry that densities are less than D_s and predation pressures are reduced and recruitment equals mortality, population extinction is avoided (Bergerud, 1992a). This spacing strategy has evolved at the fitness level of the individual female but supports the persistence of the group (population).

This wide spacing of the females complicates a description of what is critical habitat, but normally the basic component is that water is available for escape. Water is the great equalizer and its value known in traditional knowledge. A Labrador hunter from Hopedale, described why deer (caribou) calve "*in mossy places and nearly always near water… with the wolves around the only chance these little ones get to have a rest is they head for water,… they go in about two or three feet and the wolf can't do nothing because the wolf's legs are shorter then the deer*" (Brice-Bennett, 1977, p.161). On August 14, 1779, Captain Cartwright noted along the Labrador coast "*When pursued in the summer time they (deer) always make for the nearest water, in which no land animal has the least chance with them*" (Townsend, 1911). Large lakes with many islands, such as Lake Nipigon, Trout Lake, and Lac St Joseph in Ontario should be listed as critical habitat. The small islands in these lakes are absolutely safe; wolves are not prepared to swim between islands that don't have moose, only to have the females and calves that are living near the shore of the island swim to another island (Bergerud *et al.*, 1990). More lakes further north will have to be added to the list as temperatures advance and these lakes are free of ice in May/June. For montane animals, the critical habitat would commonly be the high alpine ridges used to space away from moose and wolves below, but these alpine ridges are not nearly as safe as shoreline retreats.

Old growth forest and lichens stands are not critical habitat. The southern limit of caribou is not based on lichen abundance. In the last glacial period, as the Laurentide Ice sheet retracted 12 000 to 10 000 ybp the caribou spread north from the Appalachian Mountains, where they had persisted during the ice age, moving into mixed conifer and hardwoods and jack pine/spruce forests. They did not generally inhabit either taiga or tundra lichen ranges; only 5 of

Table 1. Comparison of moose densities in Ontario 1974-85 *vs*. 2001 and management goals for Ontario Wildlife Management Units as projected in 2001 that still have a continuous caribou distribution (Fig. 3). Files provided the author from OMNR files, Thunder Bay office in 2006[5].

WMU Area		Moose per km^2			% change estimated	Wolves per 1000 km^2	
No.	km^2 x 1000	74-85	01	Goal	2001 to Goal	2001	Goal[1]
1A	78.9)			0.04	0	5.3	5.3
1C	93.0)	0.003	0.08	0.08	0	6.4	6.4
1D	111.3)			0.004	0	4.3	4.3
2[2]	7.0	0.08	0.13	0.25	92	**7.8**	**11.0**[3]
16A	14.3)		0.04	0.06	50	5.3	5.9
16B	8.4)	0.05	0.11	0.15	36	**7.2**	**8.3**
16C[4]	9.8)		0.10	0.16	60	7	**8.6**
17	27.8	0.05	0.04	0.06	50	5.3	5.9
18A	7.8)		0.11	0.17	54	**7.3**	**8.9**
18B	11.1)	0.07	0.03	0.04	33	5.1	5.3
19	9.6)		0.18	0.19	6	**9.1**	**9.4**
24	18.6	0.07	0.11	0.13	18	**7.2**	**7.8**
25	38.6	0.01	0.04	0.05	25	5.3	5.6
26	25.9	0.02	0.05	0.05	0	5.6	5.6

[1] calculated from: $Y=4.239+27.217x$, wolf densities regressed on moose densities (see Bergerud *et al*. this conference, Fig. 10), this equation is conservative since the caribou biomass is not included.

[2] Includes Woodland Caribou Provincial Park.

[3] **In bold:** wolf densities that will cause the decline of caribou.

[4] Includes a portion of Wabakimi Provincial Park.

[5] In February 2007, OMNR supplied me with their latest targets (2003). These targets (goals) were essentially the same as their goals in 2001 except moose had been censused in WMU 1C at 3369 (0.04/km^2) rather than rough estimate in 2001 of 7000 animals. The philosophy remained unchanged 2001 to 2003 of setting targets based on maximum moose projections without consideration of the impact that more moose would have wolf numbers and the negative spin-off to caribou.

21 fossil locations were in the taiga/tundra (Bergerud & Luttich, 2003). In the late Holocene, 4000 to 500 ybp, they were south again residing in forests of pine and northern hardwoods (Faunmap, 1994, Bergerud & Luttich, 2003). The southern boundary was not old growth forests and not lichen dependent but determined by the abundance of spermatophytic species that supported deer, moose, and elk populations. These cervids, inturn, sustain a suite of predators: mountain lions (*Felis concolor*), wolves, and bears that were too abundant for caribou to persist (top-down not bottom-up). **The diversity of mammal species set the southern limit for the distribution of caribou and not the abundance of lichens**.

We have wasted so much time measuring lichen abundance for a bottom-up answer to the low caribou numbers. I overlooked lynx predation in Newfoundland for years (Bergerud, 1971) measuring lichens, because I had been taught that predation did not regulation population numbers (Errington, 1946; Errington, 1967).

Caribou are constantly switching winter lichen ranges. They adapted long ago to rotating their range use from overgrazing and trampling, from the loss of habitat from forest fires and the changing snow cover. Further, they can maintain their numbers and physical condition foraging on earlier lichen successions, evergreen shrubs, ground hemlock, horsetail, winter greens, etc. (Bergerud & Nolan, 1970; Bergerud, 1972; Miller, 1976; Bergerud review, 1977; Luick review, 1977). In this study, caribou on the Slate Islands maintained densities greater than 4/km^2 for the past 60+ years without meaningful amounts of terrestrial and few arboreal lichens and inhabiting what was originally a relatively young forest (Cringan, 1956). True, animals on the Slate Islands were at times in poor physical condition in the fall, but that was not due to the quality of the food but due the extreme densities of animals. On the Slate Island, the fecal nitrogen (FN) in three years was 40% higher in May and early June than for five other herds in North America - the mean FN for females on the Slate Islands was 3.38±0.117%, and for males 3.53 ± 0.111%, compared to 1.81 ± 0.079% for females and 2.20 ± 0.067% for males in five other herds (Bergerud, 1996: Table 1 p. 96.)

When the last female is killed by wolves in the lichen-rich undisturbed Pukaskwa National Park -- and time is short as the remaining animals may number less than 10 -- the herd will be gone. The caribou on Michipicoten residing in a **hardwood forest** may be the last relic herd in northeastern Ontario - but the island is now a park and if a wolf reaches the island, would control be allowed? Can we finally reject the closely held view that caribou are wilderness animals that require climax forests and lichens, and saving such habitats is the panacea for persistence? This climax-lichen theory has hindered our understanding of the adaptability of the species for the past 50 years.

The Balance of Nature

When caribou biologists attempt to reduce wolf populations to increase caribou stocks, they are blamed for intruding into the Balance of Nature, a community of animals that has evolved together where the community is greater than the sum of the individual species and there is a system of checks and balances that prevents extinction. Charles Elton, the father of ecology (Elton, 1924; 1927) said *"it is assumed that an undisturbed animal community lives in a certain harmony … the balance of nature. The picture has the advantage of being an intelligible and apparently logical result of natural selection in producing the best possible world for each species. It has the disadvantage of being untrue"* (Connell & Sousa (1983) quoting Elton). Connell & Sousa (1983), in their extensive review of the stability and persistence of a wide variety of animal populations from protozoans to rodents, concluded that the evidence in the past 50 years upholds Elton's description. The Balance of Nature is not a scientific hypothesis, since there is no disproof that the advocates will accept. It is a closely held idea that is not testable. The Balance of Nature advocates, as a last argument blame imbalances between predator and prey as an artifact of man's intrusion.

The most widely quoted balance of nature example in wildlife management is the interaction of wolves and moose on Isle Royale, Michigan (Mech, 1966). The moose have not gone extinct and there was evidence of territorial self regulation in the wolf population. However, Isle Royale is an experimentally unnatural area, as is the Slate Islands. The artifacts of that study were that there was little opportunity for egress-ingress of the wolves, the major pathway by which they adjust their numbers, and that there were no bears on the island, a major predator of moose. Van Ballenberghe *et al.* (1975) challenged the belief of self regulation by showing that wolf numbers were based on prey biomass not territorial exclusion. Keith (1983) and then Fuller (1989) showed that in an open system, wolves are constantly dispersing, and we now calculate wolf numbers on the basis of prey biomass equations.

In the period 1959 to 1974, there appeared to be an equilibrium between wolves and moose on Isle Royale (Mech, 1966, Peterson, 1977). But since that time, the equilibrium has been lost. Wolves developed canine parvovirus (CPV) in 1980 or 1981 and crashed (Peterson *et al.*, 1998) and in the 1990s, there was subsequently a doubling in moose number until 1995 (see Fig. 1 in Wilmers *et al.*, 2006). Pimm (1991), in a penetrating discussion of the Balance of Nature, argues that assumed equilibriums between predator and prey commonly disappear in long term investigations. In the 1990s, McLaren & Peterson (1994) documented that the growth rings of balsam fir (*Abies balsamea)* on Isle Royale had depressed growth in periods when wolves were rare - these authors postulated a wolf-induced trophic cascade (wolves>moose>fir)- top-down.

The concept that wolves and caribou evolved together and therefore will continue to coexist is not valid. The Faunmap's (1994) tabulation of mammalian fossils in the United States south of Canada from 40 000 to 10 000 ybp shows 22 fossil locations of wolves west of 98W lat. and only three east where the woodland caribou persisted during the Wisconsin ice age. From 30 000 to 10 000 ybp, the eastern woodland caribou persisted only in the Appalachian Mountains (Bergerud & Luttich 2003, and in press). Other common species of mammals in the Appalachians during these years were the Jefferson ground sloth (*Megalonyx Jeffersonii* (4 records), tapirs, *Tapirus* (9 records), *Mylohyus,* the long-nosed peccary (11 records), and *Platygonus compressus,* the flathead peccary (7 fossils). The most common predator was the black bear (6 records). No wolf fossils from 40 000 to 10 000 have been found in those mountains. The fossil record besides the species listed includes armadillos, prairie ground squirrels, skunks, and jaguars (Churcher *et al.*, 1989; Faunmap, 1994). This was not the boreal community where caribou and wolves interact today and are supposed to have evolved their balance of nature.

The Herculean study of the fossil mammal fauna of the Late Quaternary at 2945 sites in the United States (Faunmap, 1994) was published in *Science* by 20 distinguished investigators (Graham *et al.*, 1996). They summarized that the record of fossil mammals supported the Gleasonian community model rather than the Clementsian community model that stresses competitive interaction. The Gleasonian model assumes that species respond to environmental changes in accordance with individual tolerance with varying rates of range shift. These author's concluded (page

1601) "*modern community patterns emerged only in the last few thousand years and many late Pleistocene communities do not have modern analogs.*" Hence, each species through individual selection evolves its own distinct behavior/habitat strategies to persist, but they are not guaranteed to avoid extinction. Each species walks its own road down through time - there is no balance of nature.

Adaptive management of wolves

Will we leave the fate of woodland caribou to mitigation of habitat/disturbance questions, or will we reduce the natural mortality rate of caribou by wolf reductions? Mitigation endeavors in lieu of wolf reduction will not succeed if the cause of the declining population is too many wolves. Mitigation recommendations commonly call for reducing road net works/seismic lines, access for wolves, reducing and or redistributing logging, oil development, and etcetera. These problems didn't exist in Pukaskwa National Park. Furthermore, the PNP population had satisfactory summer survival. Yet, those caribou are facing extinction from predation even though in the 1990s only two wolf packs existed relatively close to the caribou along the coast.

Nor should we blame human development for the supposed advantages they have given wolves. Caribou are better able in coping with development than wolves. The Central Arctic Herd grew from 5000 in 1977 to 27 000 in 1999 as the oil field developed (Russell *et al.* eds., 2002). The adjacent controversial Porcupine Herd calving in a wildness wildlife refuge where there has been no economic development grew from ≈ 100 000 to 178 000 by 1989 and then declined to 123 000 by 2001, experiencing heavy predation of young of the year (Griffith, 2002). We live in the age of the industrial revolution with its footprint everywhere and the depletion of the earth's resources. Intrusion into the predator-prey system cannot be avoided if we want prey persistence and diversity which will also benefit the predators. Mitigation without predator reductions will not work. Wolves are a highly intelligent species with prey switching part of its *modus operandi*; too many moose equals too many wolves and too few caribou.

Caribou/predator management will work. The woodland herds in the Yukon are the most successfully managed in North America. They have been increasing as a result of intense management (COSEWIC, 2002). The caribou herds are counted reasonably accurately and recruitment is measured annually. Moose recruitment and numbers are constantly monitored. Wolves are censused and radio tracked. In recent years, some wolf populations have been both reduced and fertility control experimented with (Hayes *et al.*, 2003). At this conference, Farnell *et al.* and Adams *et al.* reported on a management endeavor where pregnant females were captured and held in an exclosure in which predators were excluded until their calves were three weeks of age. Surveys in the fall showed 74-76% of the former captive calves still alive compared to a survival of calves born in the wild exposed to predation of 13 to 32%. This is the ultimate experiment that should convince even the most die-hard skeptic on the huge loss of calves of the montane ecotype in their first summer to predators (Bergerud *et al.*, 1984). The monitoring of caribou herds in British Columbia and Alberta has improved in recent years and they are moving towards management. Elsewhere in Canada, there are no plans to manage wolves. Most jurisdictions do not even monitor caribou numbers and recruitment (Labrador is an exception).

In Ontario, home to the Slate Islands and the PNP populations, there is no caribou management. The Ontario Ministry of Natural Resources does not count caribou herds or measure recruitment, nor does it census or radio track wolves. The Department's ungulate management program is directed at increasing moose. Woodland Caribou Park and Wabakmi Provincial Park are the southern corner-stones of the continuous distribution of caribou in Ontario, yet the goal of the biologists in 2001 for Wildlife Management Units (WMU 2 and WMU 16c) that contain these parks established for caribou, is to increase the moose populations by 92% and 60% (Table 1), see Fig. 3. Their moose strategy, if successful, will eliminate the caribou. Moose densities of 0.25 and 0.16/km^2 are far too high. The goal should be to *decrease* these moose populations so the caribou can increase. This technique is now being tested in British Columbia (D. Seip, *pers. comm.*). The behaviour of caribou in both Woodland Caribou Park and Wabakmi Park is to calve on islands (Simkin, 1965; Cumming & Beange, 1987; Bergerud *et al.*, 1990; Racey & Armstrong, 1998). The island calving strategy will continue to provide satisfactory summer calf survival, but after the lakes freeze, wolves will commonly switch from moose to caribou when snow depths increase. Global warming will increase the duration of water for escape in the spring but in the winter, ice will be reduced and slush will reduce escape advantages. This predation will lead to further fragmentation of the continuous distribution in Ontario.

Darby & Duquette (1986) listed 9 mitigating points to maintain Ontario caribou (pages 91-92). Point 8 "*implement predator control if wolf predation rates on caribou increase. This is likely to occur if moose or deer densities increase following cutting.*" Now global warming is increasing the spread of these cervid species faster than 20 years ago. Point 9 stated "*discourage moose and deer populations from increasing in or adjacent to caribou*

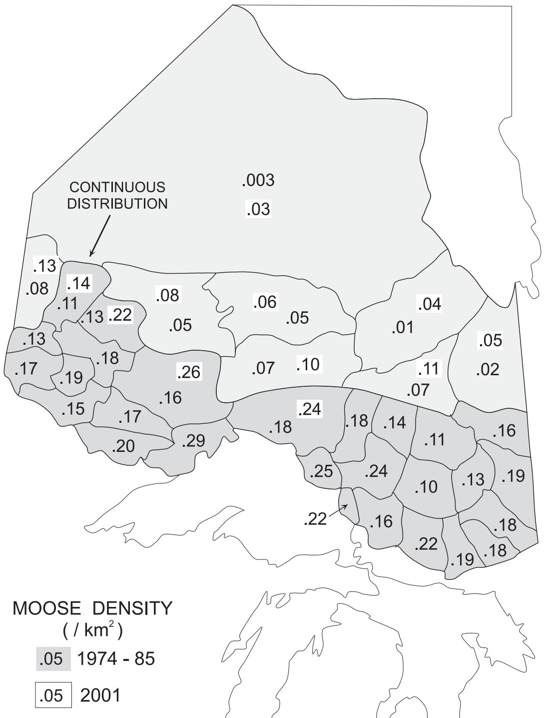

Fig. 3. The line of continuous caribou in 1985 (Darby & Duquette, 1986) bisected the boreal coniferous forest (Fig. 2) but also bisected the moose range with moose densities greater than 0.10/km² south of the discontinues distribution of caribou and the continuous distribution north of the line. Only relic herds are still found south of the line that have special escape habitat such as PNP with the Lake Superior coast and the herds on islands in Lake Superior, i.e. Slate Islands, Pic Island and Michipicoten Island (Bergerud, 1989). The moose have increased north of the line between 1985 and 2001 and wolves are predicted to exceed 6.5/km² causing herds to decline in WMUs that now have more than 0.10 moose/km². Densities are based on OMNR statistics from the Thunder Bay office provided to me in 1989 and in 2006.

range. Application of herbicides to cutovers may do this while encouraging conifer regeneration." These comments were made 20 years ago and still no one is listening, nor do many care. In Ontario, environmental groups will probably never support wolf management and instead will argue for the mitigation of disturbance factors. This argument will not save the caribou. There is no hunter clientele to argue for management, as is the case for elk in Yellowstone Park. Nor will the creation of more parks be helpful, which is the World Wildlife Fund's solution to the caribou conservation conundrum (Petersen *et al*., 1998). The Park solution means wolves cannot be managed and the rationale is based on the faulty bottom-up premise that caribou require old growth habitat with undisturbed lichens. The phenomenal success of the caribou on Pic Island (Ferguson, 1982; Ferguson *et al*., 1988), the Slate Islands and Michipicoten Island, and their demise in the lichen rich wilderness of Pukaskwa National Park give a different insight. There is no caribou conservation conundrum, only a lack of political will.

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George's Island, Labrador - A high-density predator-free refuge for a woodland caribou subpopulation?

Rebecca A. Jeffery[1], **Robert D. Otto**[2], **& Frank R. Phillips**[3]

[1] Government of Newfoundland and Labrador, Department of Environment and Conservation, Wildlife Division, P.O. Box 3014, Stn. B, Goose Bay, NL, A0P 1E0, Canada (corresponding author: rebeccajeffery@hvgb.net).
[2] Government of Newfoundland and Labrador, Department of Environment and Conservation, Wildlife Division, 117 Riverside Drive, P. O. Box 2007 Corner Brook, NL, A2H 7S1, Canada.
[3] Government of Newfoundland and Labrador, Department of Natural Resources, Forestry Resources, P.O. Box 429, Northwest River, NL, A0P 1B0, Canada.

Abstract: The movement patterns and demographic parameters were measured for caribou (*Rangifer tarandus caribou*) on George's Island (Labrador, Canada) to determine if the population is separate from the Mealy Mountain Caribou Herd. Movements between George's Island caribou and nearby Mealy Mountain caribou were examined through satellite telemetry (April 2005 to April 2006). Demographic information was collected through aerial classification surveys. The predator-free island is currently maintaining a density of 22.5-26.5 caribou/km^2. Female survival appears high and the recruitment rate in late fall-early spring was 19.0-29.2% calves. Mainland caribou moved very little throughout the year, travelling no more than 53.7 km on average from their initial collaring locations. Also, satellite data indicated no mixing between animals on George's Island and the mainland. The elevated caribou density and high proportion of calves suggest that George's Island could at times be acting as a predator-free recruitment area and that George's Island may be a subpopulation from which animals disperse to the mainland.

Key words: high density, island population, predator-free, *Rangifer tarandus caribou*, subpopulation, ungulate population.

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Introduction

The objective of this study was to better understand George's Island caribou and their relationship to the mainland caribou nearby. At the onset of the study, it was unclear if George's Island caribou were a separate population from the mainland caribou. To better understand their relationship and movements, five caribou on George's Island and a number on the mainland were outfitted with satellite collars (Jeffery, 2005). For the purposes of this paper, a population is composed of a number of smaller groups that are more homogenous within than between. These smaller groups, which may overlap, are considered subpopulations of the greater population.

George's Island, Labrador, Canada, is located at the mouth of Groswater Bay, in the Atlantic Ocean. Twelve km^2 in area and 9 km from shore, George's Island currently supports one of the highest caribou densities ever recorded. Other reports have found that high density caribou populations range from 7-8.5 caribou/km^2 (Slate Islands, Lake Superior, ON) (pers. comm. A. Bergerud) to 18.1 on St. Matthew Island, AK, (Klein, 1968), 19.1 (St. Paul Island, AK) (calculated from Scheffer, 1951), and 23 (South Georgia Island, UK) (Leader-Williams, 1988). Many populations that increase rapidly have a subsequent decline which is frequently accepted to be density-dependent (Gunn *et al.*, 2003) even though stochastic weather events may be the limiting factor (Gunn, 2003; Gunn *et al.*, 2003; Miller *et al.*, 2005b).

When and how caribou colonized George's Island is uncertain. Fishers using the area between the early 1970s and mid-1980s report no caribou on the island (pers. comm. Gene Mesher and Ben Rowe). However, caribou were reported on the island as part of a raptor

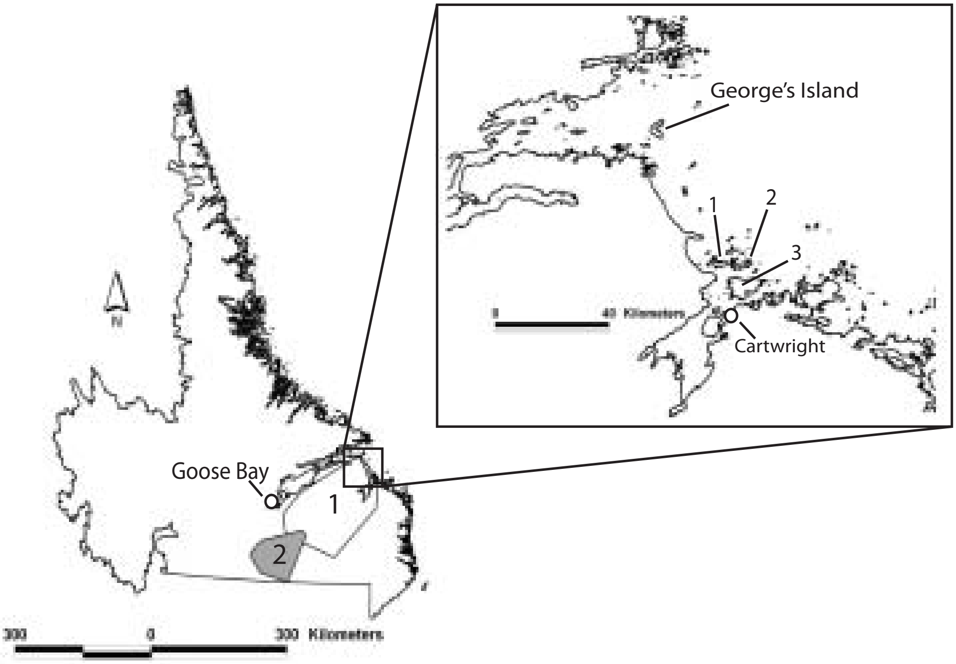

Fig. 1 Map of Labrador, Canada showing ranges of two woodland caribou subpopulations (*Rangifer tarandus caribou*): (1) Mealy Mountain caribou range (32 536 km^2) and (2) Joir River caribou range (7057 km^2). Inset shows George's Island and Horsechops (1), Newfoundland (2), and Huntington (3) Islands.

survey in July 1985 (pers. comm. Joe Brazil). Caribou were next documented in 2002 during a waterfowl survey (pers. comm. Greg Robertson), and were again observed by one of the authors in 2003 and 2004. As caribou have been present on George's Island since 1985, periodic movements to the mainland may have occurred without being observed. Caribou in the Canadian Arctic Archipelago migrate between islands, possibly to reduce grazing pressure on individual islands by accessing other ranges (Miller *et al.,* 2005a).

The caribou on George's Island are adjacent to the Mealy Mountain Woodland Caribou Herd. Protected since being listed as 'threatened' in 2002 (COSEWIC, 2002), the Mealy Mountain herd was most recently estimated at 2106 ± 1341 (Jeffery, 2005). Recent documentation (Jeffery 2005; 2006; Otto 2002; Schmelzer *et al.*, 2004) has considered the Mealy Mountain caribou a discrete population. In this paper, subpopulation structure of the Mealy Mountain herd will be investigated using movement over space and time, and by determining demographics including % calves and calves:100 females. During April 2005, collars were deployed on Mealy Mountain caribou as well as those in the adjacent Joir River area (Fig. 1). Although no population estimate has been completed, observations in 2005 by authors of this paper indicate a minimum of 48 caribou in the Joir River area. Their affiliation of these animals has not yet been determined. It is not clear if they are part of the larger Mealy Mountain herd, or if they are a separate population.

Material and methods

Study site

George's Island is 12 km^2 in area and 9 km from shore. The vegetation is sparse and stunted. Balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), Labrador tea (*Ledum latifolium*), crowberry (*Empetrum nigrum*), dwarf birch (*Betula pumila*), alder (*Alnus* sp.) and willow (*Salix* sp.) all occur on the island, especially in more sheltered areas. There are also areas of grass and sedges. There are virtually no lichens. Careful examination of the island found no large predators, but there are several other mammals, including arctic fox (*Alopex lagopus*), red fox (*Vulpes vulpes*), and arctic hare (*Lepus arcticus*). Polar bears (*Ursus maritimus)* have also been sighted in the area (pers. comm. Harry Martin) and on one occasion, an otter (*Lutra lutra*) was caught in a net nearby (pers. comm. Ben Rowe). It is likely that meadow voles (*Microtus pennsylvanicus*) and short-tailed weasels (*Mustela erminea*) also exist on the George's Island as they are present on other small islands in the vicinity (pers. comm. Harry Martin).

Collaring
Caribou were live-captured by net gun (Coda Enterprises, Mesa, AZ, USA) from an A-Star 350B helicopter and manually restrained by a crew of four people. Each animal was hooded during the capture and fitted with 2 coloured ear tags (Reyflex, Ketchum Manufacturing Inc., Brockville, ON, Canada) and a satellite collar (Telonics A-3300, Telonics Inc., Mesa, AZ, USA). Captures, including chase time, combined with handling efforts ranged from 20 to 40 minutes. Five female caribou were collared on George's Island (Fig. 1) on April 22, 2005. Part of a larger collaring effort, 18 caribou were collared on the mainland between April 19-22, 2005 (13 Mealy Mountain caribou, 5 Joir River caribou) (Jeffery, 2005).

Classification and counts
Minimum counts and classifications were completed in later winter 2005, fall 2005, and late winter 2006. Individuals were classified by age (adult or calf) and sex (presence or absence of a vulval patch) from helicopter. Recruitment is defined as the percentage of calves in the population.

Analysis
Satellite collars (Platform Terminal Transmitters or PTTs) were set to a 4-day transmission cycle (Service Argos, Landover, Maryland, USA). Argos rates the accuracy of each location on a scale from 3 to -2 indicating greatest to least accuracy. All locations with a location class less than 1 were discarded due to their inherent imprecision (Rodgers, 2001). The best and most recent location from each reporting cycle was used in the analysis.

The a) current displacement ± standard error (distance between the most recent location and capture location), b) maximum displacement ± standard error (farthest distance moved from capture location), and c) mean daily movement rate ± standard error for the year were calculated in Excel (Microsoft Corporation, 2002) for each caribou to identify differences in movement patterns between George's Island and mainland caribou. Home ranges were generated in Arcview GIS 3.2a (Environmental Systems Research Institute, Inc.) with the 'Animal Movement' extension (Hooge & Eichenlaub, 1998).

Results

At the time of submission, no collared animals have moved off George's Island since deployment in 2005. Similarly, no collared mainland caribou have crossed onto George's Island although they have travelled to other islands (Fig. 1). Mainland caribou had mean daily movement rate of 1.3 km ± 0.1 (0.7-2.1) and in the year since capture, the mean maximum displacement was 53.7 km ± 5.1 (38.1-68.2). As of April 2006, mean current displacement for mainland caribou was 18.5 km ± 3.9 (0.7-56.6).

Demographic parameters were determined for the mainland Mealy Mountain and George's Island caribou (Tables 1 and 2). Minimum counts indicated that the density on George's Island was at least 22.5 caribou/km^2 and recruitment was healthy with a high percent calves observed in all surveys (19.0-29.2) (Table 1). Based on the March-April 2006 data, George's Island has a considerably higher male:100F ratio than the other two groups. Examination of individual home ranges indicates that there is a limited

Table 1. Population dynamics for woodland caribou (*Rangifer tarandus caribou*) on George's Island, Labrador, Canada.

Date	Minimum count	Density (caribou/km^2)	% calves	Calves:100F
March 22, 2005	270	22.5	26.7	
December 19, 2005	318	26.5	29.2	55.3
April 18, 2006	274	22.8	19.0	43.7

Note: Per cent calves is the proportion of calves in the minimum count. F = females.

Table 2. Population dynamics for three groups of woodland caribou (*Rangifer tarandus caribou*) in the Mealy Mountain area, Labrador, Canada. March-April, 2006.

Group	Total	% calves	Calves:100F	Males:100F
George's Island	274	19.0	43.7	86.6
Mealy Mountain	625	17.8	34.4	59.1
Joir River	60	23.3	46.7	53.3

Note: Per cent calves is the proportion of calves in the total number of caribou. F = females.

amount of overlap between mainland animals, i.e. Joir River and Mealy Mountain caribou. Additionally, no collared caribou have moved off George's Island. Based on these findings, these groups should be considered subpopulations.

Discussion

The main objective of this study was to determine if the George's Island caribou are discrete from the mainland Mealy Mountain caribou. To date, no collared caribou have moved onto the island or off the island onto the mainland. There has been movement between the mainland and other islands in the same area vicinity. Horsechops, Newfoundland and Huntington Islands are 2.5, 4.5 and 6.5 km from shore, respectively. Satellite collar data confirms at least 1 excursion to each island and movement between Newfoundland and Huntington Islands. Approximately 70 Mealy Mountain caribou were observed on Huntington Island during April 2006, and extensive caribou sign is frequently observed on all three islands. Additionally, local knowledge confirms that land fast ice usually forms between these islands and the mainland during late winter-early spring (pers. comm. Harry Martin). George's Island, however, is not know to be regularly connected to the mainland by ice because of the greater distance from shore, and the deep water and strong current at the mouth of Lake Melville (pers. comm. Harry Martin and Derek Pottle). Consequently, conditions suitable for movement to and from the mainland may occur infrequently, i.e. a combination of a slack tide, extreme cold weather and near 100% loose ice cover such that an ice bridge may be temporarily solidified. Such conditions did exist in March 1984 when a temporary ice bridge formed that allowed snowmobile travel across Groswater Bay approximately 65 km west of George's Island (pers. comm. Harry Martin and Frank Phillips). Perhaps similar conditions existed between George's Island and the mainland during the same period as the first recorded caribou observations occurred following this event. Of interest, a group of small islands (about 0.3 km^2 total area) exists midway between George's Island and shore but showed no evidence of caribou use when examined in April 2006.

Mainland caribou moved very little; for example, their average daily movement was only 1.3 km/day, and they have stayed within 53.7 km of their initial locations. Current displacement was on average only 18.5 km from where they had been collared. Only a few caribou exhibited larger movements, wintering in coastal areas and moving inland during the calving season. Examination of individual home range placement indicated that Mealy Mountain and Joir River caribou are subpopulations of the same population. The larger population, however, seems to be composed of a number of subpopulations which, based on satellite collar locations, appear to mix infrequently. What little mixing there is occurs between groups at the margins of the home range and those in the centre. Minimal mixing between groups and areas may be part of the reason there has been no movement recorded to and from George's Island.

Caribou movement between islands has been previously observed. In the Canadian Arctic Archipelago, caribou make seasonal migrations from 30-84 km across sea ice between islands (Miller *et al.,* 2005a). Movements between islands are not limited by the presence of sea-ice as Peary caribou have been shown to swim in the open ocean between the Queen Elizabeth Islands for 1.6-2.5 km (Miller, 1995). This indicates that George's Island caribou may not be limited by a lack of land fast sea ice. The mainland adjacent to George's Island has the highest caribou density within the entire Mealy Mountain range (Jeffery 2005; 2006; Otto 2002). This could indicate that some animals are in fact leaving George's Island. Movements of George's Island caribou are unknown prior to collaring in 2005. Since their arrival to the island, there may have been movements to the mainland as the island's resources may have been depleted without such an exchange (Miller *et al.,* 2005a). Furthermore, satellite data captures the movement of adult female caribou, but not of males and yearlings. Collaring males and yearlings would provide assessment of the degree of dispersal to the mainland. Such additional data would determine if George's Island is acting as a predator-free source for the Mealy Mountain caribou population (Pulliam, 1988).

George's Island has 22.5-26.5 caribou/km^2, a higher density than other published accounts. Densities in predator-free herds are often high (18.1-23 caribou/km^2) (Klein, 1968; Leader-Willams, 1988), although exceptions do exist (Heard & Ouellet, 1994; Ouellet *et al*., 1996; Tyler, 1987). The population demographics on George's Island indicate very good calf recruitment as the calf percentage (29.2) almost reached 'the intrinsic rate-of-increase' in December 2005 (Bergerud, 1980). Other predator-free herds have experienced similar or greater proportions of calves, i.e. South Georgia Island - 25.5 to 60.6 calves:100 females (Leader-Williams, 1980); Coats Island - 93 ± 1.3:100 (Heard & Ouellet, 1994). As predators may be the most important factor contributing to calf mortality (Bergerud, 1980; Layne *et al.* 1995; Whitten *et al.* 1992), their absence may be the primary factor maintaining the high calf proportion on George's Island. Furthermore, adult mortality appears minimal. Surveys of the island, both aerially and by foot, have returned only one carcass (April 2006) and all females have survived since being collared. High adult survival combined with high recruitment is driving the caribou density on George's Island. Although unlikely, there may be a risk of polar bear predation at times. Polar bears are frequently observed along coastal Labrador and will occasionally travel much farther south than George's Island (Brazil & Goudie, 2006; Stirling and Parkinson, 2006). A nuisance polar bear was moved to the island in 2003, before the caribou population was understood.

Although there have been very few recorded mortalities on George's Island, the April 2006 survey revealed a small number of animals in very poor condition. Several animals stumbled when moving away from the helicopter and appeared weak, listless, and dull, when subjectively compared to mainland animals surveyed at the same time. Bergerud (pers. comm.) found that when nutritionally stressed, caribou on the Slate Islands became weak and emaciated. Although calf proportions have remained high on George's Island, indicating sufficient body condition for females to produce and rear young, the weak caribou observed could be a sign that the population has reached its limit. Although several studies have cited density-dependent food availability as the factor limiting reindeer and caribou herds (Klein, 1968; Leader-Williams, 1980; Skogland, 1985; Ouellet *et al.* 1996), research also indicates that severe winter weather conditions can limit food availability through snow depth, icing or stochastic events such as storms, forcing caribou to compete for resources in the areas that remain open (Adamczewski *et al.*, 1988; Solberg *et al.,* 2001). Recent work challenges Klein's explanation that the St. Matthew Island reindeer crash was density-dependent and suggests instead that eruptive populations are partially or wholly limited by stochastic weather events (Gunn, 2003; Gunn *et al.*, 2003; Miller *et al.*, 2005b). George's Island is extremely exposed to the Atlantic Ocean. Should there be a particularly severe weather event George's Island caribou would certainly be affected.

Mainland Mealy Mountain caribou can be divided into subpopulations, such as the Joir River subpopulation, based on movement and demographics. The subpopulations show varying degrees of overlap. In this context, George's Island would be considered a subpopulation as no mixing has been observed to date. However, the highest density of Mealy Mountain caribou occur directly adjacent to George's Island (Jeffery, 2005; 2006; Otto 2002) supporting the possibility that there may be some movement from George's Island to the mainland. There are still many unanswered questions about the caribou on George's Island. Without historical data, we are unable to ascertain exactly how long the population has been on the island and what its rate of growth has been. A continued long term study, including satellite tracking of both George's Island and mainland animals, and further demographic surveys, is required to better define the relationship between these groups.

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Woodland caribou persistence and extirpation in relic populations on Lake Superior

Arthur T. Bergerud[1], W. J. Dalton[2], H. Butler[1], L. Camps[3], & R. Ferguson[4]

[1] 1233 Isabella Road, Salt Spring Island, British Columbia, Canada V8K 1T5 (ryder_bergerud@hotmail.com).
[2] Ministry of Natural Resources, 70 Foster Drive, Suite 400 Sault Ste. Marie, Ontario, Canada P6A 6V5 (bill.dalton@ontario.ca).
[3] 220 Hillcrest Drive, Salt Spring Island, British Columbia, Canada V8K 1Y4 (information@naturetrek.ca).
[4] 5275 Leeward Run Drive, Alpharetta, Georgia, U.S.A. 30005 (rferguson@neenahpaper.com).

Extended abstract: The hypothesis was proposed that woodland caribou (*Rangifer tarandus caribou*) in North America had declined due to wolf predation and over-hunting rather than from a shortage of winter lichens (Bergerud, 1974). In 1974, two study areas were selected for testing: for the lichen hypothesis, we selected the Slate Islands in Lake Superior (36 km^2), a closed canopy forest without terrestrial lichens, wolves, bears, or moose; for the predation hypothesis, we selected the nearby Pukaskwa National Park (PNP) where terrestrial lichens, wolves, bears, and moose were present. Both areas were monitored from 1974 to 2003 (30 years).

The living and dead caribou on the Slates were estimated by the 'King census' strip transect (mean length 108±9.3 km, extremes 22-190, total 3026 km) and the Lincoln Index (mean tagged 45±3.6, extremes 15-78). The mean annual population on the Slate Islands based on the strip transects was 262±22 animals (extremes 104-606), or 7.3/km^2 (29 years) and from the Lincoln Index 303±64 (extremes 181-482), or 8.4/km^2 (23 years). These are the highest densities in North America and have persisted at least since 1949 (56 years). Mountain maple (*Acer spicatum*) interacted with caribou density creating a record in its age structure which corroborates persistence at relatively high density from c. 1930. The mean percentage of calves was 14.8±0.34% (20 years) in the fall and 14.1±1.95% (19 years) in late winter. The Slate Islands herd was regulated by the density dependent abundance of summer green foods and fall physical condition rather than density independent arboreal lichen availability and snow depths. Two wolves (1 wolf/150 caribou) crossed to the islands in 1993-94 and reduced two calf cohorts (3 and 4.9 per cent calves) while female adult survival declined from a mean of 82% to 71% and the population declined ≈100 animals.

In PNP, caribou/moose/wolf populations were estimated by aerial surveys (in some years assisted by telemetry). The caribou population estimates ranged from 31 in 1979 to 9 in 2003 ($Y=1267 - 0.628X$, $r=-0.783$, $n=21$, $P<0.01$) and extirpation is forecast in 2018. Animals lived within 3 km of Lake Superior (Bergerud, 1985) with an original density of 0.06/km^2, similar to many other woodland herds coexisting with wolves (Bergerud, 1992), and 100 times less than the density found on the Slate Islands. The mean moose population was 0.25±0.016/km^2 and the wolf population averaged 8.5±0.65/1000 km^2. Late winter calf percentages in PNP averaged 16.2±1.89 (25 years); the population was gradually reduced by winter wolf predation (Bergerud, 1989; 1996). The refuge habitat available is apparently insufficient for persistence in an area where the continuous distribution of woodland caribou is fragmented due to moose exceeding 0.10/km^2 and thereby supporting wolf densities ≥6.5/1000 km^2.

A second experimental study was to introduce Slate Island caribou to areas with and without wolves. A release to Bowman Island, where wolves and moose were present, failed due to predation. Bowman Island is adjacent to St. Ignace Island where caribou had persisted into the late 1940s. A second release in 1989 to the mainland in Lake Superior Provincial Park of 39 animals has persisted (<10 animals) because the animals utilize off-shore islands but numbers are also declining. A third release to Montréal Island in 1984 doubled in numbers (up to 20 animals) until Lake Superior froze in 1994 and wolves reached the island. A fourth release was to Michipicoten Island (188 km^2) in 1982 where wolves were absent and few lichens were available. This herd increased at $\lambda = 1.18$ (8 to ±200, 160 seen 2001) in 19 years. This was the island envisioned for the crucial test of the lichen/predation hypotheses (Bergerud, 1974: p.769).

These studies strongly support the idea that ecosystems without predators are limited bottom–up by food and those with wolves top-down by predation; however the proposed crucial test which has been initiated on Michipicoten Island remains to be completed and there is a limited window of opportunity for unequivocal results.

Key words: alternate prey, Canada, escape habitat, forage abundance, habitat, island biogeography, moose, mountain maple, Ontario, optimal foraging, population regulation, predation, Pukaskwa National Park, refuge habitat, Slate Islands Provincial Park, wolf.

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Introduction

Woodland caribou (*Rangifer tarandus caribou*) have recently been assessed (COSEWIC, 2002) as threatened in their Canadian range but there has been an awareness of range reduction for decades prior to this official designation (Cringan, 1956). Caribou conservation in Ontario is highly controversial and extirpation along the receding southern boundary of range remains topical (Schaefer, 2003). The hypothesis was proposed that caribou declined in North America following European settlement from wolf predation and overhunting (Bergerud, 1974) rather than the widely held view that destruction of winter lichen supplies by fires and over-grazing was the primary cause (Leopold & Darling, 1953; Edwards, 1954; Cringan, 1957; Scotter, 1964; 1967; Klein, 1970). Many biologists emphatically rejected the wolf predation hypothesis. Hence in 1974, we selected two study areas for testing the demographic/food parameters of the hypotheses.

For the lichen hypothesis, we selected the Slate Islands in Lake Superior. On these islands Cringan (1956, 1957) had studied the forage requirements of caribou in 1949. These islands supported a closed canopy forest of birch (*Betula paperifera*) and balsam fir (*Abies balsamea*); terrestrial lichens were nearly absent. The islands had been logged in the 1930s and a major fire had burned the western one-third of the largest island (Patterson) in 1902. The mammal fauna was limited to 11 species with the red fox (*Vulpes vulpes*) the only terrestrial predator of any potential consequence for woodland caribou.

For the control study, we secured a contract to investigate the caribou in Pukaskwa National Park (PNP). The park had a normal compliment of the boreal mammals including moose (*Alces alces),* wolves (*Canis lupus)*, and bears (*Ursus americanus*). We conducted studies at PNP only from 1974 to 1979. In later years the Park staff monitored caribou and moose numbers and measured the recruitment of both species. In PNP about a third of the total area (1878 km^2) had been burned in 1931 and 1936 and extensive stands of terrestrial lichens existed in open grown Jack Pine forest (*Pinus banksiana*). In addition, terrestrial lichens were available along the coast on raised bedrock formations ("balds") and arboreal lichens were present on the older conifers on the humid coast. Both areas were originally thought be populated by about 25 caribou in 1974 (Euler *et al.*, 1976; Pukaskwa National Park files - CWS 1972 faunal survey Bruce C. Johnson saw 12 caribou).

This paper provides data on the numbers of caribou in both populations from 1974 to 2003 (30 years). In addition to empirical data to distinguish between the two hypothesis (predation vs. winter lichens), experimental evidence was needed. Hempel (1966: p. 25) described a *crucial test* to decide between two rival hypothesis as "a decision between the two may be reached if some test outcome can be specified for which H_1 and H_2 predict conflicting outcomes." Bergerud (1974: p. 769) purposed the test of introducing caribou to an island with minimal lichen supplies and later, if the caribou increased, while food supplies were still adequate, introduce wolves; if the herd increases in the absence of wolves H_1 (need lichens) is refuted; if the herd then declines with the wolf introduction H_2 (predation limits) is accepted. In 1982, caribou were introduced to Michipicoten Island southeast of PNP. Michipicoten Island lies in the Great Lakes-St. Lawrence Forest Region (Rowe, 1972), which is primarily a hardwood forest with minimal lichens. Wolves have not been introduced to Michipicoten Island but in the winter of 1993-94 two wolves crossed on the ice to our Slate Island study area at a time when there was adequate forage on the Islands. In other tests of the wolf predation hypothesis versus the lichen hypothesis, caribou from the Slate Islands were introduced to areas where wolves were present (Lake Superior Provincial Park, and Bowman Island adjacent to St. Ignace Island) and where they were absent (Montréal Island).

Pic Island is another site on Lake Superior where an island provides refuge habitat sufficient to anchor a naturally persisting caribou population. Studies carried out on this population (Steve Ferguson, ATB, and RF) have been reported (Ferguson *et al.*, 1988).

Description of the main study areas

Slate Islands

In the northernmost arc of Lake Superior, the Slate Islands are a cluster of 7 significant islands plus islets (36 km^2) in the vicinity of Terrace Bay, Ontario (Butler & Bergerud, 1978). Laying almost 9 km off-shore at the closest point, the archipelago lies within a circle roughly 8 km in diameter believed to be the central uplift of a large impact crater (Grieve & Robertson, 1977). Extensive Lake Superior waters in the bays and channels inside the archipelago take on the aspect of inland lakes in sharp contrast to the behaviour of waves and winds on the lake in general.

In most winters Lake Superior does not have complete ice cover but this was seen twice over the thirty years when ice came early and stayed late. In most years, but not all, an ice bridge formed between the Slate Islands and the mainland shore at some time during the winter. When ice does form it is late by the standard of nearby inland lakes, or by the standard of lakes and ponds on the Slate Islands, due to the large thermal mass of the lake. An ice bridge by mid-January would be early and for it to stay past the first days of March would be late. Such ice bridges are prone to break-up in 24 hours if high winds develop. Given the timing, when ice on Lake Superior is available, it is not well suited to the normal seasonal migration or seasonal dispersal urges of caribou or wolves.

The regression of the start of the growing season 1967 to 1988 was Y =248336-11.182X, r=-0.482, n=22, P<0.05, Y =Julian date regressed against X =year (last 2 digits). The extrapolated date of green-up in 1967 from this regression line is June 11 and 22 years later in 1988 it had advanced to May 14. The weather station at the light house on the island was closed in 1989 and we were unable to calculate the growing season start in later years. None of the corrections we applied to concomitant statistics 1967-1988 from nearby mainland stations provided a useful extrapolate of growing season dates post 1988 for the islands. The Islands are strongly influenced by a maritime climate.

About 80% of the Slate Islands shows evidence of being burned in the late 1800s in one fire event. The western half of Mortimer Island (second largest) was burned earlier, with forest cover composition similar to other areas but advanced in age structure by possibly up to three decades. Two small decadent white birch (*Betula paperifera)* stands, with open canopies and raspberry (*Rubus strigosus*) understory, on Patterson Island (the largest), were aged to 130-150 years old in 1978. The south-western third of Patterson Island (largest) was re-burned in 1902. Horse logging for conifer pulp, evident in 1949 aerial photographs, in the 1930s was widely distributed with a concentration of activity in the lowland areas which may not have been so affected by the forest fires. Logging in the late-1800s is also said to have taken place (Cringan, 1956).

The Slate Islands forest canopy was classified based on standard 1:15 840 B&W provincial aerial photographs from 1949 and 1974. These included: (1) lakes and ponds (there are 30) 3.3% of the area, (2) meadow (sedge/grass areas) <1% trace in both 1949 and 1974, (3) alder 5.1% 1949 and 1.9% 1974, (4) birch overstory 38.0% in 1949 and decreasing to 14.0% 1974 (5) birch-fir (*Abies balsamea)* (birch dominant) 36.1% 1949 increasing to 48.5% 1974 (6) fir-birch (fir dominant) 8.7% in 1949 and 21.1% in 1974, (7) lichen-bedrock (supporting *Cladonia* lichens) 1.3% in 1949 and 1.4% 1974 (8) conifer-feathermoss 3.6% 1949 and 5.8% 1974, (mostly fir dominant and rarely pure black spruce (*Picea mariana*)) (9) conifer-sphagnum 3.9% 1949 and still 3.9% in 1974 (black spruce dominant but with a surprising number of overstory fir occurring, sometimes white cedar (*Thuja occidentalis*) dominant). The well-drained upland sites were notable for the presence of scattered large white spruce (*Picea glauca*) and they highlighted the skyline. Large white cedar also occurred on upland sites which were very steep and very fresh. Arboreal lichens were present on all tree species with variation by tree species and branch age in lichen species assemblage and quantity supported.

The herbivores competing with caribou on the Slate Islands for terrestrial forage were beaver (*Castor canadensis*), and snowshoe hares (*Lepus americanus*). Beaver impounded water for lodge building opportunities and access to forage in highly unlikely drainages, in addition to normal dam building and site occupation, and so achieved foraging access more widely than expected for similar habitats with predators present. Beaver accelerate succession to conifer overstory after canopy disturbances and deciduous species regeneration in proximity to waters they occupy, and on the Slate Islands this influence was more extensive than normal.

Pukaskwa National Park

Pukaskwa National Park occupies 1878 km^2 of the Central Boreal Uplands (Poitevin, 1989) and stretches for about 80 km along the north shore of Lake Superior, where due to a prominent jog southward the shoreline is oriented north-south in the park. The park has rugged terrain and many rivers; the largest happen to be on the northern and southern boundaries: respectively the White River and Pukaskwa River. The Swallow and Cascade Rivers are located midway down the shore and along with the Pukaskwa are travel routes for wolves to reach the Lake Superior shore.

Approximately 25% of PNP was burned in 1931 and 1936 and part of the 1936 burn regenerated with an extensive *Cladonia* cryptogam near the shore at Oiseau Bay. Extensive stands of terrestrial lichens existed in open grown jack pine forest (*Pinus banksiana*). In addition, terrestrial lichens were available along the Lake Superior near-shore on bedrock outcrops and arboreal lichens were present in the conifers. PNP, in contrast to the Slate Islands, has both an abundance of arboreal lichens within reach of the animals and the extensive lichens in old burns and on bedrock outcrops. Although the effect has not been quantified, it is presumed that the proximity to maritime climatic effects from Lake Superior, at both PNP and the Slate Islands, is favourable for arboreal lichen growth.

In the early years of our research, the caribou occupied the shorelands south from the Willow River with a concentration using the islands near Oiseau Bay. The distribution continued along the shore south to the Pukaskwa River and then east of the Park along the shore to Floating Heart Bay 26 km to the east along the shore (Bergerud & Dalton, 1990). In latter years, the herd has concentrated in the vicinity of Otter Island (south of the Cascade River) which is the major calving, rutting, and meeting location. The caribou in the past have made long movements but always stayed near the Lake Superior shore (Bergerud, 1985: Fig.1; Bergerud, 1989). One animal tagged on the Slate Islands did reach PNP during this study (Bergerud, 1989). This male would have traveled the near-shore past Pic Island and the town of Marathon.

Methods

Studies of varied intensity and kind were carried out at the Slate Islands and Pukaskwa National Park from 1974 through 2004. The methods reported below are only those relevant to the results reported and only in as much detail as required by the weight of its use.

Slate Islands floral studies

By 1979, we had established 6 moderately large exclosures (total area = 152 m^2) distributed in the 5 major forest canopy classes. Throughout the study, we made comparisons of the availability of green foods inside and adjacent to the large exclosures. Each spring in May, we weighed the lichen litter that had accumulated in these exclosures in the previous 12 months and included lichens on trees that fell within the exclosures that would have fallen within reach of caribou. Also from 1979 to 1998, we annually monitored survey lines to measure the DBH of conifers that had fallen over the trail since the previous tally. The lines were 3.3 km in length 1979-1991 and 1.7 km 1992-1998.

The growth habit of mountain maple on the Slate Islands was unusual and it was recognized that browsing may have heavily influenced this species. It was possible that a historical record of caribou population dynamics might be recorded in the age structure of stems. The age distribution of mountain maple stems was sampled in four stands. Destructive sampling of all maple stems within 10 m of a point in the interior of stands with a continuous sub-canopy of maple obtained stem 'cookies' for age analysis. Cookies (20 cm long) were taken at 0.5 m or less stem height. Stems with butt rot were sampled at the lowest height that presented a solid core suitable for aging, and age was adjusted. Ring counts were read (WJD) at two locations on each cookie with a hand lens after preparation with a thin and sharp utility knife blade, and a third if the counts disagreed. The frequency distribution of the aged stems was smoothed by generating forward and backward 3-year running averages of frequencies and taking the mean for each year, to address age assignment errors.

Foraging on shrubs and herbs was evaluated in 1985.

Slate Islands faunal studies

The population size of Slate Island caribou was estimated all years 1974 to 2003 with a walked strip transect survey (King, 1937), commonly referred to as a *King census*. Caribou tagging was initiated in 1975 and the tag-recapture (sightings) Lincoln Index (Lincoln, 1930) population estimate was calculated for 1975 to 1997.

The captures were based on baited salt traps (2-4 traps), boat herding to drive-traps at water crossings (2), a walk-through travel route trap, occasional use of drop-nets, and from boats for swimming caribou. There were 628 capture events. The main capture effort was usually conducted in the fall. We were able to capture any swimming animals encountered regardless of size and stage of the fall rut and the traps being open and set for automatic capture were similarly unbiased.

A trap card was filed for each capture event noting the date and time, location/method, capture crew, processing leader, animal sex, presence of udder, sighting and capture of calf and calf tags, body measurements, tags removed and applied, blood samples collected, fecal sample collected, weight, incisor wear, and the incisor collected for aging. Animal care protocols were maintained and animal stress parameters monitored (body temperature, respirations, exertion).

For tagging, at the outset of studies we used individually unique colour combinations of sewn vinyl ear tags (applied with numbered metal ear clips through a grommet) and collars; after c. 1978 we transitioned to numbered large cattle ear tags with colour combinations unique by male or female, and phased out collars.

There were tags in all segments of the population but there were probably tagging biases: males used water crossings more than females in the breeding season, swimming cows and their calves were selected prior to other animals available in the water at the same time, trap vulnerability bias could not be assessed, and selective spring and summer trapping effort avoided adult males and animals with antlers in velvet to avoid overheating and injuries respectively.

The mean tagged animals available each year (1975 to 1997) was 44±4.04, n=23 (unpubl. data). We did not observe any animals that had lost one or both tags based on only a single tag or a split ear in the 4-year interval post-tagging. We were able to see most animals, at least occasionally, at a salt lick established centrally on Patterson Island (the largest - 23 km^2). A second salt lick was established on Mortimer Island (second largest - 8 km^2) and monitored for a number of years to test if animals on Mortimer were infrequent visitors to Patterson Island. The survival of individual tagged animals was based on the last year an animal was seen, after waiting 3 additional years to decide if the animals had been overlooked. If an animal was later seen with tags in good condition they were added back to the tagged pool. Recaptures were re-tagged with fresh tags when a couple years had passed.

The requirement for either random tagging or random recapture for a valid capture-recapture population estimate was met with sighting effort, not capture effort. Sightings included in the Lincoln Index for the yearly estimates included all sightings from May and June: casual encounters, strip transect sightings, and salt lick observations.

King census strip transects were walked by single persons on compass courses with minimal deviation from straight lines, in forestry timber cruising compass-man style. Transects were walked at a normal walking pace, excepting required frequent stops for compass bearing taking for route extensions; as such, noise levels were moderate and approximated observed noise levels of individual caribou travelling with a mind to get somewhere. The strip transect routes were chosen for practical turning points (topographic features, lakes, bays or points, etc.), and boat drop-off and pick-ups. Routes were selected to avoid areas disturbed in recent days and with the goal to have maximal line dispersal for the level of total effort invested. Traverses were walked in May and June, with a majority in May before calving and green-up in most years, on days with little or no wind, and with the ground litter preferably damp; observing these conditions, calling for relatively good listening conditions, standardizes the expectation for flushing distance variability and is the rational for the parametric statistical assumptions.

Observers determined the length of their pace and paced the line-of-sight distance to the flushing location of caribou seen or heard. Distances to dead caribou located and snowshoe hares observed flushing were also recorded. Notes were taken on the condition of carcasses and a decision made whether it had died in the previous winter or in previous years. The definition of a valid previously unfound mortality was that the skull and/or mandible were found and collected. Without major predators, the bones generally were not strewn widely, and skulls and long bones were intact. In the early years, visibility under the forest canopy was excellent because of the elimination of deciduous browse by the caribou and the lack of deadfalls and fewer regenerating balsam fir thickets. As the study progressed, the area of blown down interlaced trees and of regenerating fir 'thicket' accumulated; average visibility declined and it was harder to listen for or see flushed animals.

For each strip transect flush, the observer filed a data card including map location, habitat, flush distance and angle from transect, behaviours, ears observed and tags seen, and if a valid view of the rear for sex determination and udder condition was accomplished.

The mean annual flushing distance of 33.3±1.12 m (30 years) was not significantly longer in 1994, 29.8 m and 1995, 27.4 m, when wolves were present. The mean distance walked per year was 99.5±9.05 km, the mean caribou seen per strip transect survey was 45±5, or the caribou per km walked was 0.48±0.038 (1974-2003, n=30). The mean area annually searched was 6.4±0.55 km^2, 18% of the archipelago.

To determine which population estimate method (*King census* or Lincoln Index) was the best predictor of population change, we calculated an independent method of change by demographic statistics (unpublished analysis); the predicted percent change Y1 to Y2 was 100 minus the survival rate Y1 + annual recruitment (R1). The mean annual change in numbers based on demography from 1980-81 to 1995-96, 16±4.9%. In comparison, the percent change based on the *King census* estimate was 38±9.2 (a perpendicular sighting distance was more deviant). For the Lincoln index, the per cent annual change was 22±3.4% and we felt it was the more reliable method, although there were years the strip transects were closer to the percent change based on demography. The correlation between the annual totals of the *King census* and the Lincoln Index estimates was significant (r=0.717, n=23 years, df=21, P<0.01).

We established a defection rate for interpreting winter pellet survey data: pellet survey counts were conducted in 7 years of the study with tally on 2 m X 20 m segments of continuous transects through proportionately representative forest communities. Captive Slate Island caribou were kept at Thunder Bay and the winter defecation rate of 23 pellet groups/day was estimated (unpubl. data).

When we arrived on the Slates in 1974, we were surprised to find a number of adult males without visible antlers (hummels). Also few of the females had antlers. Also in 1974, we encountered small animals the size of yearlings but who had the long face of an adult. Hence we only felt confident in expressing recruitment as the calf percentage of total animals rather than the more rigorous calves/100 females' index.

In 16 years, a brief period of study in March (late winter) was done to measure snow depths, locate carcasses for indications of die-off, observe foraging behaviours in die-off and non-die-off years, and compile age and sex composition tallies based on track and sign characteristics. Usually with a crew of 4+, only about 10-20 caribou per trip were seen each trip, and the animals appeared to be relatively inactive. Winter classification tallies depended on sign reading: calves separated from adults based on track size and males distinguished from females on the location of the urine spot before or behind the rear tracks and the position of the rear feet based on the drag and spread of the tracks.

Dropped antlers, old or new, on the Slate Islands were almost wholly undamaged by gnawing. Gnawing on cast antlers is a phenomenon that is ubiquitous elsewhere (we surmise that the absence of any squirrels in the fauna may explain this). In all years, dropped antlers were collected and segregated into ten classes on the basis of weathering (applies to antlers found under full forest canopy cover), and were measured and weighed. The oldest, class 1, had shell-like points gone soft, were cracked and partially buried by mosses and humus. One antler was under the humus that had accumulated since the 1902 burn (assessment by forest fire expert Dr. M. L. Heinselman). Class 10 antlers still had rich brown pigment on both surfaces and had been shed the previous fall. This class was based on comparison with antlers known to have been shed the previous winter since they were found in the baited traps left open the previous autumn. The pedicle size on the skulls of males that died in the winter was compared to the mean size of the antler burrs of class 10 antlers from the previous year to quantify whether large antlered males were more susceptible to starvation than smaller males.

An apparent salt lick had existed at Mud Lake in the center of Patterson Island in 1949 (Cringan, 1956). We started placing salt there in 1976 and made daily observations mostly in June during the study. All animals were classified including the sex of young calves. The udders of females were classified as to size to judge for barrenness in that year, the likelihood of a calf having been lost earlier (medium to small regressing udder), and the probability of the calf being nearby but unobserved (extended udder), or with calf present and the likelihood that the cow is the mother. The length of antlers was estimated using ear length as a scalar of height. Physical condition was assessed on a 10 point yes/no system (i.e. ribs showing yes or no etc.) (Bergerud, 2001: Fig. 27) and molt patterns drawn to further recognize untagged animals revisiting salt licks within the day or on following days.

Pukaskwa National Park faunal studies

The PNP caribou population was surveyed in most years following a new snowfall in March. We participated from 1974-79, and in later years the survey was made solely by park staff. The surveys were attempts at complete counts in a 5 km strip adjacent to Lake Superior for the whole north-south extent of the park, and sometimes further east along the shore. Surveys for moose and wolves and radio-tracking of caribou described a very low incidence of caribou forays away from the Lake Superior shore.

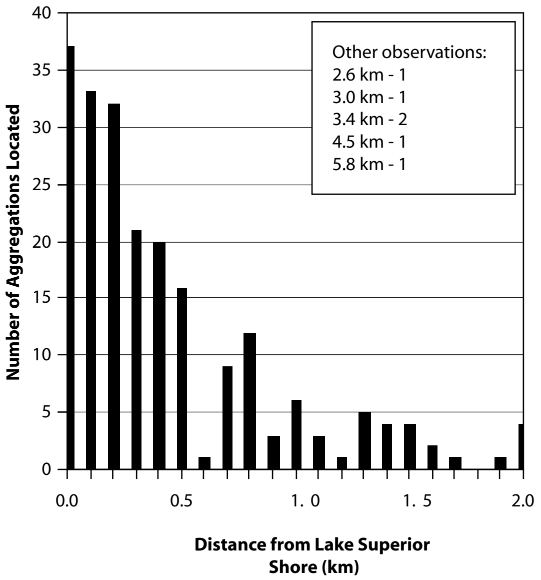

Fig. 1. Puckaskwa National Park caribou live within 1-2 km of the Lake Superior shoreline based on population surveys 1974-1988.

Caribou survey lines were flown by helicopter parallel to the shore and were more closely spaced near the shore; 97% of the tracks were within 2 km of Lake Superior (Fig. 1). The interior of PNP has the greatest snow depths in Ontario (Finlay, 1973) but is reduced along the shore. On the surveys, fresh caribou tracks were tallied and separated from moose relative to habitat locations and sinking/drag track characteristics. Caribou commonly visited small lakes digging holes for slush and these networks of tracks and holes, called spider webs (Simkin, 1965), were investigated by landings for individual counts and calf/adult male/female segregations. Clearly these were minimum counts. Additionally the radio tracking of animals captured on Otter Island showed that animals did not always remain in PNP but would travel the near-shore as far as 30 km farther east along the shore to Floating Heart Bay (Bergerud & Dalton, 1990; Neale, 2000: p45) and possibly a like distance northwest along the near-shore to Pic Island. Otter Island in Lake Superior (Bergerud, 1985: Fig. 2) is centered north-south in PNP and presented a significant opportunity for low predation risk rutting and calving (1.9 km^2 and 0.5 km offshore).

The moose were counted in winter surveys following a fresh snowfall in 1975, 1976, 1977, 1979, 1984,

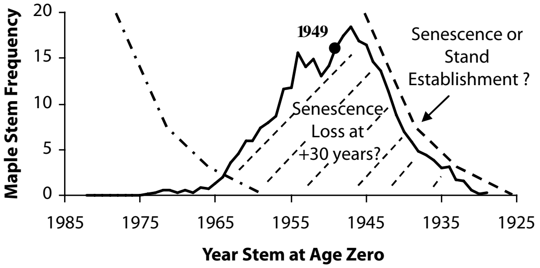

Fig. 2. Mountain maple (*Acer spicatum*) ages (*n*=318 stems) were sampled in four stands on the Slate Islands. Ages were smoothed assuming ± 3 years variability in accuracy of ring counts. Cringan (1956) measured the plant communities in 1949. The oldest stems were aged to initiation in 1929, the youngest to initiation in 1972. The shape of the frequency curve for stems initiated 1929 to 1947 suggested that natural senescence may be acting on the population of stems. Given no new recruits post-1974, and advancing senescence by 30 years would suggest the maple stem population should be nearly completely collapsed. While senescence was obvious post-1990-95, ocular estimates of the collapse under way and the rarity of observed dead sub-canopy maple stems in the stands 1975-85 do not suggest it is proceeding this fast, possibly at half this rate ± 15%; suggesting in turn that maple understorey stand establishment is actually described by this age structure.

1986, 1990, 1993, 1996, and 1999 (Bergerud *et al.*, 1983; Burrows, 2001). The counts 1975-79 involved strip transect methods (see Bergerud *et al.*, 1983) while later workers switched to the Gasaway block method (Gasaway *et al.*, 1986) with some additional modifications. Also, the counts in the 1970's were limited to PNP proper (1878 km^2) while some later counts enlarged the area to the Greater Pukaskwa Ecosystem, 10 000 km^2 (Burrows, 2001).

The wolf population was estimated in 1977, 1978, 1985, 1987, 1990, 1996, 1997, and 1998. These estimates were not very accurate and generally made in conjunction with moose surveys. Further those in the 1970s-80s were limited to PNP whereas several packs were on the boundary of the park and their total home ranges were not documented. The most accurate work was done in the 1990s (1994-99) during the Greater Pukaskwa Ecosystem studies when wolves were radio tracked (Burrows *et al.*, 1996; Forshner, 2000).

Caribou introductions

Caribou from the Slate Islands were released into areas with and without wolves. The introduction areas with wolves and moose were Lake Superior Provincial Park (1989) and Bowman Island (1985) (white-tailed deer also present) immediately adjacent to St. Ignace Island. Caribou were still present on St. Ignace in the 1940's (de Vos & Peterson, 1951). The introductions to islands without wolves or moose were: Montréal Island (1984), and Michipicoten Island (1983).

Results

Slate Islands forage resources

In June 1974, ATB & HB landed on Patterson Island for the first time and were astonished at the heavy environmental footprint of the caribou; trails led everywhere. The first impressions were that the forests were missing a shrub understory and that the arboreal lichens on conifer branches and deciduous tree trunks were browsed in the fashion of a white cedar (*Thuja occidentalis*) browse line in white-tailed deer (*Odocoileus virginianus*) wintering yards; a browse line was also evident for foliose lichens on cliff faces.

The best example of the missing understory shrubs was mountain maple whose form was altered from the norm for the area. Maple was not missing, it was present in suitable moisture and nutrient regime sites as expected. Foraging on maple was sufficient though that there was cropping of all suckering stems at the base of maple clumps. This was allowing apical dominance to remain in the stems that had reached into the forest sub-canopy in the past, so these stems were of unusually large diameter and height, and still growing. The area at the base of maple clumps, through the 1970s and to the mid-80s, had the appearance of tended and vigorous gardens with a 1-1.5 m diameter circle of high density maple suckers less than 40 cm tall. During the 1980s, the height which the suckers attained in a year was progressively less and the apparent vigour of the sucker gardens was noticeably less as the area covered at the base of maple clumps decreased. The record of browsing intensity in the maple was assayed by obtaining ages of mountain maple from four stands sampled (*n*=318) (Fig. 2): 1978 – 2 stands, 96 & 101 stems; 1982 – 2 stands, 50 & 71 stems. The oldest maples were two stems dated as becoming established in 1929; the youngest were 4 stems established in 1971 or 1972. In 1949, at the time Cringan (1956, 1957) conducted vegetation and browsing studies, the sampled stands had stems in the sub-canopy as is seen today, but also a steady, if low, recruitment of stems into the canopy.

Over the course of the study, and accelerating with time, the once vigorous stands of mountain maple commenced dying without replacement due to butt rot induced vulnerability to wind breakage. Winds also took a toll on mountain ash. This occurred in the birch and fir communities where mountain ash was

Table 1. Comparison of upland forage plant species importance (proportion of biomass in diet) to caribou in 1949 in descending order of importance (Cringan, 1956, 1957) versus 1985.

Winter Shrubs	1949	1985(%)
Acer spicatum	1st	N.A.[1]
Sorbus decora	2nd	N.A.
Salix spp.	3rd	N.A.
Cornus stolonifera	4th	[2]
Viburnum edule	5th	N.A.
Sambucus pubens	6th	[3]
Taxus candensis	7th	N.A.
Summer Shrubs	**1949**	**1985(%)**
Viburnum edule	1st	N.A.
Sobus decora	2nd	6th[4]
Acer spicatum	3rd	4th[4]
Diervilla lonicera	4th	N.A.
Populus tremuloides	5th	3rd
Rubus parviflorus	6th	1st[5]
Sambucus pubens	7th	7th
Summer Herbs	**1949**	**1985(%)**
Aster macrophyllus	1st	1st[6]
Aralia nudicaulis	2nd	8th
Epilobium angustifolium	3rd	N.A.
ferns	4th	2nd[7]
Clintonia borealis	5th	N.A.[8]
Cornus canadensis	6th	3rd
Linnaea borealis	7th	N.A.[9]

[1] N.A. - Not available.

[2] *C. stolonifera* was still present in 1985 in typical shrub form, but winter browsing was not evident, and was not preferred as summer browse (5th in importance).

[3] *S. pubens* was the most common shrub in 1985, but not winter browsed and avoided as summer browse.

[4] Available only as sprouts not as shrubs.

[5] By c.1990 *R. parviflorus* was N.A.

[6] The growth habit of *A. macrophyllus* was progressing towards a dimunitive form by the early 1990's. In the late 1970's the only foraging impact noticeable was heavy early spring use which delayed the date of full ground coverage where it occurred.

[7] Based on *Dryopteris spinulosa*, other ferns also still available.

[8] *C. borealis* was available as forage in plots measured 1977-1980.

[9] *L. borealis* was still present in 1985 but mostly in wetter habitats.

Note: Three species: *A.macrophyllus*, *D. spinulosa*, and *R. parvifolrus* made up 63% of the summer forage available in 1985.

Table 2. Comparison of the green phytomass of utilized plant species in the 6 large exclosures (total 151 m^2) basedon 10 m^2 inside and 10 m^2 adjacent outside per enclosure May and June 1994.

Dates[1]	Exclosure	Dry Grams per m^2		
		Deciduous Shrubs	Herbaceous	*Taxus canadensis*
May 17 - 24	Inside	16.1	15.0	1320.0
	Outside	0.2	3.6	0.0
	Difference	-99%	-76%	-100%
May 26 - June 1	Inside	4.0	9.6	43.8
	Outside	0.2	2.0	0.7
	Difference	-95%	-79%	-98%
June 10 - 14	Inside	9.1	13.8	255.0
	Outside	1.0	2.5	0.0
	Difference	-89%	-82%	-100%

[1] New quadrats selected each period.

Table 3. The comparison of herbaceous phytomass of the nearby Leadman Islands (4 m^2 summed) and the Slate Islands (221 m^2 summed) measured in 1985.

Plant Species	Slate Islands (gms in 221 m^2)	Leadman Islands (gms in 4 m^2)	Leadmans > Slates (factor[1])
Roseus streptopus	1.1	7.2	362
Rubus strigosus	97.5	2.2	1
Clintona borealis	7.6	22.8	166
Maianthemum canadense	51.6	17.3	19
Oxalis montona	8.4	6.4	42
Dryopteris spinulosa	159.9	329.6	114
Ribes glandulosum	161.3	36.2	12
Sorbus decora	10.4	17.3	92
Aralia nudicaulis	2.4	10.2	235

[1] e.g. (7.2/4)/(1.1/221) =362X. These results are conservative since caribou sometimes reach the Leadmans and additionally there was a major caribou die-off on the Slate Islands in 1984-85.

Table 4. Caribou forage species at or near functional extirpation from the Slate Islands but still present or re-appearing in the large exclosures in 1985.

Plant Species	Grams Inside (28 m^2)	Grams Outside (28 m^2)	%Gone
Actaea rubra	29.7	0.3	99%
Athyrium felix-femia	76.2	0.0	100%
Botrychium lunaria	0.8	0.0	100%
Taxus canadensis	41.4	0.9	98%
Goodyera repens	2.4	0.0	100%
Gautheria hispidula	30.9	1.1	96%
Listera chordata	0.3	0.1	67%
Coptis groenlandica	1.2	0.1	92%
Amelanchier sanguinea	0.1	0.0	100%
Aralia nudicaulis	0.3	0.0	100%
Populus tremuloides	0.5	0.0	100%
Taraxa cumofficinale	0.1	0.0	100%
Rosa acicularis	14.8	1.3	91%
Roseus streptopus	5.5	0.7	87%

present as scattered stems and butt rot was common, and it also occurred in the few stands where mountain ash was the dominant or co-dominant cover. The latter stands tended to occur on shallow soils over fragile bedrock or raised beaches where mountain ash was not wind-firm at mature sizes.

The aspen was also gradually reduced to very low occurrence levels during the 30 years; that is, since the beaver population was extremely high (originally at 1 colony per km^2), and they foraged at abnormal distances from water to seek aspen stems.

The analysis of forest cover composition indicated that balsam fir had increased from 1949 to 1974 and this succession continued through our 30 year study. Normal secondary succession in the boreal forest, if and when forest fires do not restart primary succession directly, is replacement of deciduous and coniferous shade intolerant pioneering species with shade tolerant coniferous species. Additionally, the vegetation survey documented functional extirpation of a number of the summer forage species that were most heavily foraged in 1949 (Table 1); several others were on the verge (Tables 1 to 4). By functional extirpation we mean that the plant was still present and vigorous in natural caribou browsing refuges but was no longer available in reach of caribou, or it was present in reach but only in a non-flowering vegetative form that was diminutive

Table 5. The arboreal lichen litter measured and removed each spring from the large exclosures compared 1979-81 versus 1989-98.

Year	Forest Cover Type		Size of Excl. (m^2)	Mean per Year		Island-wide mean annual lichen litter-fall (kg)
	Name	Island-wide Area (ha)		gm per Excl.	gm per m^2	
1979-88[1]	Birch Overstory	494	37.5	5±2	0.13	642
	Fir-Birch	245	29.1	9±1	0.30	735
	Fir-Feathermoss	206	18.3	108±18	5.90	12 154
	Birch-Fir	1714	38.6	53±8	1.37	39 079
	Birch-Fir	above	28.8	92±15	3.19	above[3]
	Spruce-Sphagnum	139	17.8	13±5	0.73	1015
	Totals and Means	**3298**	**151.8**	**46.6**	**1.90**	**53 625**
1989-98[2]	Birch Overstory	494	37.5	47±11	1.26	6
	Fir-Birch	245	29.1	55±15	1.89	5
	Fir-Feathermoss	206	18.3	218±27	11.90	25 514
	Birch-Fir	1,714	38.6	116±27	3.01	62 047
	Birch-Fir	above	28.8	122±18	4.23	above[3]
	Spruce-Sphagnum	139	17.8	77±29	4.32	6005
	Totals and Means	**3298**	**151.8**	**105.8**	**4.43**	**104 421**

[1] The estimated arboreal lichen litter 53 625 kg equals 117 975 lbs. In Nfld. caribou ate 10 lbs. per day or 210 days equals 117 975/210 equals a carrying capacity of 56 animals.

[2] The estimated arboreal lichen litter 104 421 kg equals 229 726 lbs. divided by 2100 lbs. per animal equals a carrying capacity of 109 animals.

[3] For the two exclosures in Birch-Fir the mean gms/m^2 was used in calculating kg available.

as compared with its normal form contemporarily on the adjacent mainland, and assumedly with 1949 since this phenomenon was not noted at that time (Cringan, 1956). The most dramatic example of the former was bush honeysuckle (*Diervilla lonicera*) which, while being perennial, does not extend a clone bearing root system and does not have a vegetative form that stays close to the ground. A good example of the latter was clintonia (*Clintonia borealis*) which was ubiquitous in its' normal range of preferred sites but at very low density and was evident above ground with single 10 cm or less leaves; plants persisting in this manner were always part of an extensive clonal root system.

The terrestrial lichen community was found on raised bedrock but covered only 0.5 km^2 and existed only as fragmented podetons that would contribute little to the diet. In 1981, we measured the phytomass of this lichen community on the Slates by weighing the lichen phytomass that we could pick in 5 minutes in each of 20 m^2 random quadrats. The yield from these *in situ* quadrats averaged 3.15±0.32 gm. For a control we picked 20 m^2 quadrats on the mainland immediately adjacent the Slate Islands. There the mean phytomass picked in 5 minutes averaged 173.5±28.57 gm (55 times greater). The terrestrial lichen on the Slates was less than 1 cm in height and picked from within cracks in the bedrock or it was sparsely present in clumps of feathermoss or other ground-hugging mosses. This being little changed since 1949, although Cringan (1956) estimated the difference between mainland lichen and the Slate Islands in the order of 20 times greater, and this may be the clearest indication that there was actually more lichen available in 1949. That is, in the absence of 1949 biomass measurements the reported occurrence, cover, and a qualitative description of condition might also describe the condition post-1974. Terrestrial lichen on the mainland was of a normal 10 cm or so in height and 'rooted' in an organic mat of rotting lichen.

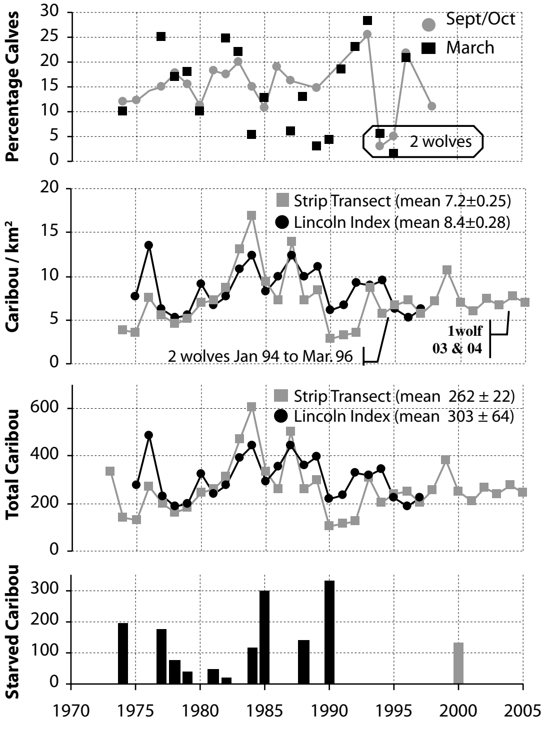

Fig. 3. The demographic parameters of the caribou on the Slate Islands 1974 to 2005. Starved caribou from spring strip transect surveys. Total caribou 1973 is backcast from 1974 sum of starved and living estimates. Total caribou in 1999 and 2000 based on less than 30 km of strip transect per year, however it was walked bya single experienced observer (L. C.); variation in estimates wider than the rest of the series. Starved caribou estimate in 2000 based on difference in total caribou estimates 1999 to 2000, no carcasess located (grey bar).

The arboreal lichen phytomass available to caribou, on branch litterfall and on blown down tress, measured in the 6 large exclosures in 19 years (1979 to 1998 broken) increased through time as the conifer forest aged (Table 5) ($Y = -20.474 + 0.266X$, $r=0.770$, $df=17$, $P<0.01$). In the early years, it might have provided biomass sufficient for 50 caribou and while in the later years of the study it was estimated to be sufficient to support 100 animals (Table 5).

Slate Islands population demography

The first *King census* strip transect estimate in 1974 was 140 animals, much greater than the estimate that had been repeated over the years of ~25. Another crew that visited the island (Euler *et al.*, 1976) quantified winter pellets to evaluate habitat preferences. Our re-analysis of their pellet count data using our habitat classification, gave a population estimate of 177. We also found dead caribou as did the other team. The estimation from the previous winter's carcass survey in the spring of 1974 was that 194 animals had died. The population the previous fall had exceeded 300 animals or 9+ animals per km^2.

For the next 23 years (1975 to 1997), the population fluctuated between 200 and 500 animals based on the Lincoln Index or from 5.0 to 12.3 caribou/km^2; or based on the strip transects 1974 to 2003, from 100 to 600 or 2.9 to 16.9/km^2 (Fig 3). The percentage of calves in the fall varied from 3 to 25% 1974-98 (excluding 1994 and 1995) and averaged 16.0±0.93%, $n=18$ years, mean sample size 125 (Fig. 3). Recruitment was much less for the 1994 and 1995 cohorts when wolves were present. The fall count in 1994 was 3.0%,

$n=166$ and in 1995, 4.9%, $n=122$. The mean winter percentage in March (excluding the 1994 and 1995 cohorts) was 15.4±1.95 (17 years, mean sample size 123). The percentage calves in March 1995 and 1996 with wolves was 5.4, $n=165$ and 1996 1.5, $n=129$ (not significantly different than in the fall). The greater variability in the winter percentages (SE 1.95) resulted since calves were already reduced in the winters of major die-off by the time we arrived, 1984-85 5.2% ($n=$ 191), 1986-87 6.1%, ($n=331$) 1989-90 3.0% ($n=135$). Some demographic parameters of general interest are listed (Table 6).

Based on the pellet count Cringan (1956) made in 1949, and our forest cover stratification for that period, we recalculated and got a similar (Cringan, pers. comm.) high figure of 150 animals using our methods. Seven pellet counts from 1978 to 1983 provided mean estimates 262±23 animals similar to the Lincoln Index for the same period, 285±37 animals. The pellet method provided an approximation of numbers but was not sufficiently accurate to predict annual changes. However, it adds cause to believe the population has probably fluctuated from 100 animals to 500+ at least since 1949.

There was an almost complete natality failure in 1990. Many pregnant cows had died prior to parturition in the winter of 1989-90. The survival rate 1989-90 for tagged females was only 15% (4 of 26) and males 12% (2 of 17). Additionally, we found the legs of newborn calves that spring at two active fox dens and the hooves of the neonates showed no wear; the newborns were either born dead or never stood. We had no 1990 fall count but the 1990-91 winter percentage of calves was 4.2% ($n=118$).

The parous percentage for tagged females was 61.7±3.30 in 19 years (mean sample 19) and was consistently higher than that of the larger samples of untagged females that included more pre-puberty animals, 59±3.12% (19 years, mean sample 169). But there were exceptions to the low rates; in 1986, the parous percentage of tagged females was 71.4 % ($n=28$), and 76.6% for untagged females ($n=286$), and in 1991 tagged females were 78.6% parous ($n=14$) and, untagged 79.8% ($n=168$). The relationship of the percentage of parous females in the spring (excluding calves of the previous year only), with the weight of captured females (inclusive of long yearlings) the previous fall was significant ($r=0.5193$, $df=13$, $P<0.05$) (Fig. 4).

The mean annual survival rate of tagged females was 82% (383/465, 16 years) and the year with the lowest survival, mentioned previously for 1989-90, was 15.4% for females and 12.2% for males. The second lowest annual survival rate for females was in 1994-95 when wolves were present 71% (24/34).

Table 6. Some demographic parameters from the Slate Islands

Survival Rates of Adults[1]

Females:

Years no wolves (excludes 1988-89) 89±1.67%, n=13 years, (334/379)= 88%

Years with wolves 1994 71% (24/34), 1995 81% (21/26)

The worst winter die-off 1989-90 15% (4/26)[2]

Males:

Years no wolves (excludes 1988-89). 84±2.62 n=13 years (254/306)=83%

Years with wolves 1994, 87% 33/38, 1995, 91% 52/57

The worst winter die-off 1989-90 12% (2/17)

Mean Pregnancy/Parous Rates (1978 to 1998 with 2 years missing)

Tagged 61.7±3.30 (mean sample size 19), minimum 33.6 (1990), maximum 82.4% (1989)

Untagged 54.9±3.12 (mean sample size 169), minimum 29.8 (1990), maximum 79.8%(1991)

Percent Male Calves

Years no wolves 54.7±2.37% (n=16 years)

Years with wolves 1994 and 1995, 3% and 5% respectively

Percent Adult Males at Salt Lick (1974 to 1996, broken series n=16 years)

33.5±2.35 (n=16 years) (mean sample 259.6)

Significantly more males in wolf yrs 52.9 (1994), 56.8 (1995) (in forest also)

Percent Calves in Fall (1974-1998, broken series n=18 years)

Years no wolves 17.8±1.18, minimum 15.0 n=10, maximum 25.4 n=63, mean sample 127.2

Years with wolves 4.0±0.95 sample 1994 166, sample 1995, 122

Percent Calves in March (1974 to 1996, broken series n=18 years)

Years no wolves 15.4±1.95 n=16, winters of major calf loss 1984 cohort 5.2, 1988 6.1, 1989 3.0, a natality failure 1990 only 4.2 calves because pregnant females died in the major die-off and also calves carried to term were stillborn or never stood, since tiny hooves with no wear found at two fox dens

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[1] Based on survival of animals tagged from four cohorts and followed for four years.

[2] 15% 4 of 26 live: no captures 1986, 1 of 8 captured 1987 live through 1989-90, 2 of 11 captured 1988 live through 1989-90, 1 of 6 captured fall 1989 live through 1989-90.

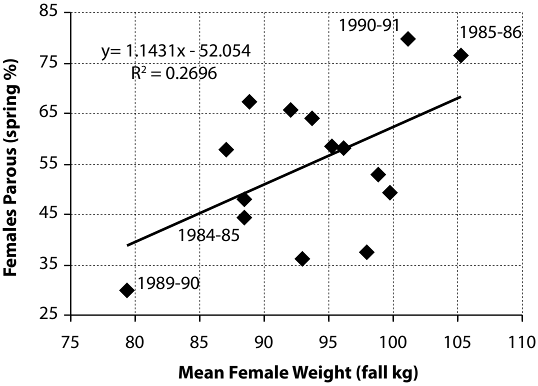

Fig. 4. The significance of the regression of the percent of females classified as parous in the spring on the mean weight of females the previous fall (inclusive of long yearlings) (r=0.5193, df=13, P<0.05) is carried by extreme observations but the conditions leading to them occurred twice in the course of the study. The winters of the most severe starvation events (Fig. 2), 1989-90 and 1984-85, with respectively the lowest and low weights entering the winter and lowest and low percentage parous the following spring, was followed by recovery over-summer of the surviving cows to record weights, and the highest percentages parous throughout the study those following springs. The mean fall sample size, females weighed, was 7.1±0.84.

Fig. 5. The greatest winter loss of Slate Islands caribou from starvation was in 1989-90. Only 23 tagged animals lived, of which 21 had ages established (Lived), and the survival of adults was only 12-15%. Forty four carcasses (Died) were recovered inclusive of tagged and untagged caribou. Of the animals that lived the 4 and 5 year olds seemed to have a particular survival advantage; these were animals with experience with the landscape, were not investing in reproduction (pregnancy in females, rut and antlers in males; two surviving males were hummels), and were not investing significantly in body growth.

We located eight dead caribou killed by wolves 1994-95. The mean survival of males over the course of the study was the same as for female 82% (320/392, n=, 16 years). But unlike the females, they had high survival in both winters when wolves were present 1994-95, 87% (33/38) and 1995-96, 91% (52/57).

The sex and age composition of the animals that we located that died over-winter from starvation (1974 to 1993) was 24 female calves, 18 male calves, 25 calves (sex unknown), 62 adult females, and 77 adult males. The large antlered males died at higher rates than males with smaller racks. The mean pedicel size of males that died in the 1984-85 die-off was 1379.2±261.65 mm^2 (n=9) compared to the random brown/brown antlers cast in the previous fall, 790±195 mm^2, n=6 (measured width x length). Older animals had higher mortality rates also in these die-offs. In the 1984-85 die-off, the mean age of adults captured in the fall was 4.4±0.48 years (n=15) and those found dead the next spring 7.5±0.29 years (n=23).

The age structure of the dead and survivors was compiled for the major starvation die-off of 1989-90 (Fig. 5). Larger males and older animals that died more than younger caribou were probably investing less in reproduction. Only 7 tagged males survived this greatest winter loss (1989-90) and two had been hummels in earlier years. Generally hummels older than yearlings represented about 5% of the adult male population. On the females side, of 15 tagged

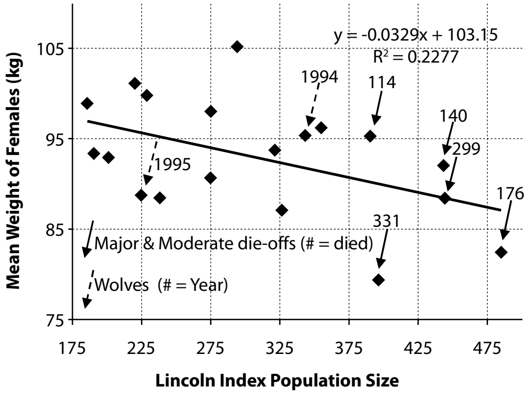

Fig. 6. There was a relationship between the size of the populaiton entering the summer and the mean weights of females that fall (r=-0.477, n=19, df=17, P<0.05), indicating a density dependant interaction with summer forage. Die-offs in the following winter were mapped to these data (solid arrows). When the population was in exceess of 390 caribou entering the winter, Lincoln estimate, a die-off of moderate to major proportions took place.

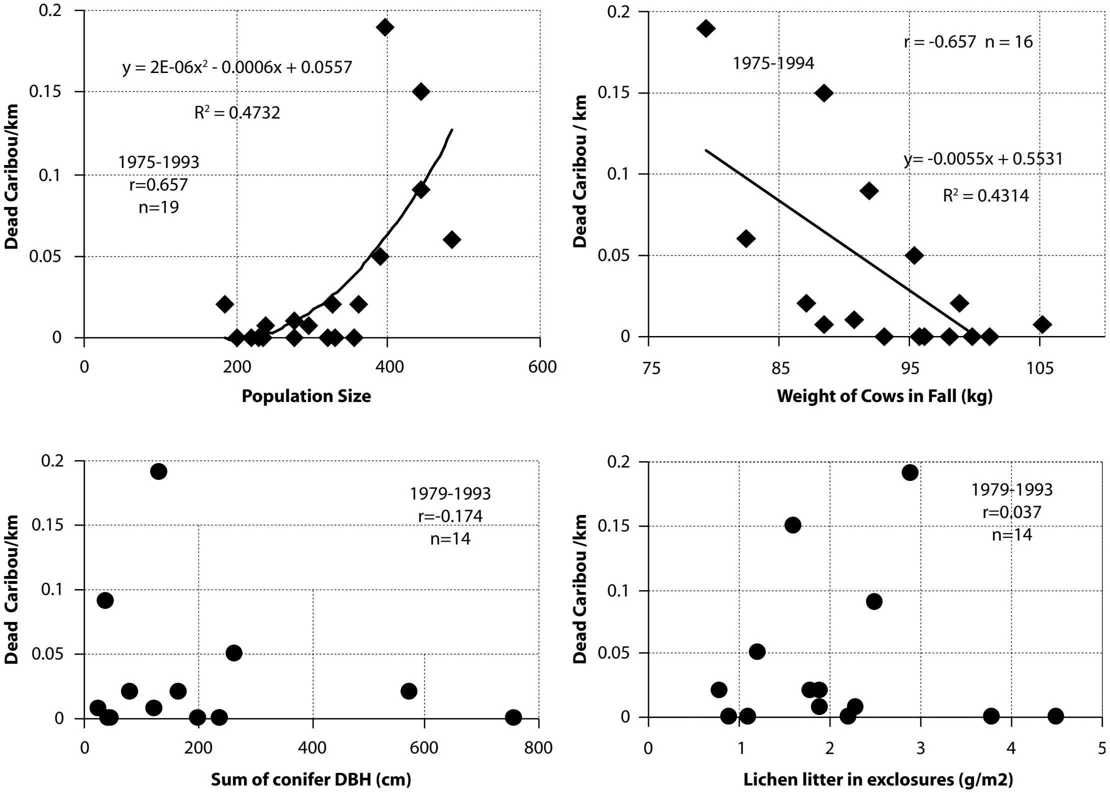

Fig. 7. Starvation die-off events (the number of caribou carcases located on 'King Census' strip transects walked in May and June each year) were correlated with the Lincoln Index population estimate the previous spring (df=17, P<.0.01), and low weights of female caribou the previous fall (df=14, P<0.01), and not with the abundance of the total over-winter lichen litter (picked clean from wind blown branches and trees in 6 caribou exclosures each spring), or with the frequency of over-winter conifer blowdown (total diameter at breast height of all conifers fallen over a trail each winter).

females surviving the crash of 1989-90, nine had not been pregnant (no udders seen) and only 6 survived that had borne calves. The oldest tagged animal that lived through that crash was a female we called Hope. She had carried her radio collar (radio signal was lost years before) since 1982. She may have had only one calf in 12 years but she was a survivor, living through 4 winters of moderate to major mortality events between 1983 and 1990 (Fig. 3), when she was 11. She had the largest home range of any of the animals we radio tracked.

The regression (Fig. 6) of fall weights of females on the spring Lincoln Index population estimates (Y = -0.0329x + 103.15, R^2 = 0.2277) indicates that population density is a predictor of winter survival (r=-0.477, n=19, df=17, P<0.05).

The population declined when the fall population exceeded 450 animals (12.5/km^2) and animals died over-winter (Figs. 3, 6). This winter mortality was not correlated with the abundance of winter lichens, but with the previous years population estimate (df=17, P<.0.01) and fall weights of female caribou (df=17, P<0.01) (Fig. 7, Table 7). This is our evidence for density-dependent population regulation based on the abundance of green summer forage. After the die-offs, the fall weights of the females increased dramatically the following year in at least three of the die-offs (Fig. 8), in two of those cases the post-die-off population density was low enough that female condition improved sufficiently over-summer to generate a parous percentage the following year which is considered the norm for caribou, the only two times this occurred in the study. The difference in weights between these two years and the third, also a number of other years (Table 7), was small and indicates a threshold was achieved.

Wolves preyed on caribou from their ice-crossing in winter 1993-94 until late March 1996. In the 2 years these wolves hunted, calf survival to October dropped from 10% to 25% in years without wolves to 5% or less (Fig. 3). The caribou population dropped in the winters of 1994-95 and 1995-96 (Figs. 3, 6) with wolves present and when the caribou population was below the density where starvation events were observed (Figs. 3, 6).

Between March and May 1996, one wolf disappeared and there is some evidence that poison had been deployed. At that time a dog accompanying tourists to the Slate Islands went into fits and was rushed to a veterinarian; it had ingested poison. After this there was no sign of wolf predation until 2003 and 2004 (Fig. 3). One wolf did persist after the poisoning incident as there was sign near and at a (former) fox denning site in the vicinity of Horace Cove until 1999. If this animal did prey on caribou it was not effective at a level that we could detect demographically or during surveys and the caribou population built up (Fig. 3).

Table 7. Pearson correlations[1] of overwinter caribou mortalities[2] located per km walked in May/June with: the winter snow depth measured on winter trips; the size of the previous years population (spring Lincoln Index); the lichen litter fall in 5 exclosures of total area 152 m^2 measured in May; and the total DBH of conifers that fell a cross a 1.7 km trail overwinter.Also, the correlation of the size of the previous fall populaion with the mean weight of females the previous fall, and exclosure lichen with total DBH of conifers across the trail.

Winter Season[3]	Previous Spring Caribou Estimate	Previous Fall Weight of Cows (kg)	Winter Trip (mo/da)	Depth of Snow (cm)	May/ June Walks (km)	Over-winter Mortality (Caribou/ km)	Exclosure Lichen/ m^2 (gm)	ΣDBH Conifers on trail (cm)
1973-74	----	----	3/7, 3/20	58	99	0.060	----	-----
1974-75	----	----	3/11-4/4	62	105	0.040	----	-----
1975-76	275	90.7	3/28	69	80	0.010	----	-----
1976-77	485	82.5	no trip	----	169	0.060	----	-----
1977-78	229	99.8	3/6-21	66	65	0.000	----	----
1978-79	186	98.9	3/18-4/2	85	130	0.020	1.9	165
1979-80	201	93.0	3/20-26	81	101	0.000	1.1	48
1980-81	326	87.1	3/24-27	25	162	0.020	0.8	81
1981-82	238	88.5	3/15-19	75	140	0.007	1.9	122
1982-83	275	98.0	3/21-24	57	133	0.000	0.9	41
1983-84	390	95.3	no trip	----	83	0.050	1.2	264
1984-85	444	88.5	3/18-22	49	158	0.150	1.6	----
1985-86	294	105.2	3/31-4/5	50	154	0.007	2.3	25
1986-87	355	96.2	no trip	----	62	0.000	2.2	241
1987-88	443	92.0	3/15-18	83	93	0.090	2.5	38
1988-89	362	----	3/29-31	70	57	0.020	1.8	574
1989-90	396	79.4	3/26-30	60	168	0.190	2.9	132
1990-91	220	101.2	4/2-5	47	135	0.000	4.5	759
1991-92	237	----	no trip	----	40	0.000	----	241
1992-93	330	----	3/21-23	69	55	0.000	3.8	200

[1] Correlation coefficients:
Overwinter mortality vs snow depths, $r = -0.094$, $n=16$ (ns).
Overwinter mortality vs fall population, $r = 0.666$, $n=18$, $df=16$, $P<0.01$.
Overwinter mortality vs exclosure lichen, $r = 0.038$, $n=14$, (ns).
Overwinter mortality vs DBH conifers, $r = -0.174$, $n=14$, (ns).
Fall population vs mean weight of females, $r = -0.568$, $n=15$. $df=13$, $P<0.05$.
Exclosure lichen vs DBH conifers, $r = 0.525$, $n = 13$, $df=11$, $P<0.10$.

[2] Overwinter caribou mortalities do not include fall rut related mortalities (antlers on adult male skulls) or accidental deaths.

[3] In c.Jan. 1994 two wolves reached the islands.

The population declined between 1999 and 2000 based on the strip census (383 estimated in 1999 and 252 in 2000). There could have been a moderate die-off (Fig. 3) but we did not find any over-winter mortalities. The census was made by the most experienced of our crew (LC). However he walked only 22 km, the lowest total in the 30 years (see Table 7). The mean line of sight distance to dead caribou in previous die-offs was 7.6±1.02m (6 die-offs and 92 carcasses). Less than 1% of the 36 km^2 of the study area was scanned. If 100 animals died they all could have been missed with such minimal coverage.

In the last two years of the study, 2003 and 2004, there were signs of a wolf on the islands. In both years, we found carcasses that had bones crushed and scattered and found scats. Studies that have continued in 2005 and 2006 have not confirmed a continued presence for this wolf.

High populations of snowshoe hares occurred on the Slates in 1979, 1988, 1995-96, with the mean population estimated at 267±44 hares (27 years), an extremely low density of 7.4 hares/km^2 with total population extremes of 61 to 813 total animals. However, interviews with the two original light house keepers, whose tour-of-duties together on the islands spanned 60+ years, both indicated higher hare numbers in prior decades. Hares were noted to have, relative to caribou in the late 1970s, more impact on *Cornus canadensis, Maianthemum canadense, and Trientalis borealis*; furthermore, they slowed the recovery of these species plus mountain maple post-clipping in clipping-recovery experiments (Bergerud, 2001: unpubl. data)

Pukaskwa National Park

The caribou population in PNP appeared to increase from 1974 to 1979 and then decreased (Fig. 9). The increase was possibly an artefact of learning or there may have been population increase in that period. The overall decline per year is $\lambda=0.97$. Recruitment averaged 16% (Fig. 9) thus mortality would approximate 18-19%. There was a high rate of disappearance of radio caribou; 23%, 6 animals in 26 radio years (1976 to 1988) (Bergerud, 1989). Eleven caribou were found dead between 1987 and 1999 (K. Wade, Warden, pers. comm.) and all but 1 or 2 were thought to have been killed by wolves.

Radio-collaring wolves in the Greater Pukaskwa Ecosystem documented 2-3 of 7 packs operating completely in the Park (Forshner, 2000: Figs. 4-8). The Cascade Lake Pack was centrally located 7 km from Otter Island and would have had the greatest impact on caribou. The Swallow River Pack was the next pack nearest to the shore and 24 km from Otter Island. The studies by Burrows *et al.* (1996), Burrows

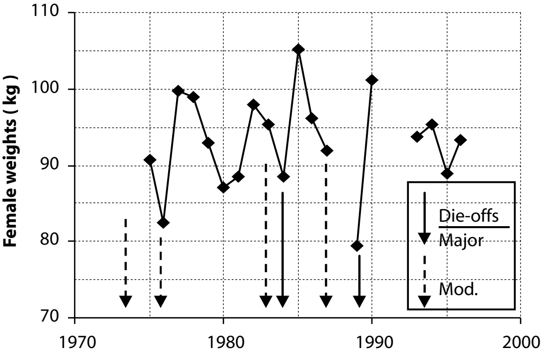

Fig. 8. The fall weights of Slate Island female caribou, and the years of moderate (100<mod.<200) and major (>=299) starvation die-offevents. The weight of females showed major gains in the two growing season observations which followed a major starvation event, and the growing season following the largest moderate event, indicating a density dependant interaction with summerfood resources.

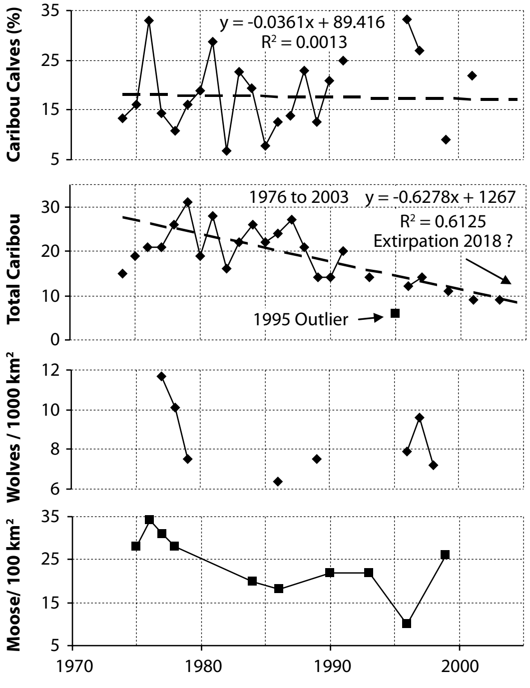

Fig. 9. Pukaskwa National Parkmoose, wolf, and caribou demographic parameters for the years 1974 to 2003. The percentage calves in winter surveys has remained constant, while the carbiou population has declined significantly (r=-0.783 n=21, df=19, P<0.01). The trend in total caribou numbers 1976-2003 suggests that extirpation is likely by the year 2018 but below 10 animals a collapse to nil could be imminent, and the chance for the population to cycle up is precariously low.

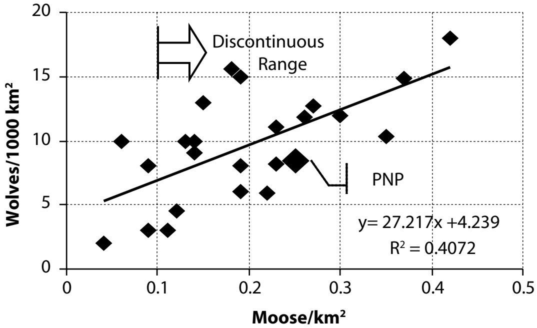

Fig. 10. The regression of wolf numbers on moose densities from published data (Forshner, 2000: Table1-1; Messier, 1994: modified) and updated for Pukaskwa National Park (r=0.638, n=24, df=22, P<0.01). Bergerud and Elliot (1986) found that R=M for caribou occurred at 6.5 wolves/1000 km², which in turn is supported by a density of 0.10 moose/km² (Bergerud 1989); thereby fragmenting the continuous range of caribou (i.e. populaitons persist in isolation or discontinuously where escape/refuge habitat is sufficient to influence R and/or M).

(2001), and Forshner (2000) showed the highest density of moose and wolves was on the north boundary of the Park and even further north where logging was taking place. However three packs probably hunted to the coast. The center of the territory of the Swallow River Pack was 15 km from the coast; the Cascade River Pack had the coast as a boundary and the center of its territory was 12 km from Otter Island; the Black Pack operated adjacent to the shore at Oiseau Bay where the caribou had disappeared by 1988 (Bergerud, 1989).

The wolf population averaged 8.5/1000 km² (Fig. 9) or 2 more /1000 km² than that predicted for stability in the regression of mortality on wolf numbers of 6.5/1000km² (n=18 herds) and recruitment on wolf densities (n=25 populations) (Bergerud & Elliott, 1986: Fig. 10 p. 1524). Recruitment averaged approximately 16% when it would be expected to be 9.6% when associated with 8.5 wolves/1000 km²; i.e. $Y=e^{3.340-0.127X}$ (Bergerud & Elliott, 1986). Given that the population was in decline, adult mortality would have been higher than the expected 15.5%; i.e. $Y= 4.766+0.669X^{1.275}$ (Bergerud & Elliott, 1986). These differences are most likely attributed to relatively high quality summer refuge habitat and inadequate winter escape habitat. The lake shore distribution and Otter Island provided the escape habitat, but land fast ice along the shore in several winters had provided the access for the wolves and the high winter predation rate. The PNP wolf population size (Fig. 9) was within variation expected based on an estimated density of moose of 0.25 moose/km² versus that predicted from a regression of wolves on moose densities in other studies (Fig. 10). Burrows *et al.* (1996) had projected the expected number of wolves in the Park based on a density of 0.25 moose/km² at 15 wolves or (8/1000 km²), close to the mean population estimate over the years (Fig. 9).

There was considerable variability in the methods used to estimate the wolf and moose populations and probably numbers of both species were relatively stable as suggested by Burrows (2001). The low moose count in 1996 may be due to weather causing tracking problems (Burrows, 2001). There is no hunting of moose in PNP and Bergerud *et al.* (1983) argued that moose numbers were regulated by wolf predation, a view rejected by Thompson & Peterson (1988).

The introduced herds

(1) In 1982, 7 animals were move onto Michipicoten Island to add to the one resident male which had been seen on the island: transplants - 1 male, 3 adult females with 3 female calves. An eighth transplant, a male, was added in 1989. The island is 188 km² and 15 km off shore. The Island is in the Great Lakes-St Lawrence Forest Region (Rowe, 1972). The dominant trees are all maples, mountain maple, sugar maple (*Acer saccharum*) and red maple (*Acer rubrum*) plus birch and aspen. Ground hemlock and white pine (*Pinus strobus*) are common and there are some boreal conifers on one ridge. The herd increased λ =1.18 (8 to ± 200, 160 counted in 2001) in 19 years.

(2) Ten animals were moved onto Montréal Island by 1984. The Island is 7 km² and 5 km from the coast. The island is mostly boreal forest of spruce, fir, and birch with terrestrial lichen common on only one sandy point. The caribou increased to approximately 20 animals by 1993 (16 seen). In 1994, when Lake Superior froze, wolves reached the island predating some and causing the balance to abandon the island.

(3) Seven animals were released on Bowman Island in 1984, in the complex of islands commonly referred to as the Rossport islands of Lake Superior (access from Rossport, Ontario). The island is adjacent to St. Ignace Island where the last caribou were seen in that vicinity in the 1940s (de Vos & Peterson, 1951). The forest cover on the island is mostly boreal forest. All the animals had radio collars. The animals disappeared by 1986. Two caribou were found killed by wolves. It is believed the others were killed on the ice in bays and channels of the Rossport islands and their collars lost (divers attempted to recover collars but the collars were not a suitable frequency for accurate underwater triangulation). The last animal alive had moved further off the coast to a small island suggesting movement to escape habitat.

(4) Thirty-nine animals were moved into Lake Superior Provincial Park in the fall of 1989. This park is in the Great Lakes-St. Lawrence Forest Region and forest cover is similar to Michipicoten Island. By June, only 1 of the 17 radio collared animals was still alive. On investigation, the majority of the carcasses had been utilized by wolves, and were either killed or scavenged by them. In retrospect, the animals moved from the Slates Islands had extremely low weights in October 1989, some of the released animals that died probably could not respond adequately to encounters with wolves. However this release has persisted in the escape habitat of the coast and a survey in February 2007 found three animals, the herd numbers less than 10 animals and is decreasing (biologist G. Eason, pers. comm.).

Discussion

Slate Islands forage resources

We observed that snowshoe hares did compete for summer foods with woodland caribou on the Slate Islands, and while not directly relevant to the competition for forage, the effect of hares was most noticeable in the limitation of white spruce recruitment. The latter may have implications for plant community succession. Specific calculations of the magnitude of hare competition for forage were not carried out. From observations of exclosure experiments (unpublished) and permanent vegetation plots (unpubl.), it was evident that hares were out-competed by the massively larger total biomass of woodland caribou.

The prime example of caribou out-competing hares was salmonberry/thimbleberry (*Rubus parviflorus*); green terminal canes were preferred by hares and essentially 100% were cropped each winter. In 1978, the mean height of the highest live bud ranged from 61.5 cm to 83.0 cm on four permanent plots where thimbleberry coverage was 100%. However, there was no qualitative difference between the height this plant achieved each summer and mainland examples until the mid-1980s. At the outset of studies, thimbleberry was lightly used as summer food by caribou with most use noted on emerging leaves and a noted lack of preference for mature leaves; this plant swamped caribou use. With the combination of functional extirpation of more highly preferred caribou summer forage species and extremely high caribou densities 1985 to 1989, caribou also consumed this species as a summer food. In a matter of a few years it was eliminated islands-wide from functional utility. Up to that point, thimbleberry had been very common in continuous large patches (100s of m in extent); after, the only place we could show this plant to visitors was in exclosures. The story is similar for other plant species but not so dramatically unambiguous. For the purposes of any conclusions drawn, the hares were considered to have a negligible impact on caribou population dynamics, or in contributing to the functional depletion of plant species.

The lengthened growing season documented for the Slate Islands, where spring green-up had advanced by almost a month from 1967 to 1988, seemed to maintain if not continue in later growing seasons. Plant phenology was closely monitored in the late 1970's and in the more recent years casual observations confirm by comparison that early green-up has continued. If all else were equal, this longer growing season would mean that plants garner greater energy reserves and this benefit would pass on to herbivores. This may not be the case where over-grazing is occurring. The opportunity to swamp herbivores with biomass and thereby allow a larger net seasonal energy gain per individual plant may be greater in a shorter growing season. A longer growing season, and larger energy transfers to the higher trophic level, might therefore accelerate the functional extirpation of plant species from the Slate Island plant communities.

The importance of energy retention at the plant level is very high. While energy transfers between trophic levels were not studied intensively in this study, we realized in time they should have been. When plant studies were initiated in 1977 on the Slate Islands (WJD), it took some time to realize that a number of *unknown* species were actually diminutive forms of common boreal forest plants. It was assumed at first that this was a localized climatic effect, in which the cold thermal mass of Lake Superior interacted with the off-shore location of the Slate Islands to thwart normal growth; that is, as seen in forest communities on the adjacent mainland. Mainland plant forms were typical of the plants throughout their range. Exclosure plots showed overgrazing depleting energy resources; plants survived in small form and at low density making them less a target for concentrated foraging. A capacity to sprout from extensive root systems was essential to this plant survival strategy. The following example is illustrative of what occurred for all the most highly grazed plant species including Canada mienthemum, starflower, big-leaf aster, and others which were available when our studies began. Clintonia, already described as being present only as specimens with single 10 cm or less leaves and not producing flowers when studies began, was present in a number of exclosures when they were erected. With each year that passed, the size of the leaves produced was more elongated; after a few years plants started producing second leaves as is their normal form, and then after 5-7 years, clintonia in exclosures would flower; and would do so each year thereafter. The importance of retained/retrieved energy in the root systems for these perennial plants is apparently critical to their presence in what is considered a normal form throughout the extent of their ranges.

Mountain maple stems in the forest sub-canopy, safe from browsing, have been harnessed by woodland caribou as nutrient pumps. The typical maple sucker gardens described earlier formed a very large portion of the summer forage available throughout the 30 years of this study. Normally, mountain maple is restricted to the understory and in a shrub form because vigorous suckers originating on the root ball in close proximity to the growing stems share and then fully acquire apical dominance. The suckers then out-compete larger stems and cause senescence and death of stems 2-4 cm diameter, and so normally restrict maximum stem age to 10 to 15 years of age. The overgrazing refuge form of mountain maple is 6-15 cm diameter stems reaching sub-canopy tree status and up to 50 years old. This is not a secure refuge in the time dimension as the trees will not live forever, but due to their shrub nature they have the ability to fill canopy openings with recruits, if they escape caribou browsing. The age distribution documents stem recruitment at low rates peaking in 1947. That this was a low rate is supported by the presence of older stems which would have been lost in whole to the apical dominance effect of being swamped by oncoming sprouts. Recruitment to the canopy has been in decline since 1950, was weak in the 1960s, and ceased altogether c. 1971 (Fig. 2). Cursory examination of the age distribution of sampled maple stems (Fig. 2) suggested that senescence mortality might set in for stems between 25 and 35 years age and be progressive (j-shape) through to age 50. Recent observations confirm that the maple sub-canopy is in serious senescence decline. Although the stands sampled did have some dead and dying stems in 1978-82, the health of those stands was still generally good and the forest floor was not littered with a steady accumulation of rotting maple stems. Also, the maple stands are outliving the predicted timeline for senescence decline. Only about half of the stems that should be dead by now according to the senescence theory are actually dead (ocular estimates WJD). Given the age of the stands and what would have been early competition for canopy space with tree species, the 1929 date for initial stems entering a sub-canopy position might correspond to the availability of this niche forming in those stands. It can be said, however, that the senescence that has set in has compromised the health of the sucker gardens too and so the energy transfer to caribou is undoubtedly in serious decline.

By virtue of the retention of a record of foraging intensity across a half century, the mountain maple tells us a lot about this caribou population. After the 1989-90 die-off when the caribou population recovered slowly from a low of approximately 100-200 caribou, the maple took full advantage and sprouts attained heights of 1-2.5 m before the population of caribou were able to catch up and kill these. For all intents and purposes, none of these sprouts have made their way into the canopy, possibly an escapement in the order of the 1971-72 escapement but we think less in fact. This sequence happened at a time when senescence was showing up in the sprout gardens and when most other forage plants were severely depleted or functionally extirpated. Earlier maple ingress into the sub-canopy was not occasioned by such severe coincident conditions; extrapolating the density that caribou were at in the past when maple escaped cannot be done directly from the 1990 case because the overall foraging situation was different. Maple escapement was probably possible in the past at the same or higher caribou density than that which fully suppressed it in this case. Whatever the fine details, the maple age record, and our caribou population monitoring since 1974, clearly document that caribou have been able to control the escapement of maple since at least c. 1930 on the Slate Islands. The absolute quantity of area in which maple occupied a sub-canopy position in those establishing stands is unknown, but it was extensive as indicated by the similarity between the four sampled stands, but still the interaction of caribou numbers with that resource is unknown. With good confidence we do extrapolate from the maple record and its current distribution that the mean population has been maintained at or above an average of approximately 200 caribou since 1950 at a minimum. Before that we know that caribou numbers were consistently high with respect to the available maple resource back at least to c. 1929.

Slate Islands population demography

Over the years we've encountered some persons (scientists, wildlife managers, and forest managers) who brush off the Slate Islands as not being able to seriously contribute to the debate on limiting factors for woodland caribou - they are islands and therefore different; we assume an impression from the theory of island biogeography that populations on islands are known to go extinct at higher rates than mainland populations is at the root. To us this is more correctly an opportunity to understand the species biology in extreme evolutionary conditions, and thereby such studies contribute to understanding the true limits to phenotypic and genetic plasticity of the species. This becomes a reality check against which all other conclusions about the species in other habitats must be considered. That is, if an assertion is not true in a natural experiment with pseudo-controlled critical variables, then it cannot be true in other circumstances. Any population that persists does so by producing sufficient recruitment and avoiding excessive mortality; observations of different behavioural tactics between ecotypic populations (Mallory & Hillis, 1998) which solve for mean R=M population viability over time do not falsify this truth.

The Slate Island population has persisted for 70+ years on an island archipelago in the absence of predators and in the absence of sufficient lichen for the maintenance of health in seemingly most if not all winters, and in periodic winters the population suffered outright starvation of moderate to large proportions. In 1949, in a period when winter availability of arboreal lichen litter-fall and tree blow-down would have been relatively negligible compared to our studies initiated in 1974, caribou browsed deciduous browse in the fashion of white-tailed deer or moose (*Alces alces*) (Cringan, 1956). This behaviour was not observed in our studies presumably because deciduous browse availability was approaching nil, or the species still available were not preferred.

In this study, females achieved pregnancy rates that are normal for caribou only in 1985 and 1990 when they weighed 100-105 kg the previous fall (Fig. 4). Cameron & Veer Hoef (1994) concluded that small shifts in mass distribution result in relatively large changes in parturition rates. Our results indicate a set-point weight for the Slate Islands that can be achieved following starvation in one growing season; with a major reduction in total caribou numbers, a female can reach her set-point in the next growing season. In June 1990, females averaged 83.6±3.26 kg (n=11) and three months later their mass was 101.2 kg resulting in 80% parous in 1991. Thus major increases in parturition rate in 1986 and 1991 occurred with major changes in mass (Figs. 4, 8). Winter forage conditions did not mitigate this rate; if winter forage would have, there was an expectation for other years that females entered winter in almost as good condition, and where die-offs did not occur, to have witnessed a high parous rate too. With animals dying over-winter, with survivors recovering on overgrazed range and starting from the worst possible body condition, in one growing season they achieved the normal pregnancy rate for females (Bergerud, 1980). It appears that a major adaptation of caribou to summer food shortage is to skip reproduction for the following year. The physiology of skipping was not investigated in this study but the small body size of younger cohorts and low average fall weights of adults suggests failure to ovulate.

The average deviation in the population estimates 1974-1992 is 38% of the mean estimate whereas from 1993-2003 it was 13.5%. There was a shift in stability in the population when the wolves arrived. This shift is not fully attributable to wolves since they were not present consistently through the period. They may have reversed an increase in the population that may have been shaping up when they first arrived in 1994 thereby stabilizing the population for 2 to 3 years in the relative sense, but the increase in caribou numbers continued after detectable wolf predation stopped in early 1996. The wolves left a footprint in the age structure of the living caribou that may have had a ripple effect on productivity as the impact of two missing cohorts (1994 and 1995) advanced through the population.

The second factor that has changed is the increase in the abundance and age of the conifer forest cover types. Two tree pathologies are present in abundance on the Slate Islands and interact with this increase in age and abundance of the conifers: armillaria root and butt rot is widespread making stems vulnerable to breakage and trees to wind-throw in windstorms; and spruce budworm although present and causing light damage earlier, was causing heavy tree mortality in the later years. Both the litter and dead fall indices 1979 to 1993 were positively curvilinear when plotted against year (Bergerud, 1996: Fig. 3).

The caribou of the Slate Islands are a good example of the "maintenance phenotype" (*sensu* Geist, 1998). The females are small bodied, the smallest of 21 populations (Butler, 1986: Fig. 11.12 p. 490). Yearlings do not reach puberty, nor do 2 year olds (Bergerud, 2001). Male and female antler lengths are the least of 17 populations (Butler, 1986: Fig. 11.10 p. 487). Again dimorphism is least on the Slate Islands of 30 populations (Butler, 1986: Fig. 11.7. p. 479). Maternal females and their calves are often apart; udder sizes at calving do no approach the size seen in other herds; males were also smallest of 19 populations; and antlerless males ("hummels") occur and do not grow any antlers until 3 or 4 years of age (and then they are diminutive) (Butler, 1986). The antlers of males have gotten smaller over the past 50 years (Bergerud, 2001). This maintenance phenotype enables them to persist in this food limited environment.

Pukaskwa National Park

The caribou population now appears headed for extinction. The count in 2007 was 5. For the interval 1974 to 1988, the dynamics suggested that wolf predation was density dependent (possibly chance encounters involved) (Bergerud, 1996: Fig. 3). Recruitment declined when numbers increased beyond 20 animals and adult mortality increased. Stochastic factors of snow depths and land fast ice were also considered to affect the contact rate between wolves and caribou. Bergerud (1989) had argued that the moose moved toward the Lake Superior shore in winters of deep snows increasing the presence of wolves. This directional movement was not supported by radio tracking 35 moose in two years (Burrows, 2001). The moose did make summer-winter movements, but they were mostly north and south, shifting to denser forest cover in winter and more deciduous in the summer. The second stochastic factor that should still be valid was the presence of land fast ice that allowed the wolves a lakeshore highway and sometime access to Otter Island (Bergerud, 1989). One counter-intuitive observation of a plus for caribou survival is that with climate change warming the area, the chance for shore-fast ice decreases. But the new negative is that the remaining animals are few and now concentrated in the vicinity of their key island. If the wolves in the two nearby packs had satellite collars that reported daily, a warden stationed at Otter Island could be alerted when wolves approached the shore and if land fast ice was present might possibly turn the packs back inland. Parks Canada has a splendid record of supporting research of this moose-caribou-wolf system and their endangered mammal. Caribou in the Park may have a chance until that day, which is coming, when white-tailed deer arrive and occupy the low snowfall belt along the Superior shore.

In summary, on the Slates Islands we studied an aging ecosystem which has been extensively modified by ungulate inhabitants, and pathologies in the forest canopy. Throughout seventy plus years, the population appears to have been primarily limited by summer food supply affecting over-winter survivorship and parous percentages with occasional stochastic interference by winter weather nudging the survivorship probabilities in either direction. The brief tenure of two wolves demonstrated the vulnerability of caribou to high wolf density. The potential for future persistence seems positive. In contrast, in spite of abundant food in all seasons, the caribou of PNP show little hope of future existence due to being flanked by healthy breeding wolf packs supported chiefly by moose as prey, and the threat of the arrival of white-tailed deer. Implementing the second stage of the crucial experiment on Michipicoten Island before caribou forage is over-grazed would buttress the less controlled examples of the Slates and other introductions which indicated that ecosystems without predators are limited bottom–up by food and those with wolves top-down by predation. The views in 1974 that predation was not regulatory has in most minds been laid aside, we have made some progress.

Acknowledgements

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Conditions for caribou persistence in the wolf-elk-caribou systems of the Canadian Rockies

Mark Hebblewhite[1], Jesse Whittington[2], Mark Bradley[3], Geoff Skinner[3], Alan Dibb[4], & Clifford A. White[2]

[1] Department of Zoology, University of British Columbia, Vancouver, BC, V6T 1Z4, Canada. *Present address*: Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, College of Forestry, University of Montana, Missoula, MT, 59812, USA (mark.hebblewhite@cfc.umt.edu).
[2] Parks Canada, Banff National Park, Box 900, Banff, Alberta, T1L 1K6, Canada.
[3] Parks Canada, Jasper National Park, Box 10, Jasper, Alberta, T0E 1E0, Canada.
[4] Parks Canada, Banff, Yoho and Kootenay National Parks, Box 220, Radium Hot Springs, B.C., V0A 1M0, Canada.

Abstract: Woodland caribou populations are considered threatened in Alberta and have declined in the Canadian Rocky Mountain National Parks of Banff and Jasper despite protection from factors causing caribou populations to decline outside of parks. Recent research emphasizes the importance of the numeric response of wolves to moose in moose-caribou-wolf systems to caribou persistence. Moose are rare in the Canadian Rockies, where the dominant ungulate prey for wolves is elk. Few studies have explored wolf-elk dynamics and none have examined implications for caribou. We used data collected in Banff to estimate the numeric response of wolves to elk from 1985 to 2005. Because no caribou kill-rate data exist for the Rockies, we explore the consequences of a range of hypothetical kill-rates based on kill-rates of alternate prey collected from 1985 to 2000 in Banff. We then multiplied the numeric response of wolves by the estimated caribou kill-rates to estimate the wolf predation response on caribou as a function of elk density. Caribou predation rates were inversely density dependent because wolf numbers depend on prey species besides caribou in multiple prey species systems. We then combined this simple wolf-elk-caribou model with observed demographic and population estimates for Banff and Jasper caribou from 2003-2004 and solved for the critical kill-rate thresholds above which caribou populations would decline. Using these critical kill-rate thresholds, Jasper caribou are likely to persist when wolf densities are below 2.1 - 4.3 wolves/1000km^2 and/or when elk densities are below 0.015- 0.033 elk/km^2. Thresholds for Banff caribou persistence are much lower because of inverse density dependence. Future research is needed on some of the necessary assumptions underlying our modeling including multi-prey wolf numeric responses, wolf kill-rates of caribou, caribou mortality by other predators, and spatial aspects of wolf-elk-caribou dynamics.

Key words: ecosystem management, endangered species, inverse density dependence, long-term range of variation, park management, predation, species at risk.

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Introduction

Common causes of species endangerment include habitat loss, fragmentation or alteration, over-hunting, and competition by invasive species, all of which can alter trophic relationships (Sinclair & Byrom, 2006). Where changes to trophic dynamics occur, predator-prey theory has been useful to understand the mechanisms causing declines and strategies to reverse them (Sinclair & Byrom 2006). For example, endangered species are often an alternate prey for an introduced or native predator (Sinclair *et al.*, 1998). Where ecosystem changes increase primary prey density, predation rates can increase to the point where endangered alternate prey can be driven to extinction (Sinclair *et al.*, 1998; Roemer *et al.*, 2002). A brief review of predator-prey theory for alternate prey reveals why.

Prey density influences both kill-rates (the functional response) and densities (the numeric response) of predators (Holling, 1959, Fig. 1). In single predator-prey systems, the functional response type (Fig. 1) determines whether predators regulate prey to low density (type II) or whether a high-density equilibrium is also possible (type III) (Messier, 1994). In single predator-prey systems predators can't drive prey extinct because predator density declines with declining prey density. In multi-prey systems, however, predator density can remain high as alternate prey decline because of primary prey (i.e., the numeric response of predators to alternate prey has a positive Y-intercept, Fig. 1, Messier, 1995). The consequences of combining a type II or III functional response with a numeric response with and without a Y-intercept for an alternate prey species are shown in Fig. 1 (from Messier, 1995). Fig. 1a illustrates predation that is inversely density dependent for the type II functional response with, but not without, a Y-intercept. As alternate prey decline, predators kill a higher percentage of the alternate prey population, triggering further declines. Thus, alternate prey density must stay above a critical density (P_c) for the population to persist (Sinclair *et al.*, 1998). Fig. 1b shows that for a type III functional response, there exists some low-density threshold (P^*) below which the total predation rate is density dependent. This implies a low-density state for alternate prey at P^* is possible. Both illustrate that given a Y-intercept, once alternate prey species decline past some threshold, regardless of the functional response type, further population declines are likely.

Woodland caribou (*Rangifer tarandus caribou*) are an endangered alternate prey species most frequently found in moose (*Alces alces*)-caribou-wolf (*Canis lupus*) systems throughout the boreal forests and western mountains of Canada (COSEWIC, 2002). Classified as threatened under the Species at Risk Act (SARA) (COSEWIC, 2002), caribou are thought to be declining throughout their range because of anthropogenic activities that are altering predator-prey dynamics (COSEWIC, 2002; McLoughlin *et al.*, 2003; Wittmer *et al.*, 2005a,b). Among the main factors is commercial forestry that converts old forests to early seral habitats, which support higher moose densities (Bergerud, 1988; Seip, 1992). Because of the strong numeric response of wolves to ungulate prey (Fuller, 1989), logging is thought to increase wolf density and thus predation rates on caribou. Anthropogenic activities have also been hypothesized to increase the functional response by increasing the effective rate of search and hence kill-rates for caribou. Seismic exploration lines, paved roads, and compacted snow trails have all been linked to increased movement by wolves (James & Stuart-Smith, 2000; Whittington, *et al.*, 2005), but despite the potential for increased predator efficiency, effects on population dynamics of caribou are uncertain. Focusing on population dynamics, Wittmer *et al.* (2005b) found inverse density dependence in predation mortality for woodland caribou in British Columbia, consistent with a type II functional response combined with a numeric response with a Y-intercept driven by increased densities of moose (Fig. 1a) (Messier, 1995). Under these conditions, caribou extinction below a critical population threshold is theoretically certain, regardless of changes to predator efficiency (Lessard, 2005).

While these mechanisms explain declines of woodland caribou outside protected areas, recent caribou declines in Banff and Jasper National Parks in the Canadian Rockies are puzzling. Anthropogenic activities such as forestry or oil and gas exploration do not occur within parks, yet caribou populations have declined since the mid 1980s paralleling provincial declines (Alberta Caribou Recovery Team, 2005, Parks Canada, unpubl. data). Furthermore, caribou in the Canadian Rockies exist in a wolf-elk (*Cervus elaphus*)-caribou system (Hebblewhite *et al.*, 2004), not in the more common moose-wolf-caribou system of the boreal and mountain caribou populations. Although wolf-elk dynamics have been studied in the Rockies (Hebblewhite *et al.*, 2004), they have received nowhere near the detailed study of moose-wolf dynamics (e.g. Messier, 1994). Thus it is uncertain whether results of wolf-moose-caribou studies can apply to the Canadian Rockies.

The purpose of this paper is to combine previous wolf-elk research with current caribou demography to understand conditions for caribou persistence in the Canadian Rockies. First, we modeled the numeric response of wolves to changing elk density using a 20-year time-series from a wolf-elk system overlapping the Banff caribou population (Hebblewhite *et al.*, 2002). Unfortunately, kill-rate data were unavailable to estimate the functional response of wolves preying on caribou. Instead, we varied kill-rates over a plausible range to explore the consequences of variation in caribou kill-rates on total predation rates for a given wolf and elk density. Finally, we compared the range of modeled caribou predation rates to observed caribou demographic data from Jasper for 2003-2004. By varying kill-rate and predation rate, we solved for the critical elk (and hence wolf) density above which present caribou populations in Banff and Jasper would decline (Sinclair *et al.*, 1998).

Study area

The study area was along the eastern slopes of the Canadian Rockies in Banff and Jasper National Parks (Banff and Jasper hereafter, Fig. 2) in the province of Alberta (AB) and a small adjacent area of British Columbia (BC). Topography is extreme, ranging from 1000 m to 3500 m in elevation, and climate is characterized by long, cold winters, and short summers with most precipitation occurring in spring. Banff is 6641 km^2 and Jasper is 10 500 km^2 in area. The land-

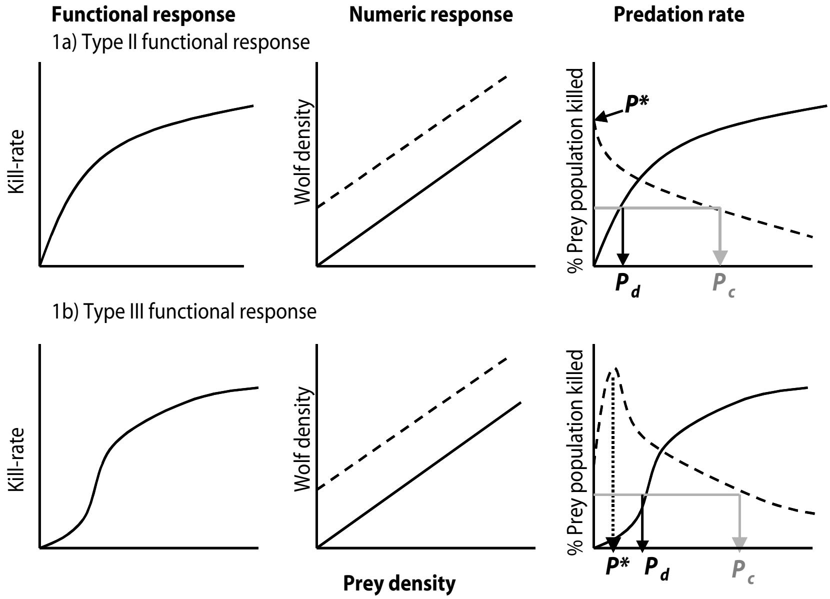

Fig. 1. Functional responses, numeric responses, and predation rates for a) type II and b) type III functional responses with (dashed line) and without (solid line) a numeric response with a Y-intercept, for a multiple prey system. For a given predation rate, some prey populations have a critical density below which their population will decline to extinction. Without a Y-intercept, the prey population is regulated to some low density, P_d, for a given critical % mortality rate (grey line). In the presence of a Y-intercept, however, predation rate is inversely density dependent, and for a given critical % mortality rate, P_c, prey density P^* declines to extinction under type II functional response, or a very low density in the presence of a type III functional response. Adapted from Messier (1994, 1995) and Dale *et al.* (1994).

scape is ecologically classified into the montane, subalpine, and alpine ecoregions (Holland & Coen, 1983). The montane ecoregion occurs in low elevation valley bottoms, contains the highest quality habitat for wolves and elk, and is characterized by lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*) forests interspersed with riparian white spruce (*Picea glauca*) – willow (*Salix* spp.) areas, aspen (*Populus tremuloides*) – parkland, and grassland systems. Subalpine and alpine ecoregions are comprised of Engelmann spruce (*Picea engelmannii*) – subalpine fir (*Abies lasiocarpa*) – lodgepole pine forest interspersed with willow-shrub meadow riparian communities, subalpine grasslands, and avalanche terrain, giving way to open shrub-forb meadows in the alpine ecoregion. In south Jasper and Banff, caribou seasonally migrate between alpine and subalpine ecoregions in the summer and winter, respectively. Elk migrate seasonally between the montane and alpine ecoregions in the summer. Wolves are the primary predator of elk, and other alternate prey species include white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), moose, bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*). See Holland & Coen (1983) and Holroyd & Van Tighem (1983) for a more detailed description of the study area.

Caribou occur in four separate sub-populations in the Canadian Rockies National Parks: one in northern Banff, one in northern Jasper, and two in southern Jasper (Fig. 2) (Alberta Woodland Caribou Recovery Team, 2005). Caribou occurring in northern Jasper (the A La Peche sub-population) migrate to winter range in the province of AB and their conservation is considered elsewhere (Smith 2004; Alberta Woodland Caribou Recovery Team, 2005). The North Banff sub-population is very small (approximately five animals) and has much lower genetic variability than the two larger south Jasper sub-populations (Parks Canada, unpubl. data). Historically, it was assumed caribou moved between the Banff and Jasper populations and adjacent provincial populations, but dispersal between subpopulations has never been confirmed (Parks Canada, unpubl. data). From a Parks Canada management perspective, management of the Jasper and Banff herds are considered part of the Alberta recovery strategy (Alberta Woodland Caribou Recovery Team, 2005), and action plans for caribou recovery are presently being developed in Jasper and Banff (Van Tighem *et al.*, 2005).

Methods

Numeric response

We estimated the numeric response of wolves to only their primary prey, elk, in a study area for which wolf and elk densities were recorded from 1987-2005 in only the Bow Valley study area (Fig. 2). Wolf numbers were assumed to respond only to the density of their primary prey, elk, not alternate prey. This approach was used instead of using a wolf- total ungulate biomass equation (Fuller, 1989) for the following reasons; 1) wolf abundance in Canadian Rockies is largely driven by elk density (Hebblewhite, 2000), 2) wolves in the Rockies are highly selective for elk (Huggard, 1993), and other studies confirmed the density of preferred prey strongly influences the multi-species wolf numeric response (Dale *et al.*, 1995, Mech *et al.*, 1998); and 3) the rugged terrain of the Rockies allows strong spatial separation of some relatively abundant secondary prey species (e.g., bighorn sheep) from elk (Holroyd & Van Tighem, 1983), limiting their influence on wolf numbers (e.g., Dale *et al.*, 1995; Mech *et al.*, 1998). Poor model fit between elk and wolf density would invalidate these assumptions and suggest alternate prey density should be included.

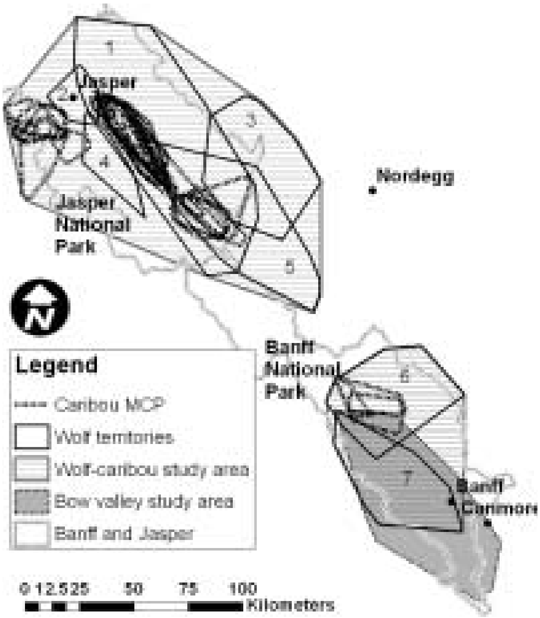

Fig. 2. Study area location in western Canada (see inset) showing annual winter home ranges for caribou (dashed) and multi-annual winter wolf territories (solid), respectively, from 2003 - 2004 in Banff National Park (Banff) and southern Jasper National Park (Jasper), Alberta, Canada. Cross-hatched areas are the Banff and Jasper wolf-caribou study areas used to estimate densities, and the shaded area is the Bow Valley study area in which wolf and elk densities were recorded from 1985 to 2003 to estimate the numeric response (see text). Numbers represent wolf packs; 1) Maligne, 2) Signal (town), 3) Brazeau, 4) Sunwapta, 5) Medicine, 6) Red Deer, and 7) Bow Valley.

We defined the Bow Valley study area for 1985-2005 using the 100% minimum convex polygon (MCP) of all locations from 3 wolf packs. We estimated wolf numbers within this area following Hebblewhite *et al.* (2002), and elk density using aerial surveys during late winter (Hebblewhite *et al.*, 2002). We only considered elk west of the Banff townsite available to wolves, because Hebblewhite *et al.* (2002) showed Banff townsite elk were regulated by food, not wolf predation, and were generally unavailable to wolves. We corrected for incomplete sightability of elk following an aerial sightability adjustment of 87% developed by Hebblewhite (2000). We then estimated the numeric response of wolf density (reported in wolves/1000km^2) to elk density by fitting linear and non-linear (type II and III) regression using least-squares in STATA (StataCorp, 2003). The highest-ranking model was selected using AIC$_c$ (Burnham & Anderson, 1998).

Functional response - kill-rate variation

In the absence of caribou kill-rates, we selected a realistic range of alternate prey kill-rates to explore the consequences for caribou dynamics. We evaluated the effects of caribou kill-rates from 0 to 0.01 caribou/day/wolf (~0 to 13 caribou/pack/ 181 day winter). For comparison, these were close to observed kill-rates for the next rarest prey species, moose (Hebblewhite *et al.*, 2004).

Total predation response

We multiplied the number of wolves predicted by the numeric response (as a function of elk density) by the range of hypothetical caribou kill-rates to predict the total number of caribou killed per unit time. We then calculated the proportion of the total caribou population killed per winter (i.e., mortality rate) as a function of the Banff and Jasper caribou densities (see below) following:

$$M_{ww} = \frac{D_w \mathrm{K}}{D_c} \qquad \text{(eq. 1)}$$

where M_{ww} is the wolf-caused winter mortality rate, D_w is the wolf density as predicted from the numeric response to elk density, K is the caribou kill rate per wolf, and D_c is the caribou density.

Caribou demography and population size

We evaluated the effects of the mortality rates from eq. 1 on caribou population growth rate given demography for the south Jasper sub-population (not Banff because of low sample size) using the approach of Hatter & Bergerud (1991). Lambda (λ), population growth rate in year t was estimated during biological years 2003 and 2004 following:

$$\text{(eq. 2)} \qquad \lambda_t = \frac{(1\text{-}M_t)}{(1\text{-}R_t)}$$

where M_t is adult female mortality rate (or 1- S_t, the survival rate) and R_t is the recruitment rate of female calves:100 cows (assuming a 50:50 sex ratio) at 12 months of age. Confidence intervals for λ were calculated using 95% confidence intervals for M_t and R_t.

To estimate adult female survival we captured female caribou in from 2001-2005 using helicopter netgunning. GPS collars (Lotek GPS 2200 collars, Aurora, ON) were deployed from 2002-2005 on 18 caribou which were monitored 1.6 years each (SD±0.4). We analyzed survival using Cox-proportional hazards regression (Therneau and Grambsch 2000) for one pooled survival rate. The sample size of collared caribou in any year (~n=11) was ~29% of the total adult female population size, thus we adjusted standard errors of survival estimators with a finite population correction factor of $((N - n)/N)$ where N was the average number of females during the study (2003-2004), and n was the average annual sample of radio-marked females (Thompson, 1992). The number of adult females using population estimates and calf:cow ratios (see below), assuming 35% of adult caribou were male (Smith, 2004). We also determined cause specific mortality (wolf, other) rates from radio-collared females in this and an earlier study (Brown *et al.*, 1994).

We estimated the size of Banff and Jasper caribou populations during fall 2004 and 2005 using helicopter (Bell 206 Jet Ranger) aerial surveys when sightability was highest because of the rut (Brown *et al.*, 1994; Parks Canada, unpubl. data). In Jasper we corrected for incomplete sightability by using the proportion of radio-marked caribou observed, and calculated 95% confidence intervals using the joint hyper-geometric maximum likelihood estimator (White & Garrott, 1990). Banff surveys were considered a complete census because of low sample sizes. We determined March recruitment rates using fall calf:cow ratios obtained on aerial surveys and then adjusting for an additional 15% overwinter mortality following Smith (2004). We adopted this approach because of the difficulty of distinguishing subadult males from females during March calf:cow surveys. Fall classification was conducted after observing caribou on aerial surveys (see below) by landing close enough to classify individuals using a 60x spotting scope, and thus represented true calf:cow ratios. Standard errors on calf:cow ratios were calculated assuming binomial error distribution (Czaplewski *et al.*, 1983). Standard errors were adjusted using a finite population correction factor based on the number of females following the approach described above for survival.

Calculating caribou, elk, and wolf density

We defined the entire wolf-caribou study area (Fig. 2) using a minimum convex polygon (MCP) surrounding all caribou MCP's and overlapping winter wolf MCP's from 2003-2005 to define densities at the appropriate scale of wolf packs occupying caribou ranges (Lessard, 2005). We estimated 100% multi-winter MCP's from GPS collar (LOTEK GPS 3300sw, and ATS GPS 2000) locations from wolves and caribou in Jasper (Parks Canada, N. Webb, University of Alberta, unpubl. data) and Banff (Hebblewhite *et al.*, 2006). Caribou density within the study area was obtained from the aerial surveys described above. We estimated wolf density using radio-telemetry based methods (Burch *et al.*, 2005). Wolf radio-telemetry data was collected from the two Banff packs and three of the five Jasper wolf packs (Signal, Brazeau, and Medicine) in 2003/04 and 2004/05. The Maligne Pack was only radio-collared in 2004/05, and the Sunwapta Pack not until 2005/06. Because snow-tracking data (unpubl.data) confirmed these 2 packs used the same areas during 2003-2005, we used the 2004/05 MCP for the Maligne pack and the 2005/06 MCP for the Sunwapta pack. We estimated winter wolf pack counts from aerial observations and ground snow tracking to calculate wolf density within this wolf-caribou study area following Burch *et al.* (2005), but did not adjust for lone wolves.

In Banff, elk density was calculated from aerial survey data in the western Bow Valley and Red deer valleys (Hebblewhite *et al.*, 2002; Hebblewhite *et al.*, 2006), corrected for aerial sightability as described above. Elk in Jasper were only surveyed from the ground during early winter in 2004 and 2005. We used a ground sightability model developed in west Yellowstone by Eberhardt *et al.* (1998) to correct ground counts. One further problem was dealing with elk unavailable to wolves surrounding the town of Jasper. Based on research in Banff, we assumed 200 elk surrounding the town of Jasper were unavailable to Jasper wolves (e.g., Hebblewhite *et al.*, 2002).

Evaluating consequences for caribou persistence

We substituted wolf, elk and caribou densities from Jasper and Banff into eq. 1 to calculate wolf-caused caribou mortality rates over a range of kill-rates. We then combined eq. 1 and eq. 2 to solve for caribou kill-rates that predicted λ = 0 by making two assumptions. First, the proportion of caribou killed by wolves in winter was estimated based on data as

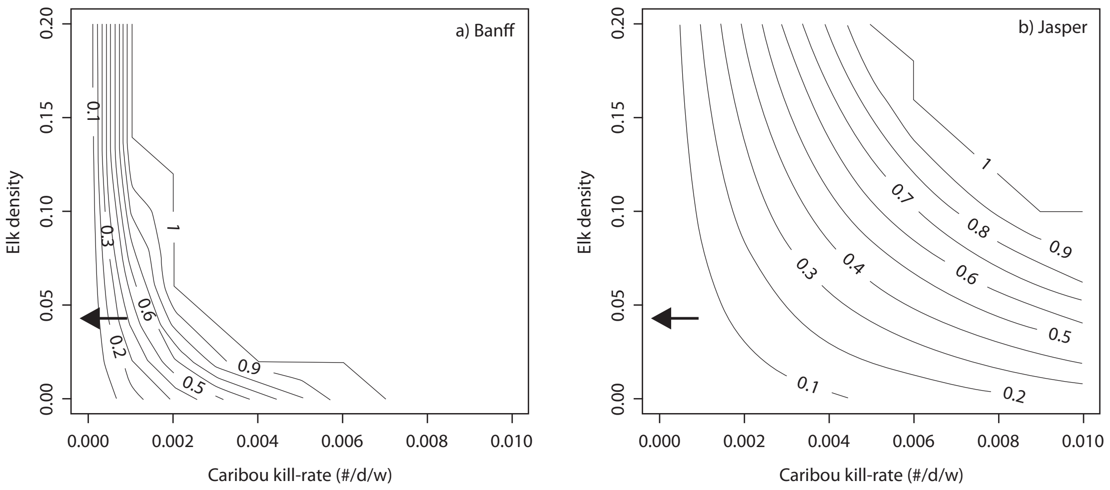

Fig. 3. Proportion of the a) Banff and b) Jasper caribou populations killed per winter (contours) by wolves as a function of elk density and a range of hypothetical wolf kill-rates (caribou killed per day per pack). Given current demography, caribou decline above a threshold of 0.15 and 0.20 wolf-caused mortality rate in Banff and Jasper. Differences between Banff and Jasper arise because of inverse density dependence in total predation rate driven by elk density (arrows mark current elk density).

0.75 (see below) to convert to annual rates. Second, the proportion of adult caribou killed that was female was assumed to be 0.75 (based on Adams *et al.*, 1995). Calf mortality was accounted for by recruitment. Combining eq. 1 and 2, we solved the following equation for $\lambda_\tau = 0$

(eq. 3)
$$\lambda_t = \frac{\left[1 - \frac{M_{ww}}{\alpha}\tau + \omega(1-S_t)\right]}{(1-R_t)}$$

where M_{ww} is from eq. 1, α is the proportion of caribou killed in the winter (0.75), τ is the proportion of adult caribou killed by wolves that are female (0.75), ω is the proportion of baseline mortality that is non-wolf related, S_t is the adult female survival rate, and R_t is from eq. 2. We used radiocollared mortalities from this (2001-2006) and an earlier study (Brown *et al.*, 1994) to estimate ω. The first term in the numerator is the annual wolf caused mortality rate and the second term is the non-wolf caused mortality rate. Setting $\lambda = 0$ yields the threshold kill-rate above which caribou decline, given current elk and wolf densities, and can also be expressed as the maximum wolf-caused mortality rate. Using this threshold kill-rate, and setting $\lambda = 0$, we then solved for the wolf (D_w) and elk density (D_e) above which caribou would decline.

In any modeling effort, uncertainty and sensitivity of model parameters on final model conclusions should be addressed (e.g., Wisdom & Mills, 1997). We addressed uncertainty in threshold estimates of kill-rate and elk/wolf densities by incorporating uncertainty in R_τ and M_τ in eq. 3. Sensitivity of equation 4 was assessed by examining the % change in λ as a result of infinitesimally small, one-at-a-time changes (e.g., Wisdom & Mills, 1997) in parameters for Jasper and Banff populations using PopTools (Hood, 2001). Sensitivity is standardized so that values sum to 1 for ease of comparison between populations.

Results

Numeric and functional responses

A linear numeric response was the best fitting of the three models fit to the wolf and elk density data; linear ΔAICc = 0, decelerating type II ΔAICc = 1.66, and the sigmoid type III ΔAICc = 4.83. Elk density explained 74% of the variance in wolf density ($F_{1,17} = 49.2$, $P < 0.0005$), according to the following model $D_w = 0.00082 + 0.0374D_e$. The strong relationship supported our approach to model wolf density using only primary prey density. Critically, the Y-intercept was significant (SE = 0.00032, $P = 0.020$). Note that Messier (2005) confirmed the Y-intercept was the most important aspect of the numeric response for multi-prey systems: considering a type II numeric response with a Y-intercept would not change our results (Messier, 2005).

Effects of caribou kill-rates and elk density on the total predation response

Results of using eq. 3 to explore the relationship between caribou kill-rates, wolf and elk density from Table 1 on caribou predation rate for the two caribou populations are summarized in Fig. 3. Generally, as

Table 1. Summary table of caribou demography and caribou, wolf and elk density for the Banff National Park and Jasper National Park caribou sub-populations, 2003 – 2004. The Banff and Jasper study areas were 4283 km^2 and 12 512 km^2 in size, respectively.

	Banff			Jasper		
Caribou	2003	2004	Mean	2003	2004	Mean
Number	4	5	4.50	107 (86-174)[e]	100 (56-336)[e]	103.5
Proportion of population collared	0.25	0.20		0.10	0.07	
Density (# / $1000km^2$)	0.93	1.17	1.05	8.55	7.99	8.27
Adult female survival[a]	1	1	1.00	0.93 (0.81 – 0.98)		
Recruitment[b]	0.25	0	0.13	0.42 (34-51)	0.32 (24-32)	0.37
Lambda[c]	--	--	--	1.18 (0.92-1.32)	1.11 (0.87-1.24)	1.14
Elk						
Number[d]	130	169	149	406	539	473
Density (# / km^2)	0.030	0.039	0.03	0.032	0.043	0.038
Wolf						
Number	14	16	15	30	41	35.5
Density (# / $1000km^2$)	3.27	3.74	3.50	2.40	3.28	2.84

[a] Adult female survival SE adjusted for finite population size.

[b] Number of calves per 100 cows in March calculated assuming 15% mortality overwinter from Fall calf:cow surveys, 90% confidence interval adjusted for finite population size.

[c] Lambda calculated for Banff as N_{t+1}/N_t (unreported caribou count in 2006 used for 2005 lambda was 4), and eq. 3 following Hatter & Bergerud (1991).

[d] Banff aerial elk counts adjusted for aerial sightability following Hebblewhite (2000), Jasper ground elk roadside counts adjusted for ground sightability following Eberhardt *et al*. (1998).

[e] Hypergeometric 95% confidence interval on mark-resight population estimator.

caribou kill-rates increase, regardless of density (or vice versa), the total predation rate increased for both populations (Fig. 3). However, the dramatically higher susceptibility of the Banff population to increasing kill-rate (Fig. 3a) is because lower caribou density (Table 1) causes strong inverse density dependence with changes to elk density in predation rate, a function of the Y-intercept in the numeric response (e.g., Fig. 1a). In contrast, the Jasper population can withstand much higher elk and caribou kill-rates because of their relatively higher density (Table 1, Fig. 3b).

Caribou demography and population size

Banff surveys counted 4 and 5 total caribou in 2003 and 2004 (Table 1). In Jasper, caribou population size appeared stable throughout the study, at 107 and 100 (Table 1). Confidence intervals from mark-recapture estimates were wide as a result of sparse counts and the low collared proportion resighted in 2004 (3 of 7, vs 8 of 11 in 2003). Survival for 29-caribou years over the pooled two-year period was 0.932 (Table 1) with wide confidence intervals despite the finite population correction (22% of adult females were collared). Wolves killed ~50% of radiocollared caribou during both the early (6 of 12) and present (2002-2006) studies (3 of 7). Other predators (bears), road-kills, and accidents (drowning, avalanches) comprised the remaining sources of mortality. Thus, we set ω = 0.5 in Eq. 3. Furthermore, in contrast to many other populations (e.g., Wittmer *et al*., 2005a), 6 of 8 (75%) wolf-caused caribou mortalities occurred during winter, thus we set α = 0.75 in Eq. 3. Fall recruitment rates adjusted for 15% overwinter mortality were 42 calves:100 cows in 2003, and 32:100 in 2004 (Table 1). A higher proportion of females were observed during recruitment surveys, 40% and 48% in 2003 and 2004, respectively, narrowing confidence intervals (Table 1). Population growth rates (λ) were 1.18, and 1.14 in 2003-2005, with confidence intervals overlapping zero (Table 1).

Table 2. Threshold elk and wolf densities above which caribou populations decline (i.e., $\lambda < 1$) at kill-rate values (see subscripts) that caused mortality to exceed recruitment for the southern Jasper National Park and Banff National Park caribou populations. Differences in Jasper thresholds between years were a result of higher calf recruitment in 2003. See eq. 3 and text for how thresholds were calculated.

	Elk density (# / km^2)	95% CI[d]	Wolf density (#/1000km^2)	95% CI[d]
JNP 2003[a]	0.078	0.04 – 0.14	4.3	1.9 – 7.9
JNP 2004[b]	0.033	0.02 – 0.06	2.1	1.0 – 3.7
BNP 2003/04[c]	0.015	0 – 0.20	1.8	1.0 – 2.0

[a] Evaluated at a kill-rate of 0.0034 caribou/day/wolf from eq. 3.

[b] Evaluated at a kill-rate of 0.0068 caribou/day/wolf from eq. 3.

[c] Evaluated at a kill-rate of 0.00035 caribou/day/wolf, and Banff thresholds were calculated assuming adult female survival and juvenile recruitment were equal to Jasper.

[d] 95% confidence intervals reported by evaluating eq. 3 using 95% CI for R_t and M_t.

Table 3. Sensitivity analyses for eq. 3 revealing the proportion of the variance in population growth rate, λ, explained by parameters, for the southern Jasper and Banff caribou sub-populations, 2003-2004. Sensitivity was evaluated using one at a time proportional changes to each parameter holding effects of other parameters constant at the values reported in Table 1, and are reported as standardized sensitivities summing to 1.

		Jasper		Banff	
Parameter	Description	Sensitivity	Rank	Sensitivity	Rank
a	% Caribou killed in the winter	0.001	8	0.001	8
t	% Adult female caribou killed by wolves	0.001	7	0.001	7
w	% Non-wolf mortality	0.025	6	0.006	6
St	Adult female caribou survival	0.187	2	0.045	5
Rt	Recruitment rate	0.447	1	0.098	4
Dw	Wolf density	0.158	3	0.128	3
Dc	Caribou density	0.054	5	0.425	1
K	Caribiou kill-rate/ wolf/ day	0.128	4	0.298	2

Caribou, elk, and wolf density

For the Banff wolf-study area, caribou density was extremely low, less than 1.2 caribou/1000 km^2. Caribou density in Jasper was seven times higher around 8 caribou/1000 km^2 (Table 1). Elk densities were similar in Jasper and Banff (Table 1). We report elk densities in Banff for both the Red Deer and Bow Valley - elk densities in the Bow Valley were more than 50% lower in 2005 (0.016 elk/km^2) than that of the Red Deer Valley (0.038 elk/km^2, Table 1).

Evaluating consequences for caribou persistence

Substituting observed wolf, elk, and caribou density and demography from Jasper into equation 3 yielded a threshold of 0.0034 caribou/day/wolf in 2004 to 0.0068 in 2004, or 4-9 caribou/winter/pack above which caribou would decline at present recruitment rates. We assumed adult female survival in Banff was the same as Jasper because there was too few collared caribou for survival estimation. Using Jasper survival rates with Banff recruitment yielded a threshold caribou kill-rate of 0.0006 caribou/day/wolf, or <1 caribou/winter/wolf pack. These kill-rate thresholds corresponded to maximum sustainable annual caribou mortality rates caused by wolves of 0.15 and 0.17 in Jasper during 2004 and 2003, respectively, and 0.05 in Banff. Thus, rearranging equation 3 using this general wolf-caused mortality threshold to solve for elk (and thus wolf density) yielded threshold elk and wolf densities (averaged for 2003 and 2004) in Jasper of 0.056 elk/km^2 and 3.2 wolves/ 1000 km^2, respectively (Table 2). In Banff, thresholds were much lower following Fig. 1 such that caribou populations would be expected to decline above elk and wolf densities of 0.02 elk/km^2 and 1.8 wolves / 1000 km^2 (Table 2).

Sensitivity and uncertainty

Thresholds for caribou persistence were quite variable given wide variation in survival recruitment (Table 2). Jasper caribou would be expected to decline given the upper 95% confidence interval for R_t and S_t once elk densities exceeded 0.14 elk/km^2, with a corresponding wolf density of 7.9 wolves/1000 km^2 (Table 2). In Banff, even assuming the upper 95% CI for demographic rates yielded upper thresholds of 0.21 elk/km^2 and 2.1 wolves/km^2 (Table 2). Sensitivity analysis revealed differences between Jasper and Banff in the consequences of perturbations in parameter values to λ. With higher caribou density in Jasper (Table 1), λ was most sensitive to changes in recruitment (the proportion of the variance in λ explained by this parameter = 0.447), adult survival (0.187), wolf density (0.158) and wolf kill-rates of caribou (0.129, Table 3). Other parameters had sensitivities <0.05. In contrast, under low caribou density in Banff, λ was most sensitive to changes in caribou density (0.425), wolf kill-rate of caribou (0.127), wolf density (0.127), and recruitment (0.099), with other parameters having <0.05 effects on λ (Table 3). Notably, parameters for which data were assumed for both populations, i.e., α, τ, ω, had minimal effect on λ in sensitivity analyses.

Discussion

Our simple modeling approach used caribou vital rates, the numeric response of wolves to elk density, and caribou, wolf, and elk density to solve for the critical kill-rates that would predict stable growth rates of caribou. We then calculated the threshold for elk and wolf densities above which caribou growth rates would decline. At present densities, given even modest wolf predation rates, extirpation of caribou in Banff is likely, while the higher density Jasper caribou population appears to be within the ranges of viability. The difference between the Banff and Jasper populations is consistent with inverse density dependence in predation rates by wolves subsisting on primary prey (elk) as caribou decline (Fig. 1a). These results echo other recent studies of endangered prey species. Sinclair *et al.* (1998) showed several species of endangered Australian marsupials being driven extinct by predators because of high densities of primary prey. On the Channel Islands off the coast of California, Roemer *et al.* (2002) found predation by golden eagles (*Aquila chrysaetos*) was driving endangered channel island fox (*Urocyon littoralis*) extinct because eagles were numerically buoyed by abundant feral pigs (*Sus scrofa*). These cases are clear examples of apparent competition between a primary and secondary prey species driven by human-caused perturbations.

A consensus that caribou abundance is mediated by the abundance of primary prey is emerging from both empirical (Bergerud, 1988; Seip, 1992; Kinley & Apps, 2001; Wittmer *et al.*, 2005a) and theoretical grounds (Lessard, 2005; Lessard *et al.*, 2005). As perhaps the strongest evidence for this, Wittmer *et al.* (2005b) clearly demonstrated inverse density dependence in caribou population growth rates immediately west of our study area in southeastern BC. Only one caribou sub-population with less than 200 caribou had positive population growth rates over a 10-year period (Wittmer *et al.*, 2005a; b). Wittmer *et al.* (2005b) concluded predator density, buoyed by high moose and deer density, and not food limitation related to habitat loss of old growth forests, were driving caribou declines.

Recent modeling suggest our thresholds for caribou persistence in wolf-elk systems may be lower than boreal or foothills populations. In the foothills of the Rockies, Lessard (2005) showed caribou declined when wolf densities exceeded ~8 wolves/1000 km^2 following increases in moose because of forestry. This was remarkably close to Bergerud's (1988) threshold of 6.5 wolves/1000 km^2 for caribou declines amongst boreal caribou populations. Reasons for the difference between boreal and foothills thresholds and ours could arise from differences between moose and elk, lower net primary production, and lower caribou density in the Rockies. Almost 50% of the Canadian Rockies is rock and ice, and are likely more spatially complex than boreal systems. Patchy mountain landscapes may lead to higher travel and encounter rates for predators because predators searching for patches of primary prey (elk) are more likely to travel through areas of alternate prey (caribou) (Huggard, 1993; Lessard, 2005). Solitary living moose may also ensure frequent encounters relative to group living elk. Elk may have lower per-capita encounter rates because groups, not individuals, are encountered, and wolves would experience group-level patch depression (Huggard, 1993). This could also contribute to higher wolf encounter rates with caribou (Huggard, 1993; Lessard, 2005). Reduced net primary productivity in mountain environments would reduce productivity of both elk and caribou populations, leading to higher vulnerability to predation (Lessard, 2005).

Sensitivity analyses further support the role of inverse density dependence in predation rate. Caribou growth rates showed remarkably different sensitivity between Jasper and Banff (Table 3). At higher caribou density in Jasper, key parameters influencing λ were recruitment rate, adult female survival, wolf density and wolf kill-rate of caribou. Recruitment rate and adult survival explained ~65% of the variance in λ. In contrast, λ for the low density Banff caribou was most sensitive to caribou density, wolf kill-rates, and wolf density. Recruitment rate and survival of adults explained less than one-fifth the variance in λ in Banff as in Jasper (Table 3). Because caribou density is determined at the wolf pack scale, the top three factors influencing λ in Banff were wolf predation related.

Jasper caribou vital rates and demography were similar or higher than other mountain and boreal caribou populations. Southern Jasper adult survival, calf recruitment and population growth rate was similar to the northern Jasper A La Peche herd, where survival was 0.919, calf recruitment 28:100, and population growth was 1.061 (Smith, 2004, Table 1). Outside of National Parks in the foothills of Alberta, however, caribou populations were stable ($\lambda=\sim1.0$) in the Red Rock-Prairie Creek area or rapidly declining in the Little Smoky river ($\lambda=0.88$). And on the western slopes of the Canadian Rockies in British Columbia, survival varied from 0.55 to 0.96 and calf: adult ratios averaged ~12:100, and these low vital rates were causing ~7 of 10 populations to decline (Wittmer *et al.*, 2005b). Boreal caribou populations in Alberta had similar or slightly lower survival rates of 0.86 – 0.93 (McLoughlin *et al.*, 2003), and variable recruitment of 11-22 calves:100 cows that resulted in 2 of 6 populations declining. For calf recruitment, Bergerud & Elliot (1998) reported that under wolf densities of 6.5, caribou calf:cow ratios would need to be > 19:100. Thus, Jasper vital rates were higher than in landscapes influenced by oil and gas exploration and forestry, consistent with hypotheses for anthropogenic influences on caribou decline in Alberta and British Columbia. While caribou in Jasper have certainly declined from the late 1980s when population size was approximately 200, the population may be increasing or stable at present. Survival rates were 0.66 during an earlier study (Brown *et al.*, 1994) when most mortality was wolf related and regional wolf numbers were high following recolonization (e.g., Hebblewhite *et al.*, 2006). One interpretation is recolonizing wolves reduced caribou densities in Banff and Jasper in the 1980's, but following declines in elk in Jasper at least, wolves stabilized to below thresholds for caribou declines. Regardless, given the grim state of caribou outside parks (Smith, 2004; Wittmer *et al.*, 2005b), the relatively high growth rates observed in this study suggests an important potential role of Jasper as a regional source population in the future.

Persistence of the Banff population is unlikely considering results of previous studies (Kinley & Apps, 2001; McLoughlin *et al.*, 2003; Wittmer *et al.*, 2005a; b). Of the smaller subpopulations of caribou in southeastern BC reported by Wittmer *et al.* (2005b), the southern Purcells ($n=6$) and George mountain herds ($n=4$), were extirpated by 2006 (R. Serrouya, pers. comm.). These two subpopulations had intrinsic growth rates (r) of -0.18 (Wittmer *et al.*, 2005b). Based on maximum counts of the Banff caribou population of 25-40 in 1988 (Parks Canada, unpubl. data) and 4 in 2005 (Table 1), r for Banff for this period = -0.13. Given present wolf and elk densities, especially in the Red Deer Valley, extirpation appears likely. Furthermore, demographic stochasticity will significantly reduce expected growth rates even more, making extinction almost certain (Boyce *et al.*, 2006). To recover Banff caribou, active recovery strategies such as those adopted for other small endangered caribou populations in the Alberta and British Columbia recovery plans will be required (e.g., Alberta Woodland Caribou Recovery Team, 2005).

Such grim predictions seem warranted because neither empirical studies (Wittmer *et al.*, 2005a) nor modeling (Lessard *et al.*, 2005) found evidence for the low-density spatial refugia scenario in Fig. 1b under a type III functional response. A spatial refuge would ensure that wolves were not able to extirpate alternate prey like caribou at high primary prey densities such as seen in Fig. 1b where P^* is >0; P^* represents the density surviving because of the spatial refuge. Lessard (2005) described conditions that would favor existence of spatial refugia: habitat differentiation between elk and caribou, favored habitats (e.g., old-growth) by caribou must not be limiting, low spatial overlap between caribou and elk, elk density must be higher than caribou density, and the ratio of the scale of predator search behavior is small relative to both ungulate and habitat patch scales. Lessard (2005) indicated that in foothills caribou existing with industrial development, many conditions would be violated. In the Canadian National Parks, however, the first four conditions may arguably be met, dependent on the spatial structure of prescribed fire management. In the absence of human development, fire is the dominant natural process that influences the spatial arrangement of favored caribou habitat (late seral), habitat overlap, and patch size (Shepherd, 2006). Restoration of the role of fire in maintaining vegetation communities is an important objective of Parks Canada's management plans (White *et al.*, 1998; Parks Canada, 1997). Shepherd (2006) showed that Jasper caribou selected forests older than 150 years. Prescribed burning should maintain the long-term spatial patterns of fire frequency that favored persistence of old growth forests at higher elevations and on north-east aspects (Tande, 1979; Rogeau *et al.*, 2004). Implementation of a widespread and diffuse prescribed fire program that burned in or near preferred caribou habitat would reduce spatial overlap and create smaller habitat patches increasing predation rates on caribou. The most difficult condition for a refuge, however, is the spatial structure of wolf search behavior relative to size of forest patches and overlap between caribou and elk. Generally, Lessard (2005)'s results imply prescribed fire should occur in large patches far from caribou ranges. But how far will depend on the spatial scale of wolves, and whether the large-scale numeric response of wolves to elk density following fire could eliminate small-scale spatial refugia for caribou. Spatial extensions of the modeling framework developed here with elk and wolf spatial models (e.g., Hebblewhite *et al.*, 2005a) will be required to test for the presence of spatial refugia and the interaction with prescribed fire.

Our simple modeling approach pooled caribou from two separate subpopulations within southern Jasper, the Tonquin and Maligne-Brazeau herds. Density thresholds presented here assume the southern Jasper herd is not subdivided, and are therefore likely optimistic. Movements between these two herds have not been observed (Parks Canada, unpubl. data). Effective caribou density could therefore be lower in each of these sub-herds than our modeling results for the pooled 'population'. This would render both herds more susceptible to inverse density dependence in wolf predation depending, again, on the spatial overlap of wolves, elk and caribou. Future analyses should examine spatial caribou meta-population dynamics.

The simple approach we took to modeling caribou population dynamics clearly has room for other improvements. The lack of kill-rate data of wolves on caribou in the Rockies and elsewhere (Lessard, 2005) poses a major problem to modeling predator-prey dynamics, and is surely a major weakness in our analysis. New approaches could be used to estimate kill-rates of wolves using GPS locations for wolves to predict prey species kill-rates (Sand *et al.*, 2005). Diet composition studies through scat analysis could aid interpretation of GPS kill-rate analyses. Another major limitation was obviously low confidence in adult female survival and density estimates, deficiencies being presently addressed with increased VHF collar deployment on Caribou in Jasper. Furthermore, calculation of elk density in Jasper was problematic because of the unknown availability of townsite elk to wolves, and research to determine how to adjust Jasper elk density for unavailable elk would be helpful. Also, eq. 3 assumes calf mortality is independent of wolf density, a necessary, but weak, assumption given present data limitations. While sensitivity analysis supported the parameter values we used for α, τ, and ω in our model (Table 2), low sample sizes were used to estimate cause-specific mortality. Perhaps the greatest limitation of our approach has to do with alternate mortality, ω. Many studies illustrate the critical role of grizzly bear predation on neonate caribou calf survival (Adams *et al.*, 1995). Our assumption of constant mortality by other 'predators' including grizzly bears despite changing elk density makes our thresholds for caribou persistence optimistic (Bergerud & Elliot, 1998). Unfortunately, few data exist to model grizzly bear numeric responses to prey density. Certainly, prescribed fire in or near caribou ranges could increase predation rates from grizzly bears foraging on productive post-fire vegetation (Hamer, 1999).

When these results are combined with studies of the long-term range of variability in the Canadian Rockies, a convergent theme emerges of low-density elk populations as the long-term norm. Our thresholds for caribou persistence are close to those required for willow and aspen persistence (White *et al.*, 1998; Hebblewhite *et al.*, 2005b). Evidence for low elk densities are also found in early explorer's journals (Kay *et al.*, 2000) or archaeological evidence (Langemann & Perry, 2002). The only remaining difficulty is reconciling how elk density was maintained at low density under higher frequencies of forest fire (Rhemtulla *et al.*, 2002; White *et al.*, 2003) that would indirectly increase predation on caribou. Predation by multiple predators, including wolves, grizzly bears, and humans would have been required to limit elk to low enough densities that wolf densities would be low enough for caribou persistence. Regardless of debates over long-term ecosystem states, management policies that maintain elk, and hence wolf density in the Canadian Rockies, appear a prudent management direction for caribou restoration.

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The influence of variable snowpacks on habitat use by mountain caribou

Trevor A. Kinley[1], Trevor Goward[2], Bruce N. McLellan[3] & Robert Serrouya[4]

[1] Sylvan Consulting Ltd., RR5 3519 Toby Creek Road, Invermere, BC, Canada, V0A 1K5 (sylcon@telus.net).
[2] Enlichened Consulting Ltd., Edgewood Blue, Box 131, Clearwater, BC, Canada, V0E 1N0 (tgoward@interchange.ubc.ca).
[3] Ministry of Forests, Box 9158 RPO #3, Revelstoke, BC, Canada, V0E 3K0 (bruce.mclellan@gov.bc.ca).
[4] Box 1522, Revelstoke, BC, Canada, VOE 2S0 (rserrouya@telus.net).

Abstract: Mountain caribou (*Rangifer tarandus caribou*) in southeastern British Columbia subsist for most of the winter on arboreal hair lichen, mostly *Bryoria* spp. Foraging occurs mainly in old subalpine fir (*Abies lasiocarpa*) forests near treeline. Here, the lower limit of *Bryoria* in the canopy is dictated by snowpack depth because hair lichens die when buried in snow. *Bryoria* is often beyond the reach of caribou in early winter, prompting caribou to move downslope to where lichen occurs lower in the canopy and other foraging modes are possible. Snowpacks are normally deep enough by late winter that caribou can reach *Bryoria* where it is most abundant, at high elevations. Extending this to inter-annual comparisons, *Bryoria* should be less accessible during late winter of low-snow years following normal winters, or of normal to low-snow years after deep-snow winters. We hypothesized that when maximum snowpack in late winter is low relative to the deepest of the previous 5 years, mountain caribou will use lower elevations to facilitate foraging ("lichen-snow-caribou" or LSC hypothesis). We tested this with late-winter data from 13 subpopulations. In the dry climatic region generally and for minor snowfall differences in wet and very wet regions, caribou did not shift downslope or in fact were at higher elevations during relatively low-snow years, possibly reflecting the ease of locomotion. The LSC hypothesis was supported within wet and very wet regions when snowpacks were about 1 m or more lower than in recent years. Elevation declined by 300 m (median) to 600 m (25th percentile) for snowpack differences of at least 1.5 m. Greater use of lodgepole pine and western hemlock stands sometimes also occurred. Management strategies emphasizing subalpine fir stands near treeline should be re-examined to ensure protection of a broader range of winter habitats used by caribou under variable snowpack conditions.

Key words: *Bryoria*, elevation, forage, forest management, lichen, locomotion, *Rangifer tarandus caribou*, winter.

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Introduction

Woodland caribou (*Rangifer tarandus caribou*) inhabiting the high-snowfall region of southeastern British Columbia, Canada, are known provincially as mountain caribou[1] (Heard & Vagt, 1998). Mountain caribou and other woodland caribou falling within the Southern Mountains national ecological area are considered threatened nationally (Thomas & Gray, 2002). Mountain caribou have recently undergone a rapid population decline (Wittmer *et al*., 2005) and are provincially "red-listed" (Conservation Data Centre, 2006).

Mountain caribou are defined largely by their reliance for winter forage on arboreal hair lichen of the genus *Bryoria*, which they obtain mainly in old treeline forests dominated by subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*; Edwards and Ritcey, 1960; Simpson *et al*., 1987; Rominger *et al*., 1996; Terry *et al*., 2000; Kinley *et al*., 2003). Hair lichens as a group are sensitive to prolonged wetting (Goward, 1998; Coxson & Coyne, 2003). Presumably because of this, the lower limit of *Bryoria* in the canopy is dictated by the maximum settled depth of the winter snowpack. Thus, where average snowpacks are deep, *Bryoria* on standing trees tends to be unavailable to caribou in early winter, i.e. until snow has accumulated sufficiently to lift caribou within reach of the lichen. The normal foraging reach of caribou is 1.6 to 2.2 m above the point to

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[1] In some other jurisdictions, the term "mountain caribou" refers to another ecotype of woodland caribou inhabiting mountainous areas but not primarily reliant on arboreal lichen.

which they sink into the snowpack (Antifeau, 1987). When the *Bryoria* trimline is higher than this, caribou must adopt additional or other foraging modes. Alternatives include using lichen from wind-thrown trees or fallen branches, or using terrestrial plants or lichens. These options are normally accompanied by downslope movement to areas of lower snow depth, where hair lichens occur lower in the canopy and cratering for terrestrial forage is also feasible (Antifeau, 1987; Simpson *et al.*, 1987; Rominger & Oldemeyer, 1989, 1990; Apps *et al.*, 2001; Stevenson *et al.*, 2001). In most of western North America, *Bryoria* is most abundant at upper forested elevations where its most copious growth (at least in the lower canopy) is in well-spaced old growth forests (Goward & Campbell, 2005). Compared to *Alectoria* – the other dominant hair lichen genus in mid- to high-elevation forest – *Bryoria* is strongly preferred by caribou (Rominger *et al.*, 1996), perhaps because of its higher protein levels (Antifeau, 1987). Given that *Bryoria* increases in abundance at higher elevations while *Alectoria* is more common in valley bottoms, and perhaps also because of the higher incidence of predators in valley bottoms during winter (Kinley & Apps, 2001), caribou minimize their time at lower elevations, despite the greater availability of terrestrial vascular forage there (Rominger & Oldemeyer, 1989, 1990).

"Early winter" is defined as the period from the onset of snow to the time when the snowpack is sufficiently deep to allow foraging of hair lichen from standing trees at high elevations. "Late winter" then lasts until caribou begin seeking terrestrial vascular forage exposed as snow melts in spring (Stevenson *et al.*, 2001). In drier regions where snowpacks are typically shallow, little downslope movement is evident during early winter and that season may be very short, whereas in areas with greater snowfall, caribou may remain at low elevations for nearly half of each winter (Terry *et al.*, 2000; Apps *et al.*, 2001; Stevenson *et al.*, 2001; Kinley *et al.*, 2003).

Such elevational shifts within a subpopulation can be variable within and between years (Antifeau, 1987; Rominger & Oldemeyer, 1990; Apps *et al.*, 2001). Inter-annual differences may relate in part to snow depth in a given winter relative to that of the years preceding. Winters of exceptionally deep snow cause the *Bryoria* trimline to recede upward, thereby potentially placing it beyond the foraging reach of caribou in subsequent years (Goward, 2003). This observation led Goward (2002, 2003) to posit the Lichen-Snow-Caribou (LSC) hypothesis which states that there will be less *Bryoria* within foraging reach of caribou for several years following a season of unusually deep snowpacks, that is, until *Bryoria* re-establishes over lower branches (see also Utzig, 2005). This pattern should be less true at lower elevations. Despite the lesser abundance of *Bryoria* there (Goward, 1998; Goward & Campbell, 2005), any *Bryoria* or *Alectoria* present is more likely to be within foraging reach of caribou due to the limited variability in snowpack at lower elevations. Therefore, the LSC hypothesis predicts that caribou will tend to use lower elevations, or remain there longer, in low-snow winters following an exceptionally deep snowpack. We predict that this phenomenon may also be detectable during shallow-snowpack years following normal winters, i.e. that *relative* snowpack depth is a key predictor of elevation use. More specifically, we hypothesize that when the maximum snowpack in any winter is low relative to the deepest snowpack of the previous 5 years, mountain caribou will: (1) use lower elevations or spend a greater proportion of their time there, or (2) otherwise shift habitat-use patterns to facilitate foraging. Because mountain caribou in many areas are obliged to use lower elevations during early winter regardless of current snow depth, these predictions apply to late winter. The 5-year effect period is an estimate of the minimum period potentially required for *Bryoria* to recolonize lower branches – mostly from thalli dislodged from higher in the canopy – in amounts potentially usable by caribou (T. Goward, pers. obs.), though full recovery likely takes much longer.

Despite the extensive literature regarding mountain caribou habitat selection, previous authors have not specifically tested the LSC hypothesis. We address differences between years in relation to recent maximum snowpacks, whereas most others compared used habitats to available habitats or compared seasons regardless of inter-annual snowpack patterns (Simpson *et al.*, 1987; Rominger & Oldemeyer, 1990; Terry *et al.*, 2000; Apps *et al.*, 2001; Johnson *et al.*, 2004), looked at single years (Servheen & Lyon, 1989; Kinley *et al.*, 2003), or compared groups of caribou rather than years (Warren *et al.*, 1996). Rominger & Oldemeyer (1989) did compare early-winter habitat use in relation to snowpack accumulation. They found that terrestrial foraging extended longer with slow snow accumulation, but did not specifically address the elevations used in slow- versus rapid-accumulation years. Antifeau (1987) also examined habitat use relative to snowpack, sinking depth, energetics, and lichen availability, pointing to the energetic advantages of using low elevations during early winter when lichen was unavailable at upper elevations, and higher elevations during late winter. He also found differences in elevation use in relation to snow accumulation rate but did not examine the effect of extreme inter-annual snowpack differences.

An alternative hypothesis exists to explain the downslope movements made in many subpopulations during early winter. Such movements could potentially relate to the difficulty of locomotion in the unconsolidated snowpacks typical of that season, rather than or in addition to an inability to access sufficient *Bryoria* then (Edwards & Ritcey, 1959; Antifeau, 1987). Perhaps caribou move downslope in deep-snow regions primarily to reach areas with greater ease of movement until the snowpack becomes consolidated at upper elevations. If so, unusually heavy snowfalls during late winter should also impair the ability of caribou to move at upper elevations. If this locomotion hypothesis were valid, we would expect that caribou would more commonly occur at lower elevations during deep-snow years, rather than during low-snow years as predicted by the LSC hypothesis.

Understanding whether or to what extent shifts in the lichen trimline affect movements and habitat use by mountain caribou has potentially profound implications for habitat requirements, forest management and population viability, particularly in view of changing climates. In this analysis, we reviewed existing telemetry and snow-survey data from throughout the range of mountain caribou to determine whether the LSC hypothesis was supported or whether there was greater support for the locomotion hypothesis. For each of 13 mountain caribou subpopulations investigated, we compared late-winter habitat use during years having shallow versus deep relative snowpacks, to determine whether habitat use was affected by presumed upward shifts in the *Bryoria* trimline.

Methods

Study area

Mountain caribou exist as a series of 18 subpopulations (Wittmer *et al.*, 2005) in a high-precipitation, mountainous, continental region of southeastern British Columbia, Canada, and small portions of adjacent northern Idaho and Washington, USA. Elevations within this 60 000 km^2 area range from 450 to 3500 m. Three principal biogeoclimatic zones occur here, defined on the basis of climate and climax vegetation (Meidinger & Pojar, 1991; Meidinger, 2006; Research Branch, 2006). (1) At the lowest elevations, the Interior Cedar – Hemlock zone (ICH) has climax forests consisting of western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*). Other biogeoclimatic zones are intermixed with or replace the ICH in places, including the Montane Spruce (MS) in the extreme southeast, and the Sub-Boreal Spruce (SBS) in the north. In both cases, climax forests are mainly of hybrid white spruce (*Picea glauca* x *engelmannii*). (2) Above the ICH is the Engelmann Spruce – Subalpine Fir zone (ESSF), in which climax stands are closed-canopied Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) that, near the upper limits of the zone, become more open ("woodland") and then very open and clumpy ("parkland"). With increasing elevation, subalpine fir is often mixed with whitebark pine (*Pinus albicaulis*) and, in the south, alpine larch (*Larix lyalli*) in the woodland and parkland subzones. (3) The Interior Mountain-heather Alpine zone (IMA) in the south and Boreal Altai Fescue Alpine zone (BAFA) in the north are at the highest elevations and are non-forested. Wildfire and other natural and human-caused disturbances have resulted in variable proportions of non-climax tree species in all zones below the ESSF woodland. Of note is the relative abundance of lodgepole pine (*Pinus contorta*), except in the highest-precipitation areas toward the center of mountain caribou range.

Late-winter habitat generally consists of the uppermost portions of the closed-canopied ESSF along with the ESSF woodland and ESSF parkland, while early-winter habitat normally includes the ICH and closed-canopied ESSF (Stevenson *et al.*, 2001) and sometimes the ESSF woodland.

Snow data

We obtained snow-depth data collected near the first day of each month from January 1980 through May 2004 (River Forecast Centre, 2006). A representative snow course was chosen for each subpopulation based on its location and completeness of data. For months when snow-depth values were missing, we regressed snow-depth against available snow-pillow (mass) data from that snow course for that month in other years, then estimated snow depth based on the current month's snow mass. Where this was not possible, we estimated depth based on values from an adjacent course in a similar biogeoclimatic subzone, in relation to regressions of snow depth between the 2 courses from other years for that month. Because snow courses occurred across a range of elevations, we then adjusted snow depths to values that would be expected at elevations where late-winter habitat normally occurs, defined as local boundaries between the closed-canopied ESSF and the ESSF woodland subzone. We determined this elevation – snow depth relationship by comparing data from all pairs of snow courses within mountain caribou range where the 2 courses were within 5 km of each other but were separated by 390 to 770 m of elevation. We developed regression equations of mean snowpack difference (cm) per elevation (m) for 6 pairs of courses from very wet or wet subzones of the ESSF and separately for 2 pairs from dry subzones (Research Branch, 2006). We then used the slope of the appropriate equation (0.1811 cm snow/m of elevation for wet and very wet subzones and 0.0849 cm snow/m of elevation for dry subzones) to extrapolate snow depth from the snow course elevation to the local ESSF woodland lower boundary. While acknowledging the simplistic assumptions inherent in this approach, we feel the resulting approximations reflect trends in snow depth.

Each winter was then assigned to categories of either low relative snowpack (hereafter "low-snow years") or normal to deep relative snowpack (hereafter "deep-snow years") based on the following criteria. If the maximum snow depth during the winter (regardless of month) was 50-99 cm lower than that of any year within the previous 5 years and was also lower than the 25-year mean of maximum annual snow depths, it was considered to be a low-snow year. If it was within 25 cm of the maximum recorded during each of the previous 5 years (or exceeded that value) and was also greater than the 25-year mean of maximal snow depths, it was considered to be a deep-snow year. If it did not fit either of these categories, it was disregarded. This process was then repeated, replacing the 50-99 cm "cutpoint" with 100-149 cm and then 150+ cm (only 2 data points fell beyond 200 cm). Deep-snow years remained unchanged in each case. This allowed us to compare low- to deep-snow years based on up to 3 definitions of "low-snow", thereby making it possible to evaluate the sensitivity of caribou to various classes of relative snow-depth.

Caribou location data

We collated radiotelemetry data gathered from 411 caribou between 1987 and 2004 under previous or existing research projects within all subpopulations. We divided the Wells Gray subpopulation as defined by Wittmer *et al.* (2005) into 3 groups based on major physiographic and caribou habitat-use differences (Apps & Kinley, 2000). These new groups included Wells Gray-Mountain, Wells Gray-Highland North and Wells Gray-Highland South. Adult caribou on which conventional VHF radiocollars were deployed were of both sexes and were captured using net guns fired from helicopters. They were monitored aerially during the winter, using standard radiotelemetry techniques (Fuller *et al.*, 2005) on a roughly weekly to monthly schedule. Where GPS collars were also deployed they were generally also monitored using the collars' VHF beacons, so we used such manually collected data because it was most comparable to the VHF-collar data. Where GPS collars were not aerially monitored, we used locations logged by the collars, but rejected records based on fewer than 4 satellites or not obtained between 8 AM and 5 PM (the approximate period in which aerial telemetry occurred). We then thinned the remaining GPS-collar data to get 1 randomly selected point per week (or longer if no data meeting our criteria were available) and added this to data obtained through conventional radiotelemetry. Some of the study animals for the South Selkirks subpopulation had been translocated there. Though habitat use by these animals was similar to that of residents (Warren *et al.*, 1996) we deleted, as a precautionary measure, any data from the winter of their arrival and the following winter.

We based our analysis on data obtained between 1 January and 15 April. This end date is the earliest among years that animals in the highest-snowfall region of mountain caribou range shifted from late-winter to spring behavior (Apps *et al.*, 2001), so we selected it for all subpopulations to ensure that we were not considering spring foraging behavior. The 1 January analysis start is the approximate mean date at which the shift from early-winter to late-winter foraging begins (Apps *et al.*, 2001; Stevenson *et al.*, 2001; Kinley *et al.*, 2003). While this date is variable among subpopulations and years, it was less critical for our analysis than was the choice of end date because the transition from early to late winter essentially represents a continuum.

Habitat use measures

In a GIS environment, we obtained attributes of each caribou radiolocation in relation to 3 habitat variables (Table 1). Digital data included elevation (Geographic Data BC, 1996) and forest cover projected to 2000 (Forest Analysis and Inventory Branch, 2000). This was true of all but the South Selkirks subpopulation which, because it straddles 3 states or provinces and many land-ownership jurisdictions, was not covered by any single database. Accordingly, we used a forest-cover database developed specifically for that subpopulation (T. Layser, USDA Forest Service, Priest Lake, Idaho, unpubl. data) which grouped tree species into categories that could be correlated to our 3 species groups. However, it included only a 2-part (forest versus non-forest) rather than 3-part scheme for cover classification, so that variable was not assessed for this subpopulation.

Data analysis

For each subpopulation and for each of the 3 definitions of low-snow late-winters, we compared all caribou locations from all low-snow years combined to those from all deep-snow years, using the variables in Table 1. Comparisons were made only when a subpopulation had at least 10 telemetry locations in each of low-snow and deep-snow years. In addition, we pooled all subpopulations falling entirely within wet or very wet subzones of the ESSF (i.e. excluding

Table 1. Habitat variables derived for each caribou radiolocation.

Variable	Description	States or Range	Scale
Elevation	metres asl	continuous	250-m pixels
Cover	broad cover class	• NF: non-forest (generally alpine) • AF: alpine forest (open canopied, near treeline) • F: forest (≈ commercial forest)	1:20 000
Leading Tree Species	most common species in over-story, grouped in ecological classes (only for AF and F cover types)	• B: subalpine fir (*Abies lasiocarpa*), whitebark pine (*Pinus albicaulis*), alpine larch (*Larix lyalli*), Engelmann and hybrid white spruce (*Picea englemannii* and *P. glauca* x *englemannii*), mountain hemlock (*Tsuga mertensiana*) • H: western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), Douglas-fir (*Pseudotsuga menziesii*), all broadleaf species • P: lodgepole pine (*Pinus contorta*), western white pine (*P. monticola*), western larch (*Larix occidentalis*)	1:20 000

Purcells-Central, Purcells-South and South Selkirks) to examine the aggregate effect for caribou in the deeper snowpack regions. For each of low-snow and deep-snow years, this pooled sample included an equal, random selection of telemetry locations from each subpopulation, based on the subpopulation with the lowest sample size (minimum 10 locations per year type). We tested nominal data (cover and leading species) with chi-square tests and elevation data with Wilcoxon rank sum tests to assess significance, using the program JMP IN 5.1 (SAS Institute Inc., Cary, North Carolina). We used the nonparametric Wilcoxon test rather than the parametric t-test because elevation distributions were not normal, and because we were more interested in differences in the median and associated indicators of distribution (percentiles) than in the mean. We report differences in responses between low-snow and deep-snow years, rather than the absolute values of each, to facilitate comparisons among subpopulations. To adjust for multiple comparisons from the same dataset, we define P_{CRIT} as 0.05/the number of tests per population. For each year of data for each subpopulation within the wet and very wet climatic regions, we also compared snowpack (in relation to the deepest in the previous 5 years) to median relative elevation of caribou locations. Relative elevation was the absolute elevation of caribou locations scaled to the elevation range used by that population, which was the difference between the 1st and 99th percentiles of elevation used by any animal of that population during early winter or late winter (1 Nov – 15 Apr) of all years combined.

Results

Of the 20 possible caribou groupings, 13 had sufficient data to test the hypothesis for at least 1 of the relative snowpack cutpoints. When late-winter snowpack variability was 50-99 cm, 0 of 11 subpopulations used significantly lower elevations in low-snow years than in deep-snow years, and the Purcells-Central subpopulation used higher elevations (Table 2). At snowpack variability of 100-149 cm, 4 of 8 subpopulations occurred at significantly lower elevations, 2 had apparently lower but non-significant elevation values, 1 (Columbia-North) had lower 25th and 75th percentile elevations but a non-significantly higher median and caribou in 1 (Purcells-Central, occurring in the dry climate region) used higher elevations. When snowpack variability exceeded 150 cm, caribou in 3 of 4 subpopulations used lower elevations, while median elevation in the other (South Selkirks, occurring partly in the dry climate region) did not differ. Differences between low-snow and deep-snow years were most evident at the 25th percentile of elevation.

At 50-99 cm snowpack variability, use of cover types did not differ significantly between low- and deep-snow years for any subpopulation (Table 2). For differences of 100-149 cm, caribou in Wells Gray-Highland North, Wells Gray-Mountain and Frisby-Boulder used more forested areas. When snowpack differences were greater than 150 cm, Frisby-Boulder caribou used more forested areas, data for Columbia-South and Nakusp were indicative of greater forest use (but were not significant), and no cover data were available for South Selkirks.

When snowpack variability was 50-99 cm, leading tree species among forest and alpine forest cover types differed between deep- and low-snow years only for Purcells-Central, where caribou locations were more commonly associated with subalpine fir during low-snow years (Table 2). At 100-149 cm variability, Purcells-Central caribou were again more commonly associated with the subalpine fir group during low snow years and those in Wells Gray-Highland North were more commonly associated with lodgepole pine and western hemlock, as were caribou in South Selkirks and Nakusp at 150+ cm of negative snowpack difference.

For data from combined subpopulations of the wet and very wet subzones, changes in habitat use were evident under conditions of greater inter-annual snowpack variability (Fig. 1). At 50-99 cm snowpack variability, little difference was evident between low-snow and deep-snow years, although there was a weak indication of greater use of subalpine fir at the expense of western hemlock. When variability was 100-149 cm, elevation declined, use of cover classes differed (an apparent shift from non-forest and alpine forest to forest), and data were indicative of greater use of western hemlock during low-snow years. When snowpack variability exceeded 150 cm, low snow years were characterized by lower and more variable elevations (median and 75th percentile declined by about 300 m while the 25th percentile declined by nearly 600 m

Table 2. Late-winter habitat use by mountain caribou in relatively low-snow years. Reported values are differences (elevation) or classes having increased use (cover and leading tree species; including absolute percentage increase) in low snow versus deep-snow years. Significance: * = $P < 0.05$/tests per subpopulation. Blanks indicate no or insufficient sample, or no habitat data available.

					Variables				
					Elevation (m)				
Subpopulation (NW to SE)	Climatic Region[1]	Snowpack Difference (cm)	n (low)	n (high)	median	25th %	75th %	Cover[2]	Leading Tree Species[3]
Hart Ranges	wet	50 - 99	71	95				NF (11)	unchanged
		100-149							
		150+							
Barkerville	wet	50 - 99	125	86	-36	-12	-3	NF (2)	B (5)
		100-149	22	86	* -106	-142	-49	F (14)	B(1), P(1)
		150+							
Wells Gray-Highland North	wet	50 - 99	90	205	-22	-36	5	F (5)	unchanged
		100-149	47	205	* -93	-153	-87	* F (41)	* P(12), H(1)
		150+							
Wells Gray-Mountain	wet	50 - 99	132	235	30	24	32	NF (4)	B (13)
		100-149	187	235	* -107	-133	-44	* F (19)	B (7)
		150+							
Columbia-North	very wet & wet	50 - 99	110	203	-86	-198	-2	NF(2), AF(1)	H (13)
		100-149	173	203	-50	111	-53	AF(5), NF(2)	H (3)
		150+							
Frisby-Boulder	very wet & wet	50 - 99							
		100-149	20	25	-92	-20	-105	* F (47)	B (13)
		150+	10	25	* -236	-492	-212	* F (62)	H (18)
Columbia-South	very wet & wet	50 - 99	64	97	-24	81	11	NF(9), AF(1)	B (19)
		100-149	147	97	-89	-75	-39	NF (18)	H (3)
		150+	153	97	* -312	-422	-166	F (7)	B (3)
Kinbasket	wet & very wet	50 - 99	65	71	-113	-228	-2	AF (14)	H (6)
		100-149							
		150+							
Duncan	wet	50 - 99	42	24	-42	-159	-83	F(17), AF(1)	H (1)
		100-149	23	24	* -409	-550	-388	F(28), AF(5)	H (28)
		150+							
Nakusp	wet	50 - 99	111	328	47	24	28	NF(5), AF(3)	P(2), B(1)
		100-149							
		150+	14	328	* -448	-520	-368	F (29)	* H(49), P(15)
South Selkirks	wet & dry	50 - 99							
		100-149							
		150+	98	228	36	-28	69		* P(25), H(10)
Purcells-Central	dry	50 - 99	30	81	* 166	117	128	AF(14), NF(11)	* B (29)
		100-149	30	81	* 128	117	131	AF(24), NF(1)	* B (30)
		150+							
Purcells-South	dry & wet	50 - 99	97	142	-27	-6	-30	AF(4), NF(1)	B (3)
		100-149							
		150+							

[1] based on subzone names within the Engelmann Spruce–Subalpine Fir zone.

[2] NF = non-forest; AF = alpine forest; F = forest (≈ commercial forest).

[3] B = subalpine fir group; H = western hemlock group; Pl = lodgepole pine group.

relative to deep-snow years). There was also a non-significant shift to less use of non-forest and alpine forest and greater use of western hemlock.

Considering all data for the wet and very wet climatic regions as individual data points, the use of the highest relative elevations generally occurred when snowpacks were just below the deepest in recent years (Fig. 2). When snowpack differences were considerably lower (roughly 80-90 cm or greater), relative elevation declined. There may also have been a slight elevation decline when snowpacks exceeded those of recent years (Fig. 2).

Discussion

Snowpack variability of less than about 1 m caused little change in elevation by mountain caribou during low-snow years. Possibly the *Bryoria* trimline was sufficiently irregular within or across stands due to the presence of sheltered microsites (such as within clumps of trees) to sustain caribou when the change in relative snowpack was minimal. Alternatively, moderately low-snow conditions may have been of benefit by improving the ease of locomotion at high elevations and allowing caribou to remain there or even move higher than usual. However, when the maximum snow depth was at least 1.5 m lower than in recent years, subpopulations of the wet and very wet regions used increasingly lower elevations, consistent with the LSC hypothesis. In particular, the lower limit of caribou activity declined dramatically, with the 25th percentile of elevation shifting nearly 600 m downward during the lowest-snow years. This disproportionately low 25th percentile in comparison to declines in the median and 75th percentile of about 300 m indicated greater variability in elevation during low-snow years.

The downward shift during low-snow years was not evident for subpopulations occurring at least partly within the dry climatic region. Caribou of the only subpopulation completely in the dry region (Purcells-Central) were actually higher during low-snow winters. Drier areas typically have lower snowpacks so *Bryoria* would be expected to be available early in the winter there. Thus, snowpack variability in such areas may have little impact on the availability of *Bryoria* to caribou, obviating the need to move downslope during winters with relatively low snowpacks. Foraging for terrestrial food sources can occur at high elevations in dry regions (Kinley *et al.*, 2003) so low-snow winters may allow caribou to travel more easily and extend ground-foraging for longer periods while also taking advantage of the greater total *Bryoria* biomass at upper elevations. Also, the uppermost elevations correlate roughly with windswept slopes and ridges where *Bryoria* occurs lower in the forest canopy (T. Goward, pers. obs.) and where there should be reduced upward movement of the *Bryoria* trimline during deep-snow years. Therefore, even if *Bryoria* availability does decrease somewhat during relatively low-snow years in dry regions, shifting to windswept sites at very high elevations could mitigate that effect. Overall, patterns observed in shallow-snowpack regions are not obviously consistent with the LSC hypothesis and may in

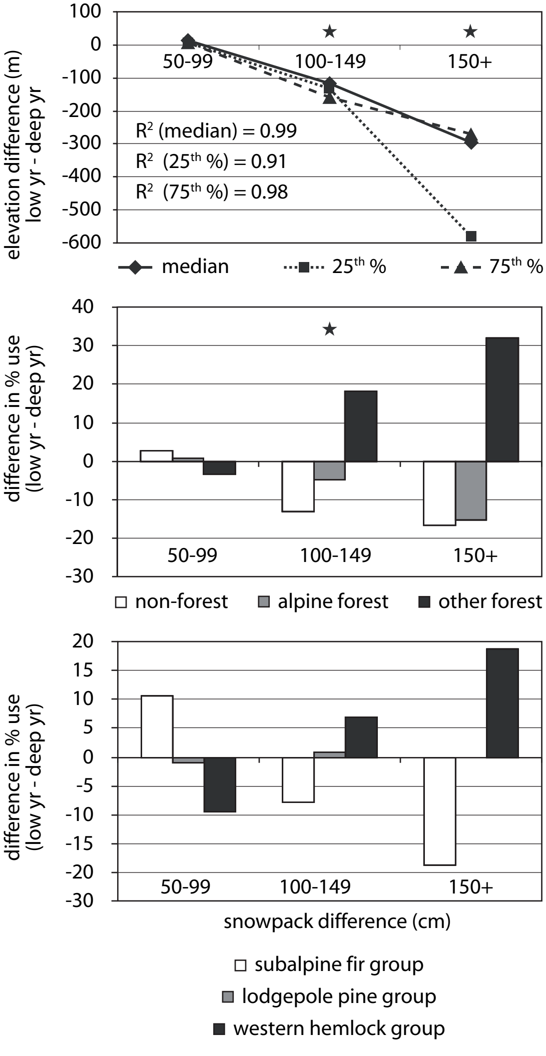

Fig. 1. Late-winter habitat use by mountain caribou in low-snow relative to deep-snow years based on equal random samples from all available subpopulations in wet and very wet ESSF subzones (*n*=336 low/192 deep locations from 8 subpopulations at 50-99 cm, 140/168 from 7 subpopulations at 100-149 cm and 30/75 from 3 subpopulations at 150+ cm; * = sig. difference at indicated snowpack difference).

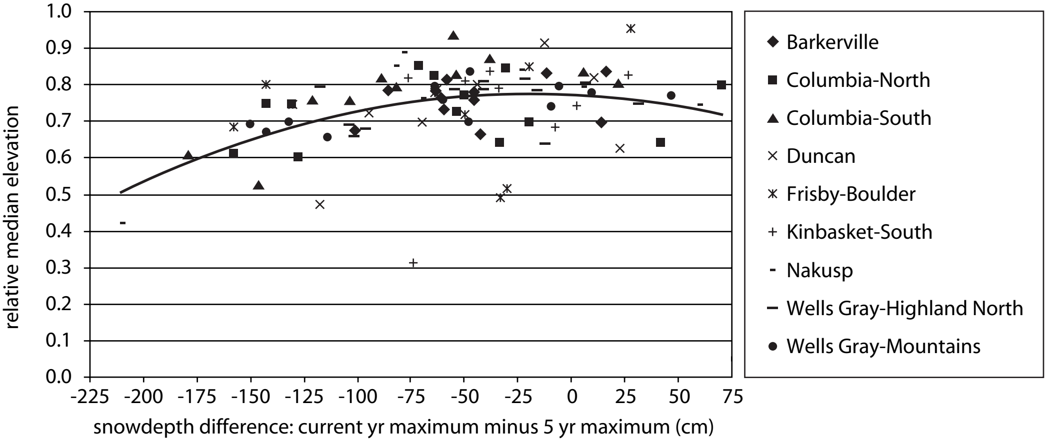

Fig. 2. Relative elevation in relation to relative snow depth for mountain caribou in the wet and very wet climatic regions (n = 9 subpopulations, 91 subpopulation-years). Relative elevation = (median elevation for late winter – 1st percentile of winter elevation for all years combined) / (99th percentile - 1st percentile of winter elevation). Trend line is 2nd-order polynomial for all data.

fact reflect the validity of the locomotion hypothesis under certain conditions.

Within the wetter regions, it would be expected that the observed downward shifts in elevation would be accompanied by an increased use of forests, especially hemlock stands, given both the distribution of those habitat types with respect to elevation and previous observations showing that hemlock stands are heavily used when caribou occur at low elevations (Apps *et al.*, 2001). Significant results, while consistent with this expectation, were sparse. This may simply reflect the overarching importance of snowpack with reference to *Bryoria* availability; when conditions necessitate caribou moving downslope, the vegetation they encounter may be of less importance than simply reaching an elevation where snowpack variability is less extreme. There may also be bimodal patterns within individual subpopulations of the wetter regions when snowpacks are only slightly lower than in recent years. In such years, some animals may move downslope while others may move upslope to seek windswept sites, as hypothesized above for caribou of the dry region. This would be consistent with the (non-significant) results indicating that when snowpack variability was minimal caribou in low-snow years actually appeared at least as likely to shift toward greater use of non-forest or alpine forest and stands dominated by subalpine fir.

In sum, our results indicate that (1) when snowpacks are considerably lower than those of recent years, mountain caribou in deep-snowfall regions make more extensive use of low-elevation sites, consistent with the LSC hypothesis; (2) this shift is sometimes associated with increased use of stands of both lodgepole pine and western hemlock, and (3) when the negative snowpack difference is slight for deep-snowfall regions, and for shallow-snow regions generally, low-snow years are characterized by little difference or even an increase in elevation, potentially consistent with the locomotion hypothesis. Thus, it appears that caribou responses to snowpack variability fall along a gradient, with snowpack differences of roughly 1 m necessary to initiate significant downslope movement during low-snow years. It is not clear whether this situation holds at the northern limit of mountain caribou range as there was limited data for the largest and northernmost subpopulation (Hart Ranges) and insufficient data for any analysis of the other 3 most northerly ones (North Cariboo Mountains, Narrow Lake, George Mountain).

Our results for most subpopulations point more strongly than has previous habitat modeling (e.g. Apps *et al.*, 2001) to the potential need for low-elevation habitat in sustaining caribou for extended periods during some winters. The risk of having limited areas protected at low elevations includes the potential lack of forage and the reduced separation from predators inhabiting valley bottoms. Another implication of such shifts is that caribou sightability during late-winter population surveys may be highly variable among years, so using the same correction factor each year may be inappropriate. Our telemetry data spanned only 6 – 13 years per population with maximum expected snowpack variability of just over 2 m, but given the trends observed it is likely that elevation shifts in wet regions would be even larger when extreme inter-annual snowpack differences occur, and at some point should precipitate significant downward movement even within drier regions.

It also appears that the characteristics of low-elevation stands used in late winter may differ from those used during early winter, even when at roughly the same elevation. Presumably, low-elevation sites used in late winter must provide high volumes of accessible *Bryoria* or have the potential to provide windthrown branches bearing this lichen on a winter-long basis. This is because terrestrial foods are not likely to be available or even detectable later in the winter within wet or very wet regions, even in a shallow-snow year. For example, the Char Creek snow station in the South Selkirks is near the boundary of a dry ESSF subzone and lies at only 1310 m elevation (700 m below normal late-winter habitat), but the lowest maximum snow depth in the 40-year record was 95 cm (River Forecast Centre, 2006). The shift toward lodgepole pine stands during low-snow years within 3 subpopulations (including 2 in the wet climatic region) may reflect the necessity of finding non-terrestrial foods when low elevations are used during late winter. While pine is more abundant at lower elevations, it has not previously been shown to be associated with preferred mountain caribou habitats (Apps *et al.*, 2001; Stevenson *et al.*, 2001; Johnson *et al.*, 2004). However, when forced to move downslope, caribou may take advantage of the short lifespan of lodgepole pine and its preponderance of dead lower branches to find windthrown pine snags or branches bearing *Bryoria*, in addition to gleaning lichen from the pine trunks.

All land-use plans in mountain caribou habitat allow for the preservation or special management of some lower-elevation stands in recognition of their importance for early-winter habitat or as movement corridors (Mountain Caribou Technical Advisory Committee, 2002). However, protected habitat has generally been concentrated in the upper ESSF (ibid.), some caribou management plans specifically allow the harvest of lodgepole pine in otherwise protected zones (Abbott, 2005), and no local allocation of habitat protection "budgets" has been explicitly based on the implications of the LSC hypothesis. We therefore recommend that any revisions to land-use plans include consideration for the key role that low-elevation habitat may play under low snowpack conditions, particularly in wetter ecosystems.

It should be noted that telemetry data for our analysis was often limited or unavailable for key years and the scale of our snowpack data was coarse (i.e. maximum depth per winter, interpolated over elevations and limited by the availability of snow stations) so our results may not precisely reflect patterns within any given subpopulation. Future analyses based on years with greater environmental variability and with more localized, real-time data on snow depth and caribou sinking depth, combined with field observations of caribou activity, temporal shifts in the *Bryoria* trimline and within-stand variability in *Bryoria* trimline heights, are required if local habitat protection plans are to more precisely reflect inter-annual differences in habitat use. In particular, the current inability to test the LSC hypothesis for the most northerly subpopulations is a significant gap. There is also a need to determine the time required to redevelop significant loads of *Bryoria* in the lower canopy after an upward shift in the trimline, in relation to the typical interval between years of exceptionally deep or shallow snowpacks.

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Assessing the length of the post-disturbance recovery period for woodland caribou habitat after fire and logging in west-central Manitoba

Juha M. Metsaranta

Department of Renewable Resources, University of Alberta, Edmonton, Alberta T6G 2H1, Canada (juha@ualberta.ca).

Abstract: This study examined the habitat characteristics of areas used by woodland caribou and areas disturbed by fire or logging in the Naosap caribou range in west-central Manitoba. The population inhabiting this area is currently considered to be of high conservation concern. The purpose was to determine how long after disturbance forests again resembled caribou habitat and whether there were differences in the recovery period between fire disturbed and logged areas. Sample transects were located in areas used by caribou and areas disturbed by fire or logging. Previously, it was shown that variables positively associated with habitat suitability in this region were species composition (presence of black spruce), an index of arboreal lichen abundance and tree size, while variables negatively associated with habitat suitability were deadfall abundance and species composition (presence of trembling aspen). It was hypothesized that if disturbed sites had become suitable caribou habitat, then they should be statistically indistinguishable from sites used by caribou based on these variables. Using cluster analysis, it was found that 2 statistical clusters showed the highest level of agreement with sampling clusters, with 88% of plots used by caribou classified into one cluster, and 74% of disturbed plots classified into the other. Although a small proportion (12%) of disturbed plots resembled used plots, 30 years (the age of the oldest disturbed plot) was not enough time, in general, for forest to return to conditions resembling caribou habitat in this region.

Key words: arboreal lichen, coarse woody debris, habitat disturbance, habitat suitability, forest fire, forest management, logging, succession.

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Introduction

A reduction in the historical range of woodland caribou in the province of Manitoba is thought to have occurred (Johnson, 1993) that is similar to trends found elsewhere in Canada (Bergerud, 1974; Schaeffer, 2003). This investigation was conducted between 1998 and 2002 in the Naosap caribou range in west-central Manitoba, Canada (Fig. 1), a population currently considered to be of high conservation concern (Manitoba Conservation, 2005). Caribou in the Naosap area are potentially affected by highway and rail transportation corridors, road development associated with forestry operations, transmission line construction, and habitat disturbance from logging or forest fires. One potential habitat management scheme that could be used to conserve woodland caribou populations involves ensuring that some critical proportion of the landscape remains in conditions that are suitable for woodland caribou. However, it is generally not known how many years after disturbance that sites return to suitable conditions and if this recovery period is different after fire and logging disturbance.

Differences in post-disturbance pathways following logging and fire have been noted in both a caribou habitat (Coxson & Marsh, 2001) and non-caribou habitat context (Carleton & MacLennan, 1994; Timoney *et al.*, 1997). Logging tends to result in an increase in deciduous habitats (Carleton & MacLennan, 1994) that are more suitable to moose and other ungulates than to caribou (Rettie & Messier, 2000). Similarly, some forest management practices may favour the creation of forest conditions with increased forage availability for other ungulates (Strong & Gates, 2006). While caribou may exist in such forests in the absence of predators, the general result of this is an alteration of predator-prey dynamics

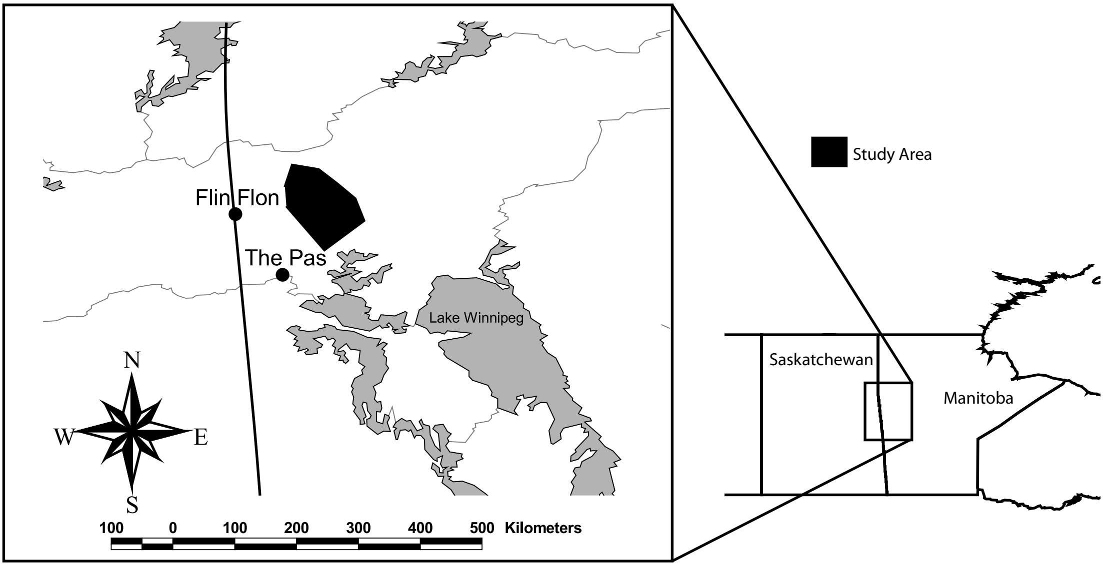

Fig. 1. The location of the Naosap caribou range in west-central Manitoba, Canada.

to the overall detriment of caribou (Bergerud & Elliot, 1986; Seip, 1992).

Most studies of post-disturbance recovery of caribou habitat have focused on lichen regeneration (Webb, 1998; Coxson & Marsh, 2001; Coxson *et al.*, 2003). Fire is generally thought to have detrimental impacts on lichen abundance in the short term (Schaeffer & Pruitt, 1991). However, post-logging lichen regeneration can initially be faster than the post-fire regeneration of lichen and may be augmented by forest management practices like thinning or winter harvesting (Coxson & Marsh, 2001; Coxson *et al.*, 2003; Daintith *et al.*, 2005). Another factor that may be of importance is the post-disturbance accumulation of coarse woody debris. For example, Schaeffer and Pruitt (1991) found that the density of deadfallen trees at burned sites was much greater in 10 year old burns than in mature forests, and postulated that this may represent a significant barrier to movement of caribou. If deadfalls also concurrently represented a barrier to the movement of other ungulates (Cumming, 1980) then this could influence faunal composition of post-fire communities. Coarse woody debris accumulation follows a "U-shaped" successional pattern after fire, with high abundance immediately following fire disturbance, low abundance during mid-successional stages, and increasing abundance again during late-successional stages (Brassard & Chen, 2006). Total accumulations immediately are much lower after logging and the majority of the debris tends to be small diameter downed material and not standing dead trees (Tinker & Knight 2000, Pedlar *et al.* 2002).

This study investigated the micro-habitat characteristics of sites used by caribou in the Naosap range in west-central Manitoba during their annual cycle in relation to the characteristics of areas disturbed by fire or logging. The purpose of the study was to attempt to determine how many years after disturbance a forest becomes caribou habitat in this region and whether there were differences in this time between fire and logging. Previously, it was determined that variables positively associated with micro-habitat suitability in this region were species composition (presence of black spruce), mean tree size, and an index of arboreal lichen abundance. Variables negatively associated with suitability were species composition (presence of trembling aspen) and the density of deadfallen trees (Metsaranta *et al.*, 2003). Here, it was hypothesized that if a disturbed plot had returned to conditions that were suitable for caribou habitat, then it should be statistically indistinguishable from plots used by caribou, based on these variables. Differences between logging and fire disturbed sites for these variables were also investigated.

Material and methods

Study area

The Naosap caribou range (Fig. 1) encompasses the boundary of the Churchill River upland and the mid-boreal lowland ecoregions of the boreal shield and boreal plains ecozones. The boreal shield landscape consists of uplands and lowlands with many bedrock outcrops. This contrasts with the boreal plains landscape, which is topographically level to gently rolling,

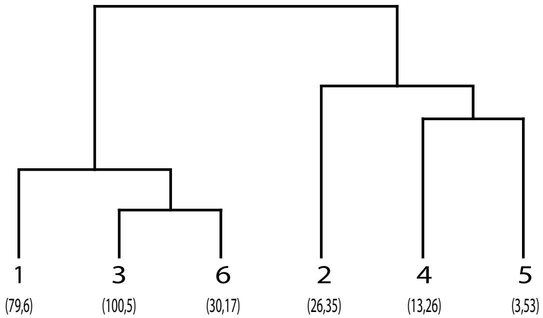

Fig. 2. Classification dendrogram for the 393 caribou habitat plots, based on micro-habitat variables most important to caribou in the Naosap caribou range in west-central Manitoba (arboreal lichen index, deadfall density, tree size, presence of trembling aspen, and presence of black spruce). Number of (used, disturbed) plots in each cluster are in parentheses.

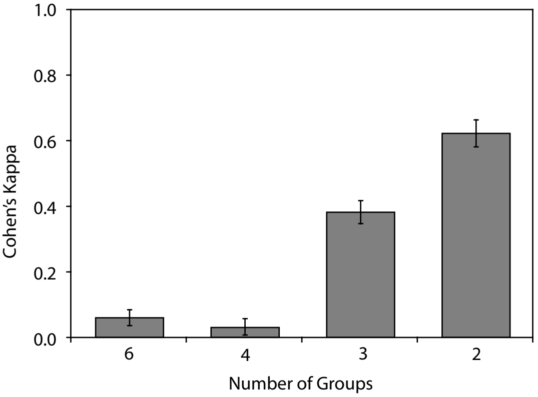

Fig. 3. Cohen's Kappa measure of agreement (+/- S.E.) at four possible levels for grouping caribou habitat plots into statistical clusters or sampling clusters in the Naosap caribou range in west-central, Manitoba. See methods for interpretation of different group memberships.

consisting of lacustrine or organic parent materials. Tree species include black spruce (*Picea mariana*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), tamarack (*Larix laricina*), trembling aspen (*Populus tremuloides*), and white birch (*Betula papyrifera*). The climate is continental, characterized by short warm summers and cold winters. Mean daily temperatures in the study area range from +17.8 °C in July to -21.4 °C in January. Mean annual rainfall and snowfall range from 323.8 mm and 154.9 cm in The Pas to 339.2 mm and 141.3 cm in Flin Flon. Snow is typically present from mid-November to early April, with maximum monthly mean depths of 30 to 39 cm occurring in January and February.

Data collection

Thirty-eight transects containing a total of 393 plots were sampled during the summer of 1999 and 2000. Twenty-four transects were located in areas used by woodland caribou (6 in each of the 4 calendar seasons), as determined by a telemetry study of habitat selection and population demographics (Metsaranta, 2002). Ten transects were located in logged areas, further classified by decade logged (1970s, 1980s, and 1990s). The oldest logged area was approximately 30 years old. Four transects were located in areas burned in 1989, ten years prior to data collection.

More details on the sampling protocol can be found in Metsaranta (2002) and Metsaranta *et al.* (2003). Briefly, transect start points were randomly selected within 500 m of roads or lakes in order to provide access. Transects were at least 500 m long, with plots located every 50 m. Data collected at each sample plot included habitat index scores (Storey & Storey, 1980), forest resource inventory characteristics (species composition, age, height, canopy closure, diameter), ecological characteristics (shrub/herb species composition), and other stand attributes thought to be important to caribou (deadfall density, visibility, and arboreal lichen abundance). A number of hierarchical plot sizes were used (2 m x 2 m for herbaceous species composition, 5 m x 5 m for shrub species composition, 10 m x 10 m for forest resource inventory characteristics, and 50 m x 50 m for habitat index scores deadfall density, and visibility). Using a regression analysis approach, it was found that the five variables best describing woodland caribou habitat at these plots were the arboreal lichen index, deadfall density, tree size, the presence of black spruce, and the presence of trembling aspen.

Data analysis

For this analysis, each of 5 variables considered important for describing woodland caribou habitat at each plot were standardized according to the maximum value for that variable. Each plot was then classified using hierarchical cluster analysis (Ward's method with Euclidean distances (Legendre & Legendre, 1998)) into 1 of 2, 3, 4, or 6 statistical clusters. In addition, each plot was also assigned into 1 of 2, 3, 4 or 6 sampling clusters, based on different combinations of plots sampled in habitat used in each of the 4 calendar seasons and plots sampled in each of the 2 types of disturbance. For the sampling clusters, the 2 group level represented used plots and disturbed plots, the 3 group level represented used plots, burned plots, and logged plots, the 4 group level represented plots used in spring/summer, plots used in fall/winter, burned plots, and logged plots, and the 6 group level represented plots used in each season (spring, summer, fall, and winter), burned plots, and logged plots. The hypothesis was that if disturbed plots had returned to conditions that resemble caribou habitat, then they should be classified into the same groups as plots used by caribou. Furthermore, if these classifications indicated true groupings, then there should be substantial agreement between statistical clusters and sampling clusters at some true level of grouping. Agreement between statistical cluster membership and sampling cluster membership for each plot at each level of grouping was assessed using Cohen's Kappa statistic (Landis & Koch, 1977). Finally, at the level of grouping with the highest level of agreement, the mean difference between the 5 variables based on both statistical clusters and sampling clusters was also assessed to see if the groupings reflected true differences.

Results

The first split in the dendrogram (Fig. 2) essentially subdivided the plots into disturbed and undisturbed groups. Clusters 1, 3, and 6 contained 88% used sampling sites and 12% disturbed sampling sites. Clusters 2, 4, and 5 on the other hand contained 26% used sampling sites and 74% disturbed sampling sites. Cohen's Kappa statistic indicated almost no agreement between true group membership and cluster membership for 4 and 6 groups, moderate agreement for 3 groups, and substantial agreement for 2 groups (Fig. 3). Taken together, these suggest that there are only 2 significant statistical groups in these data: plots used by caribou (clusters 1, 3, and 6 – the used statistical cluster) and plots disturbed by fire or logging (clusters 2, 4, and 5 – the disturbed statistical cluster). The 12% of disturbed sampling sites that were grouped with the used statistical cluster came from burned sites and logged sites of all ages, suggesting that no particular type of disturbed site of any age (5 to 30 years old) was more likely to resemble habitat used by caribou than any other type.

The arboreal lichen index and tree size were significantly higher in the plots in the used statistical clusters than in the plots in the disturbed statistical clusters, while deadfall density was significantly lower (Table 1). On average, used statistical cluster plots had an arboreal lichen index that was 0.9 units higher, had 5.2 less deadfallen trees 50 m^{-1}, and had trees that were 4.2 cm larger in diameter. Trembling aspen was present in 75% of the plots in the disturbed statistical cluster, and was absent from all plots in the used statistical cluster. Black spruce was present in 90% of used statistical cluster plots (including all of those disturbed sampling cluster plots that were considered members of this group), but only 39% of disturbed statistical cluster plots. These results are nearly identical to those obtained if the 2 group level of the sampling clusters is used to assess the differences between these variables (Table 1). On average, used sampling cluster plots had an arboreal lichen index that was 1.3 units higher, had 5.4 less deadfallen trees 50 m^{-1}, and had trees that were 7.7 cm larger in diameter. Trembling aspen was present in 62% of disturbed sampling plots, but only 11% of used sampling plots. On the other hand, black spruce was present in 94% of used sampling plots, but only 44% of disturbed sampling plots. These similarities between statistical and sampling clusters at the 2 group level further confirm the strong agreement at this level of grouping.

Discussion

The abundance of arboreal lichen, the accumulation of deadfallen trees, and species composition were 3 factors considered important for determining microhabitat suitability for caribou in this region (Metsaranta *et al.*, 2003). All 3 of these variables were significantly different between both the statistical clusters and the sampling clusters at the 2 group level, which had the highest amount of agreement between group memberships in this study. Although a small proportion of disturbed plots (12%) resembled used plots, there were no consistent trends in which plots were misclassified, except that all of these misclassified disturbed sampling cluster plots did have black spruce present. Otherwise, the 12% of disturbed plots that resembled used plots were distributed evenly amongst the categories of disturbed plots that were sampled, meaning that plots of any age sampled (5 to 30 years old) were just as likely to be misclassified. These results indicate that 30 years is likely not enough time for forests to return to conditions which resemble the habitat types used by caribou in this region. This is consistent with observations made by Racey *et al.* (1996), who noted caribou use of a logged area 40 years after disturbance, Dunford *et al.* (2006), who noted that lichen abundance had recovered to maximum levels about 40 years after disturbance, and Joly *et al.* (2003), who noted that caribou avoid all but the periphery of burned areas up to 50 years after fire.

Past studies have shown that post-disturbance regeneration of terricolous lichens after fire and logging appear to be similar (Webb, 1998), particularly after winter harvest (Coxson & Marsh, 2001). This was not the case in this study. The percent cover of terricolous lichens was higher at logged sites (mean 9.8%) than

Table 1. Differences between (A) statistical clusters and (B) sampling clusters at the two group level for three key variables determining habitat suitability for caribou in the Naosap range, west-central Manitoba.

Variable	Mean disturbed cluster value (SD)*	Mean used Cluster value (SD)**	Mean difference (95% CI)	T (*P*-value)
(A) Statistical Clusters				
Arboreal lichen index	0.38 (0.77)	1.27 (0.91)	0.90 (0.73 to 1.06)	10.57 (<0.001)
Deadfall density (trees 50 m^{-1})	9.62 (12.59)	4.45 (5.41)	-5.17 (-7.28 to -3.05)	-4.83 (<0.001)
Mean tree size (cm dbh)	7.05 (7.38)	11.24 (4.77)	4.19 (2.87 to 5.51)	6.28 (<0.001)
(B) Sampling Clusters				
Arboreal lichen index	0.18 (0.51)	1.34 (0.89)	1.16 (1.02 to 1.3)	16.41 (<0.001)
Deadfall density (trees 50 m^{-1})	9.96 (13.08)	4.53 (5.31)	-5.43 (-7.69 to -3.16)	-4.73 (<0.001)
Mean tree size (cm dbh)	4.64 (4.69)	12.37 (5.27)	7.73 (6.72 to 8.74)	14.99 (<0.001)

* Mean age 93 years (SD 36 years, *n* = 235).

** Mean age 35 years (SD 39 years, *n* = 150).

at burned sites (mean 1.25%). In addition, only 5.5% of burned sites had an arboreal lichen index greater than 0, while 23.1% of logged sites had an arboreal lichen index greater than 0. Fire and logging also create very different post-disturbance coarse woody debris accumulation patterns (Pedlar *et al.,* 2002; Brassard & Chen, 2006). Accumulations were essentially absent after logging, as it was in this region (Metsaranta *et al.*, 2003). In the case of fire, the minimum value of coarse woody debris abundance at mid-successional stages often appears to correspond to the period of time when lichen abundance has also recovered to at or near pre-disturbance levels after fire (Brais *et al.*, 2005; Dunford *et al.* , 2006; Goward & Campbell, 2005), which may result in confounding effects when examining the effect of these 2 variables. Furthermore, studies have shown that there is a tendency for forests to regenerate to deciduous habitats after logging (Carleton & MacLennan, 1994; Timoney *et al.*, 1997) and these habitats tend to be more suitable for moose than caribou (Rettie & Messier, 2000). In the study area, coniferous regeneration was present in 94.2% of burned plots and in only a slightly smaller percentage (87.7%) of logged plots. However, deciduous regeneration was present in a much greater percentage of logged plots (83.3%) than burned plots (61.5%), indicating that post-logging forests had a much more mixed species composition than post-fire forests in this region.

It is possible that differences in post-disturbance succession can result in differences in the post-disturbance faunal communities. Some studies have suggested that moose appear to avoid areas where coarse woody debris accumulation appears to be high (Cumming, 1980), and Schaeffer and Pruitt (1991) suggested that accumulation of deadfall could impede caribou movement. In this study area, 2 surveys of moose populations (Cross, 1991; Cross, 2000) failed to detect increases in moose numbers in the large burned areas sampled in this study and areas of high deadfall accumulations had low moose activity (Cross, 2000). Moreover, caribou in the study area continued to be located in lowland habitats within burned areas, but tended to avoid burned upland habitats where presumably deadfall accumulation would be high (Metsaranta, 2002). Thus it seems that coarse woody debris accumulation is potentially an important factor reducing the post-fire habitat suitability for caribou and moose. Fire may under some circumstances create habitat conditions that are equally poor for both species, while logging can tend to create habitat conditions that differentially favour moose over caribou. These differences in post-disturbance successional pathways between logging and fire could result in differential changes in post-disturbance faunal communities that, in the case of logging, work to the detriment of caribou.

Overall, evidence suggests that fire and logging often do not differ in post-disturbance regeneration of lichen (Webb, 1998; Coxson & Marsh 2001; Coxson *et al.*, 2003), but do differ in the post-disturbance accumulation of coarse woody debris (Pedlar *et al.*, 2002; Brassard & Chen 2006) and in the types of forests that tend to regenerate post-disturbance (Carleton & MacLennan, 1994; Timoney *et al.*, 1997). In addition, it will take more than 30 years after disturbance for forests to return to conditions that resemble caribou habitat in this region. Evidence from previous studies suggests that this value is in the range of 40-50 years (Racey *et al.*, 1996; Joly *et al.*, 2003). Historically, it is likely that populations of moose and caribou have fluctuated in response to variation in habitat characteristics, primarily driven by fire disturbance (Fritz *et al.*, 1993), and thus differences in the post-disturbance successional pathways after fire and logging are of concern to the long-term persistence of caribou populations if these differences tend to favour other ungulates over caribou. Little can be done about the post-disturbance differences in coarse-woody debris accumulation between logging and fire, since fire tends to leave dead trees standing and logging removes trees for processing. However, there may be management steps that can be taken to encourage the regeneration of lichen after logging (Coxson *et al.*, 2003; Goward & Campbell, 2005). In addition, ensuring successful regeneration of coniferous species after logging is an important first step for ensuring the long-term persistence of caribou habitat in this region. This is generally consistent with forest management objectives and was also suggested by Brown *et al.* (2000) as a first step in ensuring the persistence of caribou populations in this region of Manitoba.

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Comparison of seasonal habitat selection between threatened woodland caribou ecotypes in central British Columbia

Elena S. Jones[1*], Michael P. Gillingham[1], Dale R. Seip[2] & Douglas C. Heard[3]

[1]Natural Resources and Environmental Studies, University of Northern British Columbia, 3333 University Way, Prince George, British Columbia, V2N 4Z9, Canada.
[2]British Columbia Ministry of Forests and Range, 325 -1011 4th Avenue, Prince George, British Columbia, V2L 3H9, Canada.
[3]British Columbia Ministry of Environment, 4051 18th Avenue, Prince George, British Columbia, V2N 1B3, Canada.
[*]Corresponding author: (jonese@unbc.ca).

Abstract: Woodland caribou (*Rangifer tarandus caribou*) in British Columbia have been classified into ecotypes based on differences in use of habitat in winter. Although recovery planning focuses on ecotypes, habitat use and selection varies within ecotypes. Our objectives were to compare habitat use and selection among previously identified woodland caribou herds at the transition zone between northern (Moberly, Quintette, and Kennedy herds) and mountain (Parsnip herd) ecotypes in central British Columbia. We developed selection models for each herd in spring, calving, summer/fall, early and late winter. Topographic models best predicted selection by most herds in most seasons, but importance of vegetation-cover was highlighted by disproportionate use of specific vegetation-cover types by all caribou herds (e.g., in early winter, 75% of Kennedy locations were in pine-leading stands, 84% of Parsnip locations were in fir and fir-leading stands, and 87 and 96% of locations were in alpine for the Moberly and Quintette herds, respectively). Using a combination of GPS and VHF radio-collar locations, we documented some spatial overlap among herds within the year, but use of vegetation-cover types and selection of elevations, aspects, and vegetation-cover types differed among herds and within ecotypes in all seasons. Habitat use and selection were most similar between the two northern-ecotype herds residing on the eastern side of the Rocky Mountains. This research indicates that habitat use and selection by caribou herds in all seasons is more variable than ecotype classifications suggest and demonstrates the value of undertaking herd-specific mapping of critical habitat for woodland caribou.

Key words: GPS, herd, model, *Rangifer tarandus*, resource, use, vegetation.

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Introduction

Habitat selection by large ungulates is believed to be related to the amount and availability of food and minerals, insect disturbance, weather and predator avoidance (Skogland, 1980; Bergerud *et al.*, 1984; Bowyer, 1986; Barten *et al.*, 2001). Variation in habitat selection by large ungulates is likely because one or a combination of these factors is more pronounced in different regions at different times of the year. Research that quantifies variables that influence seasonal habitat selection of large ungulates across a diverse landscape is essential to resource management and species-conservation strategies.

Woodland caribou (*Rangifer tarandus caribou*) display considerable variation in seasonal habitat use within British Columbia (Cichowski, 1993; Terry *et al.*, 1996; Poole *et al.*, 2000; Apps *et al.*, 2001; Johnson *et al.*, 2001). Differences in use of habitat and forage (ground versus arboreal lichens) by woodland caribou in winter have led to the categorization of woodland caribou into ecotypes (Bergerud, 1978; Stevenson & Hatler, 1985). Two ecotypes of woodland caribou have been identified in central British Columbia: northern and mountain (Heard & Vagt, 1998). In winter, northern caribou primarily forage on ground lichens in alpine or low-elevation pine forests, whereas mountain caribou forage on arboreal lichens in old-growth subalpine forests (Stevenson & Hatler, 1985; Heard & Vagt, 1998). Differences between woodland caribou ecotypes are likely due to varying climate and topography across woodland caribou range that acts to influence forage distribution, abundance and snow conditions (Bergerud, 1978).

Differences between northern and mountain caribou, particularly in winter, have been made evident by studies examining habitat use and selection for one ecotype of woodland caribou during winter (Cichowski, 1993; Terry *et al*., 1996; Apps *et al*., 2001; Johnson *et al*., 2001). Variation in habitat use and selection by caribou in winter has also been observed within an ecotype (Cichowski, 1993; Terry *et al*., 1996; Gustine *et al*., 2006b), and among individuals in the same herd (Seip, 1992b; Johnson *et al*., 2001; Gustine *et al*., 2006b). Examination of habitat selection among adjacent caribou herds or individuals, however, has received little attention (Rettie & Messier, 2000; Mosnier *et al*., 2003; Saher & Schmiegelow, 2005; Gustine *et al*., 2006b), and differences in use and selection (in all seasons) between northern and mountain caribou herds have not been concurrently examined.

In British Columbia, mountain caribou are listed as endangered and northern caribou are of special concern (Hatter, 2002). Woodland caribou herds in our study area have been nationally designated as “threatened” by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2002), and subsequently have been listed as “threatened” under the federal Species at Risk Act (SARA). SARA requires that recovery planning occurs for threatened species. Although recovery planning for woodland caribou in British Columbia focuses on ecotypes, variation within ecotypes of woodland caribou suggests the need to determine whether it is appropriate to apply broad land-management strategies based on ecotype delineation or suitable land-management strategies to specific herds.

We compared habitat use (specifically use of different vegetation-cover types) and developed habitat selection models for four woodland caribou herds at the transition zone from northern to mountain ecotype during spring, calving, combined summer and fall (hereafter termed summer/fall), early and late winter in order to determine whether previously identified herds (Seip, 2002) were spatially and/or ecologically distinct. Our objectives were to: 1) determine whether seasonal range overlap occurred among herds and between ecotypes; and 2) compare seasonal habitat use and selection among herds and between ecotypes. We hypothesized that herds and ecotypes would be spatially separated during each season and that northern-ecotype herds (Kennedy, Moberly and Quintette) would show similar patterns in use and selection and differ from the mountain-ecotype herd (Parsnip), particularly during winter. As habitat selection by woodland caribou may be related to climatic variation, we expected the northern-ecotype herds that inhabited the eastern side of the Rocky Mountains (Quintette and Moberly) to show the most similar patterns in selection.

Study area

The study area is approximately 8000 km^2 and is located in the Rocky Mountains of central British Columbia (Fig. 1). This area is characterized by mountains and rolling hills with variable terrain, ranging from lodgepole pine (*Pinus contorta*) and hybrid white-spruce (*Picea glauca x engelmannii*) forests at 650 m to alpine summits at 2520 m. Four biogeoclimatic zones occur within the study area (Meidinger & Pojar, 1991): Sub-Boreal Spruce (SBS), Boreal White and Black Spruce (BWBS), Engelmann Spruce-Subalpine Fir (ESSF), and Alpine Tundra (AT).

The SBS zone occurs in the valley bottoms up to elevations of approximately 1100 m. This zone is dominated by hybrid white spruce and subalpine fir (*Abies lasiocarpa*), with occasional occurrences of lodgepole pine in drier areas and black spruce (*Picea mariana*) in wetter regions (Meidinger & Pojar, 1991). The BWBS zone occurs on the eastern side of the Rocky Mountains, ranges in elevation from 650 to 1050 m, and is typically colder and drier than the SBS zone. Dominant tree species include white spruce (*Picea glauca*), black spruce and lodgepole pine. Fire is common in this zone and early-seral stands containing trembling aspen (*Populus tremuloides*) and cottonwood (*Populus balsamifera*) are numerous (Meidinger & Pojar, 1991). The ESSF zone occurs above the SBS and BWBS zones to elevations up to 1700 m (Meidinger & Pojar, 1991). The dominant tree species within the ESSF zone are Engelmann spruce (*Picea engelmannii*) and subalpine fir. As elevation increases in the ESSF zone, subalpine fir dominates and the forest becomes more open, eventually turning into parkland where stunted subalpine fir grows in clumps interspersed with alpine meadows (Meidinger & Pojar, 1991). The AT zone occurs above the ESSF zone and is usually treeless. This zone is dominated by permanent ice and snow, rock, dwarf shrubs, forbs, mosses, grasses, sedge and ground lichens.

Prevailing westerly winds typically stall over the central Rocky Mountains resulting in high precipitation on the western side of the Rockies (Demarchi, 1996). The climate in the eastern portion of the study area is drier than in the western portion. The ESSF

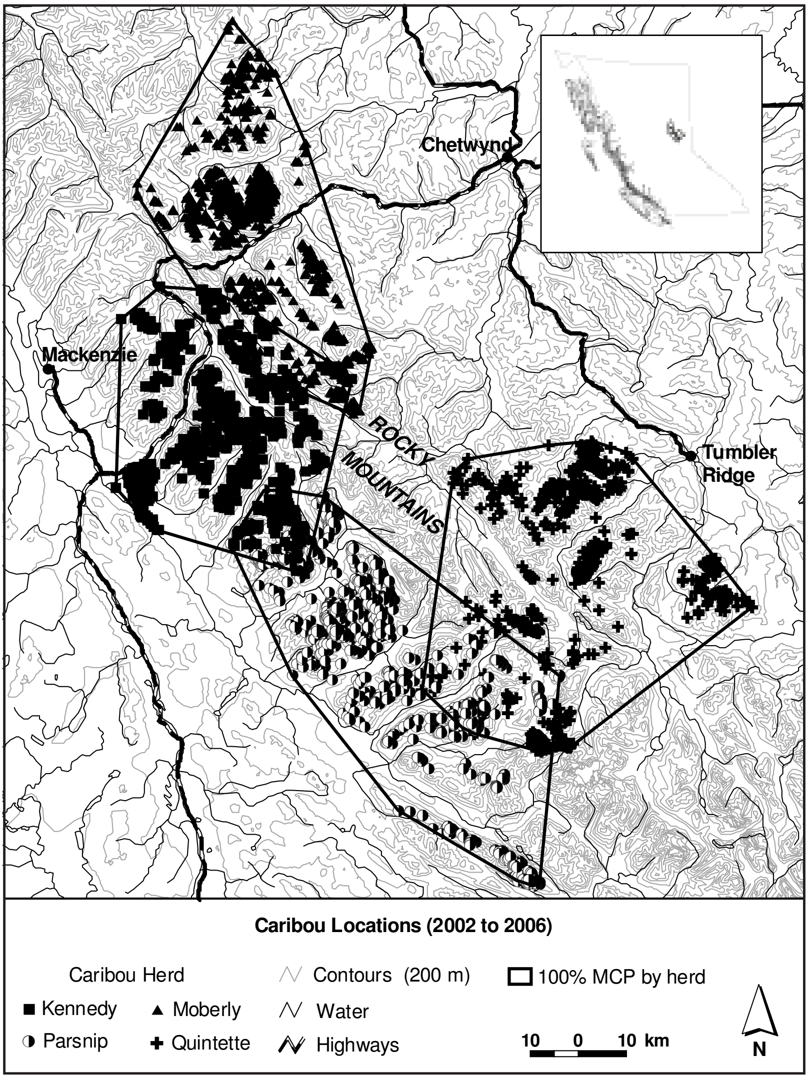

Fig. 1. Study area and caribou locations from May 2002 to January 2006 for woodland caribou in central British Columbia. The study area is depicted by a 100% minimum convex polygon (MCP) around all caribou locations for each herd.

zone on the west side of the Rockies has an annual precipitation of approximately 1530 mm compared with approximately 780 mm on the east side (Delong, 1994). The Parsnip (mountain ecotype) and Kennedy (northern ecotype) herds occur in the western portion of the study area whereas the Moberly and Quintette (northern ecotype) herds typically occupy the eastern side of the Rocky Mountains (Fig. 1). A major highway intersects both the Kennedy and Moberly herds, and a railway intersects all four of the herds. Logging has occurred and continues in the valley bottoms and low-elevation subalpine forests throughout the majority of the study area. The Quintette area is more developed than the Parsnip, Kennedy and Moberly areas from a combination of logging, oil and gas exploration and mining.

Materials and methods

Caribou locations and location accuracy

We captured 46 caribou within the four herds (Kennedy = 11, Moberly = 10, Quintette = 15, and Parsnip = 10) by net-gunning from a helicopter between April 2002 and December 2005. Herd sizes ranged from approximately 100 to 200 animals (Seip, 2002), so collared caribou represented from five to 10% of each herd. Caribou were fitted with either VHF (Lotek Fish and Wildlife Monitoring, 115 Pony

Drive, Newmarket, Ontario, Canada L3Y 7B5, Model LMRT-4) or GPS (Televilt, TVP Positioning AB, Bandygatan 2, SE-71134 Lindesberg, Sweden, Model GPS-VHF remote download) collars. Televilt GPS collars were programmed to take fixes every 4 h. All 12 Televilt collars failed to function as programmed; nine collars did not download following the first download period, and five collars stopped emitting a VHF signal and were lost. Seven of the original Televilt GPS-collared caribou were recaptured and collars were replaced with either a VHF or GPS (Advanced Telemetry Systems, 470 First Ave. No., Box 398 Isanti, Minnesota, USA 55040, Model: GPS Remote-Release Collar) collar. Locations were obtained from eight of the Televilt GPS collars during the first download period and from three recovered collars. Ten caribou were fitted with ATS GPS collars. ATS GPS collars were programmed to take fixes every 20 h and data were recovered successfully from collars on each caribou, nine on 18 April 2005, and one following its death in October 2004.

We located both VHF- and GPS-collared caribou (unless the VHF beacon had failed) using radio telemetry from a fixed-wing aircraft using the VHF beacon of both types of collars. We flew weekly in winter and spring, and bimonthly in summer and fall, weather permitting. We recorded caribou locations obtained by aerial telemetry using both a handheld GPS unit and the internal GPS unit in the aircraft to ensure that locations were recorded accurately. We believe that telemetry locations captured in this manner were accurate to within 150 m, and 59% (1143 of 1953) of the VHF locations were confirmed visually. We obtained 1953 aerial-telemetry (hereafter termed VHF) locations between 2 May 2002 and 29 January 2006: Kennedy = 491 (*n* = 11 individuals), Moberly = 565 (*n* = 10), Quintette = 422 (*n* = 15), and Parsnip = 475 (*n* = 10).

We obtained 7687 locations from 10 caribou throughout all seasons with ATS GPS collars (*n* = 2, Quintette and Kennedy; *n* = 3, Moberly and Parsnip), three of which also had data from Televilt GPS collars. We also used data from five individual caribou with Televilt GPS collars in late winter, one of which also recorded locations in early winter. As Televilt GPS collars were programmed to record data every 4 h, we ensured that these collars were consistent with the 20-h ATS GPS-collar fix rate by using only every fifth location. Data from each GPS collar were examined for atypical locations (Spatial Viewer, unpublished program by M. P. Gillingham) and one questionable location was removed. Because dilution of precision (DOP) values and the number of satellites used to obtain a location (2D or 3D) have been related to location error, we removed DOP values >25 for 3D locations (*n* = 6) and >10 for 2D locations (*n* = 46) (Rempel & Rodgers, 1997; Dussault *et al.*, 2001). Fix rates of all GPS collars combined exceeded 75% in all seasons with the exception of summer/fall when the fix rate was 63%. After generating 20-h fix locations from the Televilt collars, removing potentially erroneous 2D and 3D fixes, and excluding locations that fell into areas where vegetation-cover data did not exist (*n* = 5), 5243 GPS-collar locations were used to model seasonal habitat selection of woodland caribou: Kennedy = 1031 (*n* = 2 individuals, all seasons; *n* = 3 individuals, late winter), Moberly = 1749 (*n* = 3, all seasons; *n* = 4, early and late winter), Quintette = 1173 (*n* = 2, all seasons; *n* = 5, late winter), and Parsnip = 1290 (*n* = 3, all seasons).

Herd and seasonal definitions

We initially grouped radio-collared caribou into one of four previously identified herds (Seip, 2002) based on the capture location of each collared caribou, but some capture locations fell outside of the previously identified herd boundaries. Because ecotypes are distinguished by differences in habitat use during winter (Stevenson & Hatler, 1985), we evaluated herd assignments based on habitat use (VHF data) by individual caribou in early winter. Differences in use of vegetation-cover type (e.g., alpine, fir-leading, pine-leading) among individual caribou were more discernable than other variables that also describe habitat use by caribou (e.g., elevation, slope, aspect). Consequently, we checked original herd assignments and assigned outlying individuals to previously identified herds based on use of vegetation-cover types by individual caribou.

We categorized location data from caribou into five seasons based on migration patterns, biology and snow conditions recorded during telemetry flights, and while conducting fieldwork within the study area: spring (1 April to 14 May), calving (15 May to 14 June), summer/fall (15 June to 31 October), early winter (1 November to 14 January), and late winter (15 January to 31 March). Spring corresponded with the melting of snow and emerging green vegetation on south-facing slopes. Calving encompassed the typical calving period for woodland caribou (Bergerud *et al.*, 1984; Bergerud & Page, 1987; Gustine *et al.*, 2006a). Summer/fall began when the majority of snow had melted from the mountainous areas. Early winter began when snowfall remained on the ground in the mountainous areas and typically coincided with the movement of Kennedy caribou to the low-elevation pine stand at Kennedy Siding. Late winter began when snow depth on the west side of the mountains typically exceeded 1 m and the snowpack had settled and hardened.

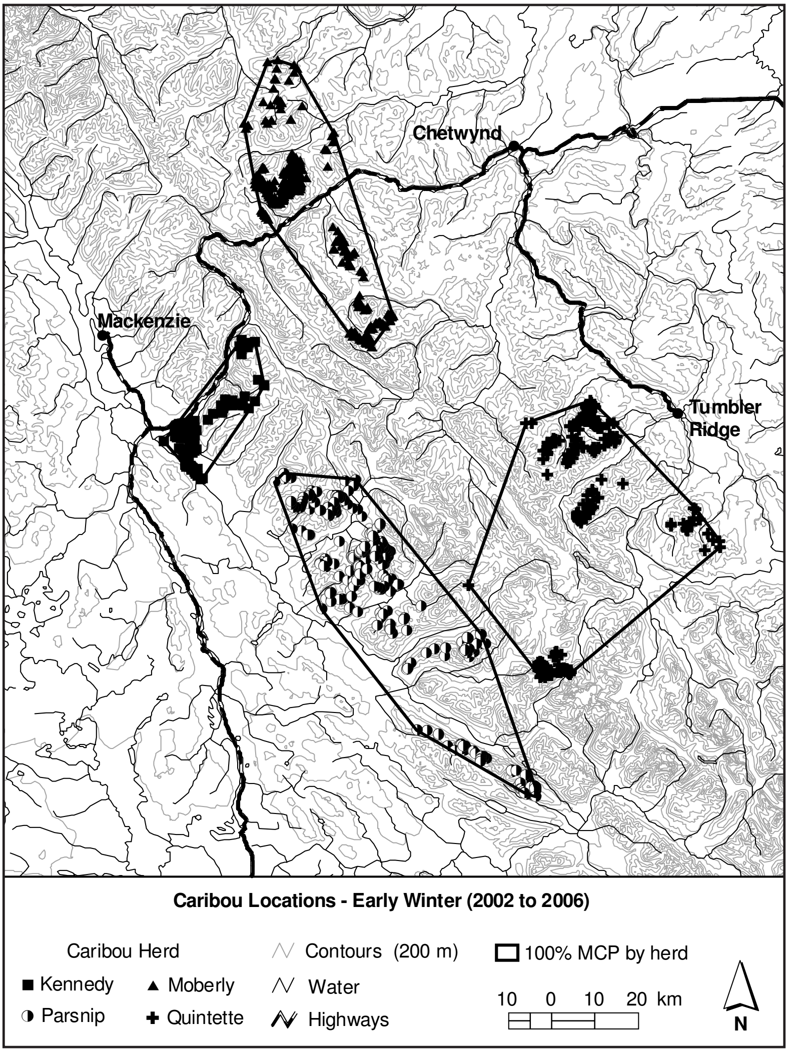

Fig. 2. Early winter locations of caribou (2002 to 2006), by herd, showing lack of spatial overlap during this season for woodland caribou in central British Columbia.

Defining availability

We examined availability at the scale of an approximate daily movement capability of caribou using the 95th percentile movement distance (Arthur *et al.*, 1996) between consecutive 20-h fixes calculated for each herd during each season. We selected the 95th percentile movement distance after examining frequency distributions by herd and season to identify the distance that a caribou was capable of moving in a 20-h period with the exception of movements that were not typical and may have been provoked by rare human or other disturbance. This distance was applied as a radius around each used caribou location to define the area available to an individual caribou. For each caribou location we generated five random locations within the defined available area. We chose to use movement distance to define availability as opposed to a seasonal home-range estimator as using movement distance allowed the sampled area available to an individual caribou to correspond to each use location for that individual (Compton *et al.*, 2002).

Because available areas may have been underestimated (caribou could have moved farther in 40 h than in 20 h) for locations occurring after a mixed fix (i.e., 40-hr time interval between two fixes), we analyzed the used/available locations as unmatched, in that comparison between used and available locations was across an entire season, as opposed to comparing use and availability for each location. This method allowed us to relate availability to use locations as is appropriate for animals with large home ranges (Compton *et al.*, 2002).

Model development

We developed a set of biologically plausible *a priori* candidate models (Table 1) to examine the influence of topographic variables, vegetation-cover type and distance to nearest road on habitat selection of woodland caribou herds in each season using the GPS-location data. Elevation, slope and aspect at each caribou location were obtained from a Digital Elevation Model (DEM) (British Columbia Ministry of Sustainable Resource Management, Base Mapping and Geomatic Services Branch, 2005). Elevation and slope were modeled as continuous variables and we used five categorical variables to model aspect: north (316 to 45 degrees), east (46 to 135 degrees), south (136 to 225 degrees), west (226 to 315 degrees), and no aspect (slope = 0).

Land cover was obtained from digitized 1:20 000 Vegetation Resource Inventory (VRI) data (British Columbia Ministry of Sustainable Resource Management, Land and Resource Data Warehouse, 2005b). We defined 11 vegetation-cover types using a combination of land-cover variables and elevation (Jones, unpubl. data): alpine, parkland, fir, fir-leading, spruce-leading, pine-leading, coniferous-unknown, young-coniferous, deciduous/shrub, open-nonvegetated and open-vegetated. We defined 'fir' as a stand containing only fir trees, whereas 'fir-leading' was a stand dominated by fir but also containing other tree species. The 'young-coniferous' cover type included all coniferous-cover types $\leq$ 40 years, thus all other coniferous classes were >40-years old. As collar locations (GPS and VHF) were not all obtained during the same year as the VRI, we calculated the age of coniferous-cover types specific to the year of each caribou location using the updated-age variable of leading-tree species in the VRI (British Columbia Ministry of Forests and Range, 2005).

Road locations were obtained from Terrestrial Resource Inventory Mapping (TRIM) data (British Columbia Ministry of Sustainable Resource Management, Land and Resource Data Warehouse, 2005a). Distance to nearest road (any type) was modeled as a continuous variable and was calculated using the Spatial Analyst extension in ArcMAP (version 8.3, ESRI, 2003). All vector data were rasterized with a 25-m output resolution using the Spatial Analyst extension in ArcMAP. Variable attributes for each used and available caribou location were obtained from final raster layers using PCI Imageworks (version 9.1, PCI Geomatics, 2003).

Categorical variables (vegetation-cover type and aspect) were modeled with deviation coding using DESMAT (Hendrickx, 2001), and classes that were rarely or never used by caribou ($n < 4$) were excluded from analysis to avoid issues of perfect or near-perfect separation (Menard, 2002). We chose to eliminate categorical variables where $n < 4$ because standard errors (SEs) of variables normalized only when $n \geq 4$. Collinearity of continuous variables in the model set was examined by herd and season and all tolerance scores exceeded the acceptable level of 0.2 (Menard, 2002). To ensure that elevation and vegetation-cover type, were not highly collinear we examined overlap in range of elevations among vegetation-cover types, and used a Kruskal-Wallis test (StataCorp, 2005) to determine whether there were differences in elevation among vegetation-cover types. Although alpine and pine-leading stands differed in elevation, there was considerable overlap (range of elevations and non-significant differences) among the remaining vegetation-cover classes. We concluded that elevation and vegetation-cover type were not inherently collinear.

Prior to modeling, we used logistic regression (Hosmer & Lemeshow, 2000) to evaluate whether selection for elevation was linear (elevation) or quadratic (elevation + elevation^2), for each herd in each season by comparing Akaike's Information Criterion for small sample sizes (AIC$_c$) for both the linear and quadratic elevation models (Burnham & Anderson, 2002). The elevation model with the lowest AIC$_c$

Table 1. Suite of ecologically plausible models, determined *a priori*, to describe selection for woodland caribou in central British Columbia.

Model Name	Model Variables
Topo Model 1	Elevation[a] + Aspect + Slope
Topo Model 2	Elevation[a] + Aspect
Vegetation - Topo Model 1	Elevation[a] + Aspect + Vegetation Cover Type
Vegetation - Topo Model 2	Elevation[a] + Vegetation Cover Type
Vegetation Model	Vegetation Cover Type
Vegetation - DTR Model	Elevation[a] + Vegetation Cover Type + Distance to Road
Topo - DTR Model	Elevation[a] + Aspect + Distance to Road
DTR Model	Distance to Road

[a] Elevation was modeled as either a linear or quadratic relationship depending on best fit (see methods and results).

score (typically the quadratic model) was used in the model set (Table 1).

We initially attempted to model selection (using logistic regression) for individual caribou, but small sample sizes resulted in large SEs of variables and the receiver operating characteristic (ROC) curves typically showed less than acceptable (<0.70) discrimination (Manel *et al.*, 2001). Because sample sizes precluded examining selection for individual caribou, we pooled GPS locations by herd and season and used logistic regression to determine the coefficients of selection (β_i) for each variable and the Huber-White sandwich estimator to obtain robust estimates of variance for these coefficients (Boyce *et al.*, 2002). All logistic-regression analyses were conducted using STATA (version 8.0, StataCorp, 2005).

We considered all models for which Akaike weights (w_i) summed to ≥0.95 to be competing models, indicating that given the entire set of models, these models explained over 95% of the variation (Burnham & Anderson, 2002); we use the term 'top' model to refer to those instances where one model explained ≥0.95 of the variation. To evaluate the predictive ability of the top model or competing models for each herd in each season, we used k-fold cross validation (Boyce *et al.*, 2002) to obtain the mean Spearman's rank correlation ($\bar{r}_s$) from five random subsets of the used/available data. Models were considered to be valid if the mean Spearman's rank correlation was significant ($P < 0.5$). We averaged validated competing models (Burnham & Anderson, 2002) to obtain a final model for each herd in each season. Significance of selection coefficients (β_i) was determined using the Wald statistic (Menard, 2002) for top models, and inferred when the confidence intervals (CIs) did not encompass zero for an averaged final model. Selection was inferred when $\beta_i > 0$ for significant variables.

Of the selection attributes we measured, only vegetation-cover type and roads can be manipulated by managers. Because the addition of topographic variables may have influenced the statistical significance of selection for vegetation-cover types, we also examined selection coefficients from the vegetation-cover type model in the absence of other variables to quantify selection or avoidance of vegetation-cover types by woodland caribou herds.

Results

Spatial separation and use of vegetation-cover types

We considered herds to be spatially separated if the 100% MCP (minimum convex polygon) around seasonal locations for a herd did not overlap with the seasonal MCP of another herd. Using those criteria, evidence of some geographical overlap among herds and ecotypes was apparent in spring, calving, summer/fall, and late winter, but not in early winter (Fig. 2). The northern-ecotype herds on the eastern side of the Rockies (Quintette and Moberly) were spatially separated during all seasons. Some spatial overlap occurred between the Parsnip and Quintette herds and the Kennedy and Moberly herds in all seasons but early winter, and the Parsnip and Kennedy herds in all seasons but early and late winter. Spatial separation may exist within the Moberly herd as collared caribou did not cross the highway (Highway 97) intersecting that herd. Perhaps these groups (north and south) should be considered separate herds, but because individuals had similar habitat-use patterns and sample size (n = 10 individuals) may not have been sufficient to determine that none of the Moberly caribou cross the highway, we modeled them as the same herd.

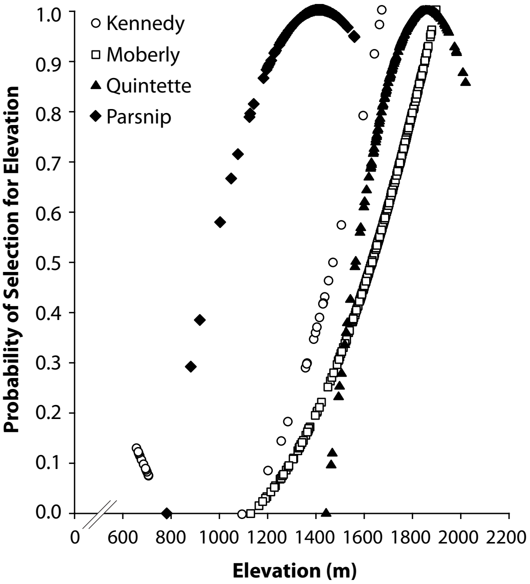

Fig. 3. Probability of selection for elevation in early winter from the top or averaged selection model, by herd, for woodland caribou in central British Columbia. The elevation function was determined by holding other variables in the model constant and calculating the sum of $\beta_{i(elevation)}$ x elevation and $\beta_{i(elevation^2)}$ x elevation^2 (scaled between 0-1) at use locations of woodland caribou for that season. Elevation and elevation^2 were significant ($P < 0.05$) for each herd.

Use of vegetation-cover types by GPS-collared caribou varied among herds and seasons (Table 2), but some patterns were evident. The northern-ecotype herds that inhabited the eastern side of the Rockies (Moberly and Quintette) were predominately located

Table 2. Percent of total number of used and available GPS (VHF in brackets) locations in vegetation-cover types, by season and herd, for woodland caribou in central British Columbia. Total number of used and available locations (*n*) for each herd is included.

	Kennedy		Moberly		Quintette		Parsnip	
Spring	Used	Available	Used	Available	Used	Available	Used	Available
n	141 (48)	705 (240)	217 (54)	1075 (270)	152 (48)	760 (240)	201 (50)	1005 (255)
Alpine	36 (63)	16 (19)	98 (81)	40 (35)	91 (94)	43 (33)	12 (6)	7 (2)
Parkland	15 (8)	10 (15)	[a]	10 (9)	[a]	4 (6)	[a]	
Fir	23 (10)	17 (10)	[a] (6)	4 (6)	5	3 (6)	42 (22)	21 (16)
Fir-leading	9 (6)	26 (27)	[a] (2)	24 (22)	3 (4)	18 (17)	29 (32)	28 (20)
Spruce-leading	[a]	17 (19)	[a] (6)	13 (17)	[a] (2)	19 (23)	4 (8)	26 (24)
Pine-leading	[a] (4)	(4)	[a] (2)	4 (7)	[a]	3 (4)	[a]	
Conif.-unknown	[a]		[a]		[a]		4 (20)	5 (25)
Young-conif.	[a]	1 (2)	[a]	2	[a]	4 (2)	[a]	
Decid./shrub	11 (2)	13 (4)	[a]	2 (2)	[a]	5 (6)	7 (10)	8 (8)
Open-nonveg.	[a] (4)		[a]		[a]	1	[a]	1 (4)
Open-veg.	6 (2)	1	2 (4)	1 (2)	[a]	1 (2)	[a] (2)	2 (2)
Calving								
n	64 (30)	325 (140)	82 (35)	415 (175)	58 (32)	285 (150)	110 (34)	555 (160)
Alpine	36 (23)	14 (21)	40 (43)	19 (26)	45 (38)	26 (27)	[a]	9 (6)
Parkland	[a] (10)	5 (11)	32 (9)	11 (9)	[a] (16)	2 (10)	[a]	
Fir	31 (10)	12 (18)	4 (6)	1 (6)	2	9	36 (29)	21 (22)
Fir-leading	9 (30)	22 (25)	11 (23)	27 (26)	41 (16)	28 (13)	45 (50)	28 (28)
Spruce-leading	22 (17)	34 (18)	10 (17)	30 (23)	12 (25)	28 (30)	13 (9)	27 (19)
Pine-leading	[a]		[a] (3)	2 (3)	[a]	2 (3)	[a]	
Conif.-unknown	[a] (3)	2	[a]		[a]		3 (12)	3 (16)
Young-conif.	[a]	2	[a]		[a]	(3)	[a]	1
Decid./shrub	2 (7)	8 (4)	2	6 (6)	[a]	4 (10)	3	9 (9)
Open-nonveg.	[a]	2	[a]	2	[a] (3)	(3)	[a]	1
Open-veg.	[a]	2 (4)	1	1 (3)	[a] (3)	2	[a]	2
Summer/Fall								
n	237 (141)	1185 (705)	354 (165)	1760 (840)	216 (132)	1075 (660)	348 (136)	1745 (675)
Alpine	8 (5)	9 (10)	55 (32)	26 (23)	53 (33)	33 (20)	2 (1)	8 (4)
Parkland	5 (6)	5 (6)	15 (15)	12 (11)	2 (8)	1 (7)	[a]	
Fir	32 (30)	16 (16)	1 (3)	4 (4)	9 (8)	9 (9)	21 (19)	25 (23)
Fir-leading	28 (35)	29 (32)	16 (32)	29 (25)	28 (25)	28 (23)	69 (60)	38 (38)
Spruce-leading	12 (11)	24 (21)	8 (15)	20 (21)	4 (21)	16 (30)	4 (8)	21 (17)
Pine-leading	9 (4)	4 (2)	[a] (1)	1 (4)	2 (3)	2 (4)	[a]	
Conif.-unknown	[a] (1)		[a]	(2)	[a]		2 (10)	1 (13)
Young-conif.	[a] (1)	1 (1)	[a]	2 (1)	1	1 (2)	[a]	
Decid./shrub	3 (4)	9 (9)	[a]	3 (6)	[a] (2)	6 (4)	1 (3)	4 (4)
Open-nonveg.	[a] (1)	2 (2)	[a]	1 (1)	[a]	1 (1)	1	1
Open-veg.	2 (3)	1 (1)	4 (2)	3 (3)	1	2 (2)	[a]	1 (1)

[a] Vegetation-cover type removed from models when use locations <4.

Table 2. Continued.

	Kennedy		Moberly		Quintette		Parsnip	
Early Winter	Used	Available	Used	Available	Used	Available	Used	Available
n	248 (106)	1225 (525)	472 (112)	2335 (555)	238 (81)	1205 (400)	237 (97)	1175 (480)
Alpine	2		87 (67)	33 (34)	96 (75)	40 (35)	[a]	3 (1)
Parkland	1 (1)	1 (1)	4 (8)	15 (9)	[a] (2)	1 (5)	[a]	
Fir	3	2 (1)	1 (1)	4 (3)	4 (1)	6 (3)	30 (28)	19 (16)
Fir-leading	4 (3)	6 (5)	6 (11)	24 (28)	[a] (5)	20 (18)	54 (35)	36 (29)
Spruce-leading	1 (1)	19 (20)	1 (7)	13 (17)	[a] (11)	17 (21)	5 (6)	24 (15)
Pine-leading	75 (67)	34 (35)	[a] (4)	3 (5)	[a] (4)	3 (13)	[a]	
Conif.-unknown	[a]		[a]		[a]		9 (30)	9 (30)
Young-conif.	13 (24)	7 (9)	[a]	2 (1)	[a]	2 (3)	[a]	
Decid./shrub	[a] (2)	23 (23)	[a] (2)	2 (2)	[a]	7 (3)	1 (1)	8 (7)
Open-nonveg.	[a] (2)	6 (7)	[a]	1	[a]	1	[a]	(1)
Open-veg.	[a] (1)	1	1 (1)	2 (1)	[a] (1)	2 (1)	[a]	1 (1)
Late Winter								
n	341 (164)	1705 (820)	623 (196)	3115 (980)	505 (129)	2535 (640)	394 (157)	1975 (785)
Alpine	23 (21)	12 (12)	85 (65)	49 (39)	90 (78)	54 (44)	2 (2)	5 (4)
Parkland	12 (7)	11 (10)	6 (7)	13 (10)	[a] (3)	3 (5)	[a]	
Fir	18 (21)	11 (10)	5 (3)	4 (4)	5 (2)	7 (5)	45 (40)	30 (22)
Fir-leading	19 (18)	25 (26)	1 (7)	15 (21)	4 (6)	20 (19)	43 (32)	34 (28)
Spruce-leading	3 (5)	17 (15)	1 (10)	12 (15)	[a] (4)	9 (16)	3 (2)	15 (16)
Pine-leading	17 (6)	9 (10)	[a] (7)	3 (7)	[a] (6)	1 (8)	[a]	
Conif.-unknown	[a]		[a]		[a]		[a] (21)	2 (20)
Young-conif.	3 (12)	2 (5)	[a]	1 (1)	[a]	(1)	[a]	
Decid./shrub	3 (5)	9 (9)	1	2 (2)	[a] (1)	4 (2)	6 (1)	10 (8)
Open-nonveg.	[a] (3)	2 (2)	[a]	1 (1)	[a]		[a]	1 (1)
Open-veg.	2 (1)	3 (3)	2 (2)	1 (1)	[a]	1 (1)	1 (2)	3 (1)

[a] Vegetation-cover type removed from models when use locations <4.

in alpine in all seasons. In contrast, the northern-ecotype herd on the western side of the Rockies (Kennedy) used five to 10 different vegetation-cover types that varied in percentage of use across seasons. The mountain-ecotype herd (Parsnip) primarily used fir and fir-leading stands in all seasons. Differences in use of vegetation-cover types were most apparent within and among ecotypes in early winter. Seventy-five percent of Kennedy locations were in pine-leading stands, 87 and 96% of locations were in alpine for the Moberly and Quintette herds, respectively, and 84% of Parsnip locations were in fir and fir-leading stands.

The VHF data were generally consistent with the patterns observed from the GPS locations (Table 2). Although we did not statistically test for differences between the GPS and VHF data, the VHF data suggested greater use of fir, fir-leading and spruce-leading stands by the northern-ecotype herds than GPS data, particularly during summer/fall. We attempted to model habitat selection using the VHF data, but small sample sizes resulted in models that we were unable to validate (using k-fold cross validation).

Up to nine vegetation-cover types were removed from selection models due to rare occurrences of use (Table 2). Specifically, spruce-leading, pine-leading, deciduous/shrub, young-coniferous, and open-vegetation classes were often removed for many herds in all seasons, with the exception of the Kennedy herd, which commonly used pine-leading and to a lesser extent young-coniferous stands in early and late winter.

Selection models

The model containing all topographic variables (Topo Model 1, Table 3) was the top model during spring, summer/fall, early winter and late winter with the exception of the Kennedy herd during summer/fall and late winter, and the Parsnip herd during summer/fall. This result indicates that vegetation-cover type or distance to nearest road did not contribute to explaining selection by these herds during these seasons and that the combination of elevation, slope and aspect best predicted selection by caribou. The predictive ability of the topographic model ranged from a mean r_s (using k-fold cross validation) of 0.787 in early winter to 0.970 in late winter (all $P < 0.01$). During calving, the model containing vegetation-cover type, elevation and aspect (Table 3) often explained the majority of variation in selection. In two instances (Moberly Topo Model 1 in spring, and Parsnip Topo Model 1 in late winter), mean r_s could not be calculated (using k-fold cross validation) because the combination of elevation + elevation^2 predicted the dependent variable perfectly.

Vegetation-cover type or distance to nearest road typically entered into the competing model set only when use of varying elevations by caribou was more common, and the selection coefficient for distance to nearest road was only significant for the Parsnip herd during summer/fall. The DTR Model (containing only the distance to nearest road variable) and the Vegetation Model (containing only the vegetation-cover type variable) never entered into the competing model set (Table 3).

Elevation

Differences in selection patterns for elevation by caribou herds were most apparent in early winter (Fig. 3), but selection for elevation varied among herds in all other seasons. Although elevation was typically modeled as a quadratic (AIC_c scores were lower for the quadratic model than the linear model, for all herds in all seasons, except Quintette in spring and calving), selection for elevation commonly showed a more linear pattern for northern-ecotype herds until elevation exceeded 1600 m (e.g., Quintette herd, Fig. 3). In contrast, selection for elevation by the mountain-ecotype herd was distinctly quadratic in all seasons (e.g., Parsnip herd, Figure 3), showing selection for mid-elevations. An inverse quadratic pattern occurred for the Kennedy herd in early and late winter as these caribou were commonly located in low-elevation pine forests during this period (e.g., Kennedy herd, Fig. 3).

The northern-ecotype caribou on the eastern side of the Rockies (Quintette and Moberly) showed the most similar patterns of use and selection for elevation. These herds were rarely located below 1200 m (range of use: Moberly, 1175 to 2005 m; Quintette, 1250 to 2035 m) and selected elevations above 1600 m in all seasons. Seasonal differences in selection patterns for elevation were still apparent between these two herds, as the Quintette caribou selected for lower elevations (>1600 m) in summer/fall and the highest elevations in late winter (>1900 m), whereas the Moberly caribou selected for lower elevations in late winter (>1600 m), and highest elevations in summer/fall and early winter (>1800 m). Elevation was not significant for the Moberly herd during calving.

The northern-ecotype herd on the west side of the Rockies (Kennedy) selected for elevations similar to the eastern herds during calving (>1800 m), but selected for lower elevations than these herds in summer/fall (>1400 m) and early winter (>1600 m). Elevation was not significant for the Kennedy herd during spring and late winter. Caribou in the Kennedy herd were located at elevations below 1200 m in all seasons except calving, and use of elevations between 700 and 800 m was common in early and late winter (range of use: Kennedy, 710 to 2010 m).

The Parsnip herd was rarely located below 1100 m (range of use: Parsnip, 835 to 1835 m) and showed selection for elevations between 1150 to 1800 m across all seasons. During spring, Parsnip caribou selected the largest range of elevations (1300 to 1800 m), and slightly lower elevations during calving and summer/fall (1250 to 1600 m). The lowest elevations were selected during early winter (1150 to 1600 m) and were similar to elevations selected in late winter (1200 to 1600 m). The Parsnip herd was notably absent from elevations outside of the selected range (only 10 locations < 1100 m), whereas the northern ecotypes were commonly located at lower elevations than selection indicates.

Slope and aspect

Selection for slopes with the lowest gradients was common among all herds in spring, early winter and late winter with the exception of the Kennedy herd where slope was not significant in late winter. Slope was not significant for any of the herds during calving or for the Kennedy and Parsnip herds during summer/fall. The Moberly and Quintette herds both avoided steeper slopes in summer/fall.

The northern-ecotype herds on the eastern side of the Rockies avoided eastern aspects in all seasons and selected for western aspects in all seasons with the exception of the Moberly herd in spring, where western aspects were not significant. Both herds selected for southern aspects in spring and the Quintette herd avoided northern aspects in spring and early winter. Both herds avoided northern aspects in late winter.

Aspect was significant for Kennedy caribou during spring, summer/fall and late winter. Similar to the Quintette herd, the Kennedy caribou selected for southern and western aspects in spring and avoided northern aspects in spring and eastern aspects in late

Table 3. Top or competing models, by season and herd, for woodland caribou in central British Columbia. Model variables are presented in Table 2. Competing models are sorted by Akaike model weights (w_i). Statistics also include the number of parameters used in each model (K), number of locations (n), receiver operating characteristic (ROC), log-likelihood (LL), Akaike's information criteria for small sample sizes (AIC$_c$), and Spearman's rank correlation ($\bar{r}_s$) using *k*-fold cross validation. All $\bar{r}_s$ from five k-fold runs were significant ($P < 0.01$).

Season	Herd	Model	K	n	ROC	LL	AIC$_c$	w_i	$\bar{r}_s$
Spring	Kennedy	Topo Model 1	7	720	0.805	-282.346	578.809	0.999	0.830
	Moberly	Topo Model 1	7	655	0.888	-257.417	528.964	1.000	[a]
	Quintette	Topo Model 1	6	634	0.825	-247.527	507.149	1.000	0.801
	Parsnip	Topo Model 1	7	1162	0.869	-375.652	765.378	1.000	0.863
Calving	Kennedy	Vegetation - Topo Model 1	9	325	0.898	-99.207	216.872	0.427	0.791
	Kennedy	Vegetation - Topo Model 2	6	325	0.888	-102.596	217.380	0.331	0.837
	Kennedy	Vegetation - DTR Model	7	325	0.889	-101.879	218.024	0.240	0.779
	Moberly	Vegetation - Topo Model 1	9	438	0.807	-161.125	340.587	0.771	0.813
	Moberly	Topo Model 2	6	438	0.792	-166.274	344.687	0.099	0.797
	Moberly	Topo Model 1	7	438	0.787	-165.466	345.127	0.080	0.863
	Quintette	Topo - DTR Model	6	292	0.789	-119.261	250.732	0.456	0.644
	Quintette	Vegetation - Topo Model 1	7	292	0.787	-118.882	252.061	0.235	0.768
	Parsnip	Vegetation - Topo Model 1	8	521	0.799	-204.677	425.573	0.354	0.851
	Parsnip	Topo Model 2	6	521	0.790	-207.227	426.570	0.215	0.862
	Parsnip	Vegetation - Topo Model 2	5	521	0.782	-208.667	427.412	0.141	0.874
	Parsnip	Topo Model 1	7	521	0.793	-206.669	427.502	0.135	0.853
	Parsnip	Topo - DTR Model	7	521	0.792	-207.108	428.379	0.087	0.884
	Parsnip	Vegetation - DTR Model	6	521	0.784	-208.366	428.849	0.069	0.858
Summer/ Fall	Kennedy	Vegetation - Topo Model 1	14	1388	0.788	-526.269	1080.804	0.937	0.936
	Kennedy	Vegetation - Topo Model 2	10	1388	0.775	-533.432	1086.996	0.042	0.938
	Moberly	Topo Model 1	7	1999	0.761	-799.042	1612.126	1.000	0.946
	Quintette	Topo Model 1	7	1178	0.721	-495.911	1005.895	1.000	0.837
	Parsnip	Vegetation - DTR Model	9	2038	0.775	-784.089	1586.250	0.898	0.930
	Parsnip	Topo Model 1	7	2038	0.776	-788.406	1590.853	0.090	0.906
Early Winter	Kennedy	Topo Model 1	8	843	0.702	-453.108	922.349	1.000	0.848
	Moberly	Topo Model 1	7	2609	0.864	-851.782	1717.596	1.000	0.787
	Quintette	Topo Model 1	7	793	0.785	-395.553	805.213	1.000	0.882
	Parsnip	Topo Model 1	7	1260	0.796	-509.466	1032.999	0.999	0.894
Late Winter	Kennedy	Vegetation - Topo Model 1	15	2013	0.745	-798.803	1627.816	0.792	0.897
	Kennedy	Vegetation - Topo Model 2	11	2013	0.739	-804.506	1631.123	0.152	0.901
	Kennedy	Vegetation - DTR Model	12	2013	0.739	-804.505	1633.142	0.055	0.920
	Moberly	Topo Model 1	7	3588	0.809	-1319.033	2652.089	1.000	0.970
	Quintette	Topo Model 1	7	2539	0.804	-1021.047	2056.126	1.000	0.911
	Parsnip	Topo Model 1	7	2260	0.790	-851.076	1716.190	1.000	[a]

[a] K-fold cross validation procedures were unsuccessful (see results).

winter. In contrast to the Quintette and Moberly herds, the Kennedy caribou selected for northern aspects in summer/fall and areas with no aspect (slope = 0) in late winter. Aspect was significant for the Parsnip herd only during calving and late winter. The Parsnip caribou selected for southern aspects during calving and similar to the Quintette and Moberly herds, selected western aspects and avoided eastern aspects in late winter. No aspect (slope = 0) was dropped from the models for the Parsnip, Moberly and Quintette herds due to zero or rare ($n < 4$) occurrences of use.

Vegetation-cover type

Vegetation-cover type only entered into the competing model set for all herds during calving, for the Parsnip herd during summer/fall and for the Kennedy herd during summer/fall and late winter (Table 3). Selection coefficients for relatively few vegetation-cover types were significant for herds during these seasons, and selected vegetation-cover types were typically lower-elevation forested stands not explained by elevation. The Moberly herd selected parkland and the Kennedy herd selected spruce-leading stands during calving. Although a higher percentage of use locations were in alpine during calving (Table 2), some individuals in these herds moved from alpine to forested stands (Kennedy) during parturition and returned to alpine after calving.

Vegetation-cover type model

Selection for mid- and high-elevation areas was evident among herds and ecotypes, and elevation typically overshadowed vegetation-cover type in explaining differences among used and available locations. Because use data (Table 2) showed a clear disparity in use of different vegetation-cover types among herds, and understanding selection for vegetation cover is an important component for recovery planning, we examined the coefficients for vegetation-cover types in the absence of other variables (Vegetation Model, Table 1).

Alpine

The northern-ecotype herds selected alpine in all seasons with the exception of the Moberly herd during spring and the Kennedy herd during summer/fall. The Moberly herd in spring was almost exclusively located in alpine (98% of locations, Table 2), but selection for alpine was not statistically significant as only two vegetation-cover types could be included in the model (all other available vegetation-cover types were removed to avoid issues of perfect or near-perfect separation), and both were used in similar proportion to availability (following removal of unused vegetation-cover types). Selection for alpine by Moberly caribou in spring is easily inferred from use. In contrast, the Parsnip herd selected alpine only during spring and avoided alpine in summer/fall.

Parkland, fir and fir-leading stands

Selection for forested stands that typically occur at high elevations (parkland, fir and fir-leading) was variable among the northern-ecotype herds in all seasons. The Moberly caribou selected for parkland during calving and summer/fall, and fir stands in late winter, while the Quintette herd selected fir stands during spring. Fir stands were avoided by the Moberly herd in summer/fall and the Quintette herd in early winter. The Kennedy herd selected fir during calving, summer/fall and late winter and never showed avoidance of fir stands. Avoidance of fir-leading stands, which commonly occurred at lower-elevations than parkland or pure fir stands, was typical for the northern-ecotype herds across all seasons. The Parsnip herd selected fir stands in all seasons and in contrast to the northern-ecotype herds, selected fir-leading stands in all seasons except spring.

Spruce-leading

Spruce-leading stands typically occur in low-elevation subalpine or valley-bottom forests. All herds avoided spruce-leading stands during calving and summer/fall and none of the herds selected spruce-leading stands in any season. None of the northern-ecotype herds were located in spruce-leading stands during spring (Table 2), and the Parsnip herd avoided spruce-leading stands during this season. In early and late winter all of the herds either avoided, or were never located, in spruce-leading stands.

Pine-leading

The northern-ecotype herds on the eastern side of the Rockies were never located in pine-leading stands with the exception of the Quintette herd during summer/fall (Table 2). In contrast, the Kennedy herd selected for pine-leading stands in summer/fall and late winter. Similar to the northern-ecotype herds on the eastern side of the Rockies, the Parsnip caribou were never located in pine-leading stands.

Deciduous/shrub, young-coniferous, open-nonvegetated, open-vegetated

These vegetation-cover types were typically dropped from the models for all herds in all seasons due to rare occurrences of use (Table 2). The GPS models showed avoidance of deciduous/shrub in summer/fall and late winter and selection of open-vegetated areas in spring for the Kennedy herd. The Moberly herd selected open-nonvegetated areas in summer/fall and open-vegetated areas in late winter. Although selection of young-coniferous stands was not significant for the Kennedy herd during winter, Kennedy caribou were commonly located in an approximately 10-year old, winter-logged clearcut within their winter range.

Discussion

Differences in habitat use (specifically use of different vegetation-cover types) and selection were apparent between ecotypes and among herds of woodland caribou, as well as within herds in different seasons. Concurrent examination of habitat use and selection among herds and ecotypes during this study indicated that differences among ecotypes of woodland caribou were not necessarily inherent in temporal variation among studies examining one herd or ecotype of woodland caribou. As well, differences in use and selection among herds and ecotypes were evident in all seasons, and not isolated only to winter.

Spatial separation and use of vegetation-cover types

Although some spatial overlap occurred among most herds (except in early winter), overlapping areas generally accounted for only a small portion of the seasonal range of each herd. Spatial overlap and separation was, in part, an artifact of the number and distribution of the collared-caribou in this study, our method of assigning individuals to herds, and our method of inferring spatial overlap. For example, spatial separation between the Moberly and Quintette herds may have been a result of the sample size and home ranges of caribou collared in these herds. During caribou captures, however, we did not find caribou in the area between the Moberly and Quintette herds, and other surveys (Seip, 2002) suggest that caribou may be absent from this region. Similarly, other methods of defining seasonal ranges may have yielded different results (Boulanger & White, 1990; Girard *et al.*, 2002) and range overlap may vary depending on herd densities (e.g., spatial overlap may increase at higher densities). Despite limitations in quantifying spatial overlap, our data suggest that spatial overlap or adjacency of herds is not synonymous with ecological overlap. Ecological differences (habitat use and selection) were most evident between herds that spatially overlapped (e.g., Quintette and Parsnip), whereas ecological similarities were most apparent among herds that were spatially separated (Moberly and Quintette).

The VHF locations indicated that patterns in use of vegetation-cover types by herd and season were generally consistent with GPS data. VHF data did differ somewhat from GPS data in use of forested vegetation-cover types for each herd, and VHF data indicated greater use of forested stands by the northern-ecotype herds. The VHF data contained fewer locations on a larger number of individuals over a greater time period. As such, variation in use of vegetation-cover types across multiple years and among individuals in a herd may have been greater than variation in the GPS data. Also, different biases are inherent to different methods of obtaining locations. Locations obtained using aerial telemetry may not be as accurate as GPS locations, and as such, VHF locations are more likely to be assigned to the wrong vegetation-cover type. GPS locations over represent use of open areas by collared animals (Rempel & Rodgers, 1997). Consequently, use of alpine by caribou may have been overestimated and use of forested vegetation-cover types by caribou may have been underestimated using GPS data. Differences in fix rates among GPS collars and collar malfunctions resulted in a different number of locations for some individuals compared to others and GPS-collar data may be biased towards individuals that contributed more locations. Because we built our models using GPS-collar data, and from only a few individuals in each herd ($n \leq 5$), inferences about selection by herds are subject to these same biases. Despite biases and inconsistencies, the GPS data was similar to the VHF data in showing general patterns of use of vegetation-cover types by caribou in each herd, suggesting that GPS-collared caribou were representative of other individuals within their herd.

Seasonal habitat selection

Habitat selection by caribou likely involves a trade-off between forage quality and abundance, and risk of predation (Bergerud *et al.*, 1984; Rettie & Messier, 2000; Barten *et al.*, 2001; Gustine *et al.*, 2006a). The influence of these factors on selection by caribou may vary at different scales. At course scales (e.g., seasonal range), caribou likely select or are able to exist in areas with a low risk of predation and then select for forage at finer scales within those areas (Bergerud *et al.*, 1990; Rettie & Messier, 2000; Gustine *et al.*, 2006a).

Similarly the trade-off between forage and risk of predation by caribou may vary in different seasons. Adults and calves are particularly vulnerable to predation during spring, calving, and summer/fall (Bergerud *et al.*, 1984; Edmonds, 1988; Seip, 1990; Seip, 1992a). Caribou herds for which calving or summer ranges overlap with moose and wolves have higher mortality rates than herds that spatially separate from areas used by wolves and moose (Bergerud & Page, 1987; Seip, 1992a). Females may compromise nutritional gains by using alpine areas where predation risk may be lower (Bergerud *et al.*, 1984; Bergerud & Page, 1987; Bergerud *et al.*, 1990; Gustine *et al.*, 2006a), but survival is higher (Seip & Cichowski, 1996) than in lower-elevation forests. During seasons when nutritional demands for caribou are high (e.g., pregnant or lactating females in spring), caribou may move to areas containing more abundant or high-quality forage and increase risk of predation (Gustine *et al.*, 2006a).

As climate and disturbance regimes differ between the eastern and western side of the Rockies (Meidinger & Pojar, 1991; Delong, 1994), caribou herds in our study may be employing different strategies in response to differences in forage quality, availability or predation risk resulting from different precipitation levels between the eastern and western portions of the study area. During calving and summer/fall, the northern ecotypes on the eastern side of the Rockies selected alpine. Other studies have found that caribou herds residing on the eastern side of the Rockies also select alpine or parkland areas, particularly during calving and summer/fall (Edmonds & Bloomfield, 1984; Culling *et al.*, 2005). In contrast to caribou herds on the eastern side of the Rockies, we found the northern ecotype herd on the western side of the Rockies commonly used and selected lower-elevation forested stands during calving and summer/fall. Ungulate density at low-elevations may be higher in the dry eastern region, and the forb layer in subalpine forests on the western side of the Rockies is more productive and less sparse than on the eastern side (Meidinger & Pojar, 1991). Caribou on the western side of the Rockies may be obtaining a combination of better forage and lower risk of predation, compared to the eastern herds, when using lower-elevation forests.

Selection by northern caribou in winter is similarly influenced by forage abundance, availability and predation risk by wolves (Johnson *et al.*, 2001). In our study, the northern-ecotype herds on the eastern side of the Rockies primarily selected alpine in winter. In contrast, the northern ecotype herd on the western side of the Rockies migrated to a low-elevation pine forest. Other northern ecotype herds on the western side of the Rockies also use low-elevation pine forests in winter (Wood, 1996; Johnson *et al.*, 2002). Other northern ecotype herds on the eastern side of the Rockies were much more variable in use or selection of different vegetation-cover types in winter (Edmonds & Bloomfield, 1984; Culling *et al.*, 2005; Saher, 2005) than eastern herds in this study.

Differences in selection by herds residing on the eastern and western side of the Rockies in our study may have been influenced by differences in snow conditions between the eastern and western regions. Snow depths are notably lower on the eastern as opposed to western side of the Rockies (Jones, unpubl. data). Movement by caribou in the subalpine forest may be more energetically costly for eastern compared to western herds because the snowpack may not harden on the drier eastern side of the Rockies (Culling *et al.*, 2005). Alpine areas in the eastern portion of our study area are typically windswept, often containing more snow-free areas than the western region. The energetic demands for cratering in alpine for caribou on the western side of the Rockies may outweigh the lower risk of predation in this vegetation-cover type (Johnson *et al.*, 2004), whereas caribou on the eastern side of the Rockies can forage in snow-free alpine areas.

Although Kennedy caribou typically have to crater through snow to access lichens in pine stands, ground lichens were more abundant in pine stands compared to alpine areas used by Kennedy caribou (Jones, unpubl. data). Caribou wintering in pine stands also have access to arboreal lichens that are not available in alpine. The energetic benefits of foraging in pine stands over alpine may outweigh the lower predation risk in alpine (Johnson *et al.*, 2004). At our scale of analysis, pine stands were not available to the mountain-ecotype herd on the western side of the Rockies in winter, signifying that availability of vegetation-cover types may also influence differences between ecotypes.

In early winter, mountain caribou in southern British Columbia typically select low-elevation forests (Servheen & Lyon, 1989; Apps *et al.*, 2001), whereas mountain caribou in the more northern regions tend to stay at higher elevations (Seip, 1992a; Terry *et al.*, 1996). Differences among regions may be related to predation risk by wolves (Terry *et al.*, 1996), variation in energetic costs of movement or lichen availability due to snow differences (Apps *et al.*, 2001), or the lack of a major early-winter food, falsebox (*Pachistima myrsinites*), in low-elevation forests in northern compared to southern areas (Terry *et al.*, 1996). In late winter, mountain caribou move to higher elevations than early winter using subalpine forest and parkland areas (Servheen & Lyon, 1989; Seip, 1990; Seip, 1992a; Apps *et al.*, 2001).

Consistent with seasonal habitat selection of mountain caribou in the more northern regions of their distribution, we found that Parsnip caribou typically selected fir and fir-leading stands between approximately 1200 to 1600 m with no evidence of selection for lower elevations in spring or early winter. These results support theories that selection by mountain caribou may be related to differences in forage or risk of predation between northern and southern regions (Terry *et al.*, 1996; Apps *et al.*, 2001).

The general pattern for both northern and mountain ecotypes appears to be use of productive forests at low-elevations in spring (Servheen & Lyon, 1989;

Cichowski, 1993; Apps *et al.*, 2001; Culling *et al.*, 2005, Saher, 2005). Caribou using low-elevation areas are likely obtaining more green forage than those occupying other areas (Servheen & Lyon, 1989; Seip, 1990; Seip, 1992b; Apps *et al.*, 2001). Our models indicated that none of the herds in this study use low-elevation forests in spring. Risk to caribou from predation by wolves may be higher in lower-elevation forested areas compared to alpine (Johnson *et al.*, 2004), and caribou may be trading off nutritional gain obtained from green forage against predation risk (Bergerud *et al.*, 1984; Bergerud & Page, 1987; Gustine *et al.*, 2006a). Conversely, we did observe variation among Parsnip caribou individuals in model predictions of selection. For example, we occasionally located two of the 10 collared mountain caribou in snow-free areas at low elevations in spring. During telemetry flights we noted that more southern areas in the Parsnip range became snow-free earlier in spring compared to northern areas and thus snow-free areas may not be available to all Parsnip caribou in spring and similarly to individuals in other herds.

Despite differences in selection and use among herds and ecotypes, our results suggest that some commonalities were apparent among herds and in each season. With the exception of the Kennedy herd in summer/fall, early and late winter, caribou selected elevations >1300 m and avoided or did not use pine-leading, spruce-leading, deciduous/shrub and young-coniferous stands. Studies conducted in other areas suggest that moose and subsequently wolf density may be higher in early-seral forests (Schwartz & Franzmann, 1989), and predation risk for caribou from wolves may be higher in pine-leading and spruce-leading stands (Johnson *et al.*, 2002). Caribou may be avoiding these vegetation-cover types across their range in order to increase spatial separation from wolves (Seip, 1992a). All herds avoided steeper slopes, and selection for western and southern aspects were common, whereas eastern and northern aspects were typically avoided. Western and southern aspects may contain more abundant vegetation in spring, calving and summer/fall, and wind patterns may result in lower snow depths on western compared to eastern aspects in early and late winter.

Scale and model limitations

Selection by woodland caribou may differ at different scales of analysis (Rettie & Messier, 2000; Apps *et al.*, 2001; Johnson *et al.*, 2001) and quantifying scale-dependent differences in selection may provide further insight into determining appropriate management strategies for woodland caribou (Johnson *et al.*, 2001). Although we recognize that examining selection at different scales may have resulted in broader conclusions, our analyses of smaller-scale levels of selection were constrained by 20-h fix intervals, vegetation-cover resolution and sample size. Using 20-h fix intervals precluded using movement rates (Johnson *et al.*, 2001) to identify scales of selection related to small-scale behavioral decisions (e.g., selection of feeding sites), and variables related to selection at these scales typically must be collected on the ground. The VRI data did not contain vegetation-cover classifications relative to a smaller scale of selection (e.g., alpine-lichen, alpine-barren) and had this data been available, our analytical tests would have likely been constrained by rare or zero cell counts in these categories as a result of small sample sizes.

Using a larger-scale definition of availability (e.g., annual home range, study area), in addition to examining availability at the scale of daily movement capability, may have further contributed to understanding selection by woodland caribou in our study area. For example, in early winter, Kennedy caribou migrate from mountainous terrain to an expansive low-elevation pine forest. At our scale of analysis, selection for pine was not significant, although 75% of locations occurred in pine-leading stands within this range. The 95th percentile movement distance for Kennedy caribou in early winter was 4960 m, and as such, the majority of available locations also occurred within this extensive pine range. Examining selection at the scale of annual home range would likely have resulted in a high availability of sites in the adjacent mountains, and selection for pine may have become apparent at this scale. Quantifying selection at larger scales, however, would have involved defining areas as available that may not have been available to caribou.

We recognize that our definition of availability was still somewhat arbitrary (e.g., we chose the 95th percentile movement distance), but available locations were constrained within biologically defined areas that caribou could almost certainly use. Our scale of analysis was analogous to a large scale definition of availability for caribou occupying mountainous terrain (because valley bottom to alpine was often available). For caribou occupying an expansive and homogenous area (e.g., low-elevation pine), however, a larger scale of analysis or classifying vegetation-cover types at a finer scale may have yielded different results. In the future, a larger scale of analysis, using a larger sample of collared caribou, would be valuable to obtain a broader understanding of the seasonal ecology of these or other caribou herds.

We may have made different inferences about selection of these herds had we modeled selection of individual caribou or selection in each year. Similarly, our classification of individuals into herds and seasonal definitions may have influenced our results. These types of analyses were constrained by having a limited number of locations (particularly in shorter seasons) for only a few individuals in each herd. For example, examination of locations for individual caribou during calving, regardless of herd or ecotype, indicated that parturition commonly occurred in the subalpine forest and caribou moved to higher elevations after their calf was born. Selection models, however, indicated that northern ecotype herds selected alpine during calving. Differences in selection during parturition and post-calving may have been apparent had these periods been modeled separately.

Topographic variables and the topographic model were useful for predicting caribou locations at the scale of analysis of this study, but likely do not encompass all variables influencing selection of habitat by woodland caribou. A different scale or type of analysis may have emphasized the importance of other variables. Location data (both GPS and VHF) clearly indicated that caribou disproportionately used specific vegetation-cover types, but vegetation-cover type performed poorly in the selection models. Topographic variables (particularly elevation) may be more related to variables that influence selection by caribou (e.g., forage quality, snow characteristics and risk of predation) than vegetation-cover type. This may be a result of inaccuracies associated with the mapping of vegetation-cover types or by defining vegetation-cover classes that are not related to factors influencing selection by caribou.

We found that selection of vegetation-cover types at our scale of analysis was not always consistent with use of vegetation-cover types by caribou. Because our method of analysis required the removal of vegetation-cover types that were rarely or never used by caribou, selection for vegetation-cover types that were occasionally used (e.g., forested calving sites) or used in similar proportion to availability (e.g., use of pine by Kennedy caribou) may have been underestimated (as available locations in unused vegetation-cover types were also excluded from the models). Similarly, vegetation-cover types that were removed from our models may have been slightly correlated with topographical (e.g., elevation) or distance to nearest road variables, resulting in a biased estimate of availability for these variables. An examination of the relationship between elevation and vegetation-cover type, however, showed considerable overlap in ranges of elevation and non-significant differences among the majority of vegetation-cover classes.

Because selection models were constrained by our scale of analysis, small samples of individual caribou, and seasonal delineation, we recommend that use and selection of vegetation-cover types by caribou be considered when identifying critical habitat for caribou herds in this study. Conversely, planning strategies that focus solely on vegetation cover (in the absence of topographic variables) may not identify suitable habitat for caribou.

This research demonstrates that seasonal use and selection by herds and ecotypes is much more variable then general ecotype descriptions suggest. Discrepancies between ecotype classifications and habitat use and selection by caribou herds in this study illustrate the importance of determining seasonal use and selection for woodland caribou herds across their range. Consequently, we recommend that recovery planning and mapping of critical habitat for woodland caribou be undertaken on a seasonal and herd-specific basis.

Although we found evidence of spatial overlap among previously identified herds, our results suggest that these herds may be ecologically different (e.g., seasonal use and selection). Despite ecological differences among herds, we do not know if herds can be considered distinct populations (in which no genetic exchange occurs). Caribou in this study may belong to one population, but respond to climatic and terrain variability at a more regional scale. Maintaining habitat predominantly used and selected by caribou, combined with reducing habitat avoided by caribou across their range, may ensure population stability by preserving or initiating genetic flow among herds of caribou.

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Managing fire for woodland caribou in Jasper and Banff National Parks

Landon Shepherd[1], **Fiona Schmiegelow**[2], **& Ellen Macdonald**[2]

[1]Parks Canada, Jasper National Park, Box 10, Jasper AB, T0E 1E0, Canada (Landon.Shepherd@pc.gc.ca).
[2]Dept. of Renewable Resources, University of Alberta, Edmonton, AB T6G 2H1, Canada.

Abstract: Woodland caribou (*Rangifer tarandus caribou*) populations in Jasper (JNP) and Banff National Parks (BNP) have declined since the 1970s, coincident with reduced fire activity in both parks, relative to historic levels. Some researchers have suggested that long periods without fire may cause habitat deterioration for woodland caribou, primarily by reducing available lichen forage. We examined winter habitat selection by woodland caribou at coarse and fine scales based on GPS-derived telemetry data and used models that included stand origin (decade), topography, and several stand structure variables that are related to time since fire, to explore relationships among caribou, lichen, and fire history. Based on the relationships illustrated by the models, we assessed how fire management could be applied to caribou conservation in JNP and BNP. At a coarse scale, caribou selected old forest (> 75 years) in landscapes that have likely experienced less frequent wildfire. While the abundance of *Cladonia* spp. influenced caribou use at fine scales, a preference for areas with older trees within stands was also significant. We conclude that short-term habitat protection for woodland caribou in JNP and BNP likely requires fire exclusion from caribou range.

Key words: *Cladonia*, fire management, forage, generalized linear models, habitat, lichen, multi-scale models, *Rangifer tarandus caribou*, resource selection functions.

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Introduction

Woodland caribou (*Rangifer tarandus caribou;* hereafter caribou) in Alberta, Canada are listed federally and provincially as a threatened species (Alberta Wildlife Act, 2002; COSEWIC, 2003). Several factors have been implicated in recent population declines: (1) direct disturbance from human activities, (2) increased predation due to increased predator access along anthropogenic linear features and increased predator abundance due to alternate prey population increases, and (3) habitat loss, primarily as a result of industrial activity (Edmonds, 1988; Seip, 1992; James & Stuart-Smith, 2000; McLoughlin *et al.*, 2003; Wittmer *et al.*, 2005).

Jasper and Banff National Parks (JNP and BNP) contain the most southerly distribution of woodland caribou in Alberta. Despite protection from industrial development, the south JNP population is in serious decline, while the northern BNP population may consist of less than 6 animals (Flanagan & Rasheed, 2002; Mercer, 2002). In the national parks, caribou population declines could be caused by habitat deterioration due to human infrastructure (Parks Canada, 2000), displacement due to human use (Whittington & Mercer, 2004), increased predator pressure due to human activities (Mercer 2002) or recently reduced frequency in fire disturbance (Tande, 1979; Rhemtulla *et al.*, 2002; Van Wagner *et al.*, 2006), which has been hypothesized to result in a reduction of lichen forage (Schaefer & Pruitt, 1991; Thomas & Armbruster, 1996). Our research examines the latter possibility.

A low frequency of fire in the Rocky Mountain National Parks in the past century has been accompanied by a change from a relatively heterogeneous landscape, including a range of forest ages and composition along with non-forested areas, to a relatively even-aged and uniform, forest structure and composition (Tande, 1979; Rhemtulla *et al.*, 2002). This shift in forest age and structure, which could be attributed to fire supression activities, should have benefited caribou, given that they have generally been found to prefer older forests (Apps *et al*., 2001; Szkorupa, 2002; Joly *et al*., 2003; Saher, 2005). However, populations have declined in recent decades (Mercer *et al*., 2004).

An assessment of fire effects on caribou requires consideration of temporal effects on habitat. Fires can make forests unsuitable for caribou for at least several decades (Thomas *et al*., 1996a; Joly *et al*., 2003), but some researchers have suggested that a lack of fire eventually leads to degradation of caribou habitat as terrestrial lichen cover declines (Schaefer & Pruitt, 1991; Coxson & Marsh, 2001). The immediate effect of fire on lichens is destruction through combustion (Johnson, 1981; Schaefer & Pruitt, 1991; Joly *et al*., 2003). Over time, following fire, lichen genera re-establish in a sequential pattern; usually *Cladonia spp*., followed by genera more commonly preferred by caribou (e.g., *Cladina* spp., *Cetraria* spp.*;* Johnson, 1981; Klein, 1982; Snyder & Woodard, 1992; Thomas & Hervieux, 1994; Thomas *et al*., 1996a). In the longer term, terrestrial lichens may decline as litter accumulates and forest floor bryophyte cover develops (Klein, 1982; Payette *et al*., 2000; Coxson & Marsh, 2001). Arboreal lichen is usually only found in abundance in older, presumably long-unburned stands (Edwards *et al*., 1960; Schaefer & Pruitt, 1991; Apps *et al*., 2001). Structural changes accompanying forest development post-fire, such as declining stand density (Arseneault, 2001; Schoennagel *et al*., 2003) and development of continuous forest canopy (Bessie & Johnson, 1995) may create stand structures preferred by caribou.

Terrain affects stand structure and fire behavior (Hirsch, 1996; Gray *et al*., 2002), and has been shown to influence caribou habitat selection (Johnson *et al*., 2004; Saher & Schmiegelow, 2005). Elevation can influence fire return intervals, with older stands tending to occur at higher elevations (Tande, 1979; Rogeau, 1996; Schoennagel *et al*., 2003) while aspect affects both fire frequency and intensity, with south and southwest aspects having more frequent and more intense fire events (Tande, 1979; Gray *et al*., 2002).

Over the last decade, Parks Canada has adopted a policy of trying to achieve annual burning of an area that would eventually emulate 50% of each Park's average long-term fire cycle (Parks Canada, 2000; 2001; 2005). Per hectare average burn rates are calculated across the extent of a park, ignoring topographic variation in the fire cycle (Parks Canada 2005). Prescribed burning is employed to meet multiple management objectives in parks and elsewhere (Van Wagner & Methven, 1980; Achuff *et al*., 1996), with effects on caribou largely unknown. Our objective was to develop and evaluate emprical models to determine whether stand age affects caribou habitat selection. We were specifically interested in whether caribou use forests younger than 75 years during winter, as this cohort is underepresented in our study region, relative to natural, historic levels; thus, restoration of this age class has become an objective of fire management efforts in the parks. Following on recent studies that have highlighted the importance of examining caribou habitat selection at different spatial scales (Rettie & Messier, 2000; Apps *et al*., 2001; Johnson *et al*., 2001; Szkorupa, 2002; Saher, 2005), we wanted to develop both fine- and coarse-scale models. At a coarse scale, we evaluated habitat selection models using variables related to time since fire along with those that may influence fire regime. Our fine scale modeling efforts focused on caribou selection related to lichen abundance, given the importance of forage availability to caribou (Rettie & Messier, 2000; Saher, 2005), but also included topography, stand age, and forest composition and structure.

Material and methods

Study area

We conducted our study in the southern half of JNP (52.5°N, 118.08°W) and the northern portion of BNP (51.3°N, 116.15°W; Fig. 1), in the Rocky Mountains of Alberta, Canada. Both areas are immediately east of the continental divide and include wide, glacier-carved valley systems. In JNP, a significant proportion of the park area consists of rock and glacial ice (19%; Holland & Coen, 1983). Forested areas include the montane (7%), lower subalpine (30%), and upper subalpine (37 %) ecological regions (Holland & Coen, 1983). The BNP valley systems for this study were all higher elevation valleys and did not include any montane zones. In the vegetated portion of the BNP study area, 44% was alpine, 30% was upper subalpine, and 25% was lower subalpine (Holland & Coen, 1983). Montane forest was primarily composed of dominant and mixed stands of lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), Douglas-fir (*Pseudotsuga menziesii*), and trembling aspen (*Populus tremuloides*). Subalpine forests included lodgepole pine, subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), black spruce, whitebark pine (*Pinus albicaulus*), and subalpine larch (*Larix lyallii* - BNP only). Stand boundaries in both study areas were determined primarily by stand initiating fire events (Tande, 1979; Achuff *et al*., 1996). Stands were up to 400 years old in the study area in JNP, (Tande, 1979; Parks Canada, unpublished data), and generally older in the BNP study area, some as old as 600 years (Rogeau, 1996; Parks Canada, unpublished data). Elevations of sample locations ranged from 1019 m to 2393 m above sea level (ASL) in JNP and 1494 m to 2589 m ASL in BNP. While not the emphasis of this study, we note that both parks support diverse predator populations, including wolf (*Canis lupus*), grizzly bear (*Ursus arctos horribilis*), black bear (*Ursus americanus*), wolverine (*Gulo gulo*), and cougar (*Felis concolor*) (Holland & Coen, 1983). For wolves, the primary ungulate prey species in both JNP or BNP is elk (*Cervus elaphus*) (White *et al.,* 2003); in contrast to other forested systems where moose (*Alces alces*) represent the primary prey (Lessard *et al.*, 2005; Wittmer *et al.*, 2005).

Study design

We used a mixed modeling approach to create a candidate set of Resource Selection Function (RSF) models at coarse and fine scales, using telemetry based animal location data. RSF models quantify habitat selection patterns based on the use of potential habitat attributes (independent variables) relative to their availability. We treated individual animals as a random effect in our models to address issues of pooling location data from multiple animals (Otis & White, 1999), and elimated correlated independent variables (r>0.50) using univariate regression to identify the variables with greatest potential explanatory power among correlated pairs. S-PLUS v.6.2 was used for all analyses (Venables & Ripley, 1999).

Animal location data

We used Global Positioning System (GPS) telemetry collar data (GPS 2200 and GPS 3300 Lotek, Inc.) from 2001-2004, collected between October 15 and April 15 of each year. From late April-October, caribou remained primarily in alpine areas in JNP and BNP, for which there is no measured fire cycle (Tande, 1979; Rogeau, 1996). We thus restricted our analyses to the period where caribou occurred primarily below treeline, yielding a total of 8124 caribou locations, collected over 3 years. Data were supplied by Parks Canada, from the first 3 years of a 5-year caribou study in JNP (Mercer *et al.*, 2004) and from the first year of BNP's caribou telemetry monitoring (Dibb, 2004). Caribou were captured in late fall each year, with 11 animals collared from 2001-03, and 8 in the winter of 2003-04. Locations were collected every 6 hours, with an average successful fix rate of 81.8%. Habitat-induced bias has been cited as a confounding factor in selection studies using GPS telemetry data (D'Eon *et al.*, 2002; Frair *et al.* 2004). Frair *et al.* (2004) found that closed conifer forest cover resulted in a GPS habitat-induced data loss that biased coefficients if data loss was ≥ 30%. Our overall GPS data loss was less than 20%, thus we did not feel it necessary to account for bias in parameter estimation. Furthermore, Hebblewhite *et al.* (in press) report that Lotek 12 channel GPS collars, as used in this study, do not have significant habitat-induced data loss, and do not require correction when used in the Central Canadian Rockies.

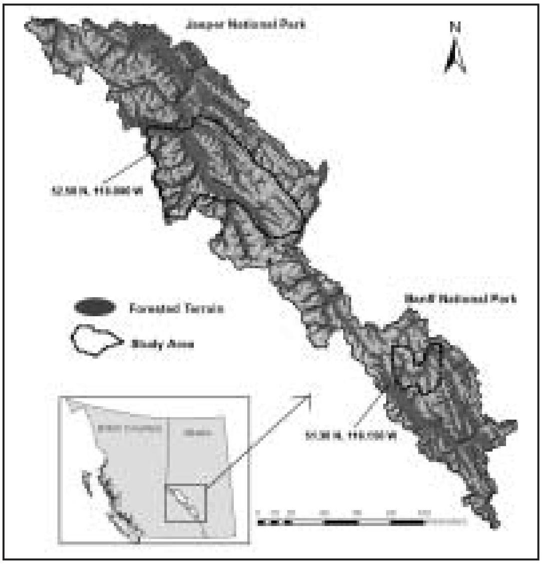

Fig. 2. Early winter locations of caribou (2002 to 2006), by herd, showing lack of spatial overlap during this season for woodland caribou in central British Columbia.

Spatial scales

Our coarse scale corresponded to stand level selection, and was chosen to reflect the scale at which fires tend to occur on the JNP and BNP landscape (Tande, 1979; Rogeau, 1996). Fine scale corresponded to foraging level selection, consistent with other studies (Johnson *et al.*, 2001; Szkorupa, 2002; Saher, 2005). At the coarse scale, available habitat was delimited by height of land and main valley-bottom rivers beyond the furthest caribou observations from 2001-2004 GPS collar data, earlier radio-telemetry locations from the area (Brown *et al.*, 1994; Thomas & Armbruster, 1996), and recorded historical caribou observations dating back to 1978 (Parks Canada, unpublished data; see Fig. 1). At the fine scale, we defined available habitat as treed areas within valleys containing GPS telemetry caribou use locations from 2001-2003. Valleys were delimited by surrounding mountain ranges and defined as the continuous forest cover on either side of a single main valley-bottom river or stream. Topography is a physically-limiting factor for caribou travel in this mountainous terrain, and thus arguably more biologically relevant than average daily distance traveled (e.g., Joly *et al.*, 2003; Johnson *et al.*, 2004). Fine scale sampling was further limited to include only those locations south of a major highway transecting JNP (Highway 16); north of which we had no caribou location data.

Coarse-scale resource selection

We used a Generalized Linear Modeling approach (GLM), applying logistic regression to compare used (caribou "use" location) and available (random) sites for a set of candidate models derived from a suite of land cover and topographic data, and conducted model training and validation using partitioned data to evaluate model performance. Locations from 2 caribou collared in 2001/2002, and 9 caribou collared in 2002/2003 were used for model training (a total of 4288 "use"; 9798 "available" locations), and validation was undertaken using two independent data sets: JNP's 2003/2004 telemetry data (8 caribou - 3048 "use"; 11 292 "available" locations) and BNP's 2003/2004 data (1 caribou - 783 "use" locations; 783 "available"). Available locations were randomly generated separately for each of the training and validation sets, from coordinates constrained to the park boundary for JNP (sample of 15 000), and subsequently restricted to the study region (i.e. the treed portion of the park), and constrained from the outset to create a number of available locations for the treed portion of BNP equal to the total number of "use" locations we had for BNP. This procedure resulted in some variation in the ratio of "use" to "available" locations in the different data sets, but we do not feel it unduly influenced our results.

Digital ecological land classification maps for JNP and BNP (Holland & Coen, 1983) identify the following vegetation types: lodgepole pine, Douglas-fir, white spruce, poplar, aspen, closed Engelmann spruce/subalpine fir, Engelmann spruce/subalpine fir/whitebark pine, shrub, meadows, or alpine. From these, we assigned each use or available location to either open forest (meadow, alpine, poplar, or aspen [which was leafless during the winter sampling period]), or closed conifer (all other categories). We used 75-year stand origin categories ("Fire.cat"), based on related research reporting development of preferred lichen forage at 70-80 years post-fire (Thomas & Armbruster, 1996; Thomas *et al.*, 1996a; Szkorupa, 2002), and created a binary variable, "fire.old", to compare old stands (>150 years) to younger stands (<150 years). Aspect categories correspond to the eight cardinal and semi-cardinal compass directions. All elevation, stand origin date, slope, and aspect data were obtained from the parks digital elevation models (20m resolution) and stand origin maps (Tande, 1979; Rogeau, 1996; Parks Canada, unpublished data). Table 1 summarizes all variables evaluated in the coarse scale models.

Candidate coarse scale models contained combinations of stand origin, structure, and topographic variables (Table 2). We included linear and non-linear forms of stand origin variables as well as stand origin interactions with topography to determine whether these influenced caribou selection (beta coefficients significant at $\alpha < 0.05$). We compared our suite of candidate models using the Akaike Information Criterion (AIC; Burnham & Anderson, 1998), including only significant predictor variables (beta coefficients with $\alpha < 0.05$), as AIC calculations for large sample sizes tend to favor over-parameterization of models (Link & Barker, 2006). To determine the relative significances of "levels" within categorical variables, we used the Sidak post-hoc multiple comparison test (Venables & Ripley, 1999) to rank levels based on beta coefficients. Ranking of selection preference is recommended by Keating & Cherry (2004) for use/availability RSF studies. We summed the number of times each level was selected over another (given a 95% confidence interval) to determine an overall category ranking. Those with highest ranks were considered preferred by caribou.

Model performance was evaluated using Spearman rank correlation to compare relative probability values from the validation data sets, which were divided into 9 bins of 0.0-0.10, 0.11-.20, 0.21-0.30, 0.31-0.40, 0.41-0.50, 0.51-0.60, 0.61-0.70, 0.71-0.80, and 0.81-1.00, with interpolated values from the training model (see Boyce *et al.*, 2002). The 10th bin (0.91-1.00) was grouped with the 9th because only 3 predicted probabilities were greater than 0.90.

Fine-scale resource selection

Our fine scale selection analysis included a large number of biologically plausible variables related to stand age, forest structure and topography, and it was necessary to reduce this set to generate candidate RSF models for analysis. We first used univariate logistic regression to identify variables that accounted for deviance of at least one. We further reduced this list of potential predictors using a stepwise approach to create three groups of candidate models: 1) lichen based, 2) forest age and structure based, and 3) lichen and forest age and structure combined. The use of frequentist techniques can bias parameter estimation and model selection when mixed with an information-theoretic approach (Burnham & Anderson, 1998; Whittingham *et al.* 2006). We have employed it recognizing these limitations, and acknowledge the exploratory nature of our analyses.

In order to populate fine scale models, we sampled 38 field plots in 2003 ("use" locations), and 154 field plots in 2004 (90 "use"; 64 "available"). The 2003 use sites were selected from a random draw of filtered locations from the two caribou collared in 2001/02 (see Animal Location Data and Spatial Scales), whereas in 2004, we randomly selected 10 use sites from each of 9 animals. Year was evaluated as a variable within our set of candidate models, to assess the potential influence of differences in sample design. We sampled 64 randomly located sites (available sites) within valleys containing caribou use locations, while excluding areas within 300 m of a use location; 300m is one order of magnitude larger than the reported error for a study on uncorrected GPS collar accuracy in mountainous terrain (D'Eon *et al*., 2002). Since GPS caribou location data from BNP were not available during the 2004 sampling season, fine scale selection analysis used JNP sample data only.

At each sample location, we used 2 diagonally-adjacent 10m by 10m quadrats laid out on a north-south by east-west grid to delineate the plot area, and recorded local slope and aspect in degrees. For each tree (≥ 5 cm diameter at 130 cm above ground (DBH)), we recorded species, DBH, and arboreal lichen abundance by categories (<0.1g: *class 0*, 0.1-5 g: *class 1*, 5.1-50 g: *class 2*, 50.1-250 g: *class 3* as per Stevenson *et al*., 1998). To quantify arboreal lichen abundance, we used counts of numbers of trees per plot in each of the different lichen abundance classes (Stevenson *et al*., 1998) and also evaluated a binary variable that coded plots as having at least one Class 3 tree (estimated > 50 grams of lichen) or not. To quantify terrestrial lichens we estimated percent

Table 1. Definitions of independent variables used in the coarse scale selection models. The description of the "Fire Category" (stand age categories) variable also includes percent of study area for each category.

Variable	Data type	Description
fire	continuous	stand origin date based on park stand origin map
fire.cat	categorical	six stand origin categories of 75-year intervals; <75 yrs old (9% of study area), 75-150 yrs (43%), 151-225 yrs (16%), 226-300 yrs (20%), 301-375 yrs (7%), >375 yrs (4%)*
fire.old	binary	stand origin date of either <150 yrs ago or >150 yrs ago
elev	continuous	elevation in meters above sea level from a digital elevation model (DEM)
slope	continuous	slope in degrees from the park DEM
aspect.cat	categorical	eight aspect categories of 45 degree intervals: north*, northeast, east, southeast, south, southwest, west, and northwest
aspect.cat1	binary	south and southwest aspect (157.6-247.5 degrees azimuth) versus any other aspect
closure	binary	closed forest versus open based on Holland & Coen (1983); open stands include meadow, shrub, alpine and deciduous coded sites

*reference categories for each categorical variable.

Table 2. Definitions of independent variables that were included in the top 10 fine scale selection models.

Variable	Data type	Description
cladonia.cov	continuous	average percent *Cladonia* cover (from 5 quadrats per sample location)
#saplings	count	number of saplings (in one 2m x 2m plot)
all.lichen.cov	continuous	average percent cover of lichens (from 5 quadrats per sample location)
#logs	count	number of logs from line intersect count
%notPl.Se.Fa	continuous	percent of trees in plot that are not pine, spruce or fir
max.core	continuous	highest tree age (ring count from increment core) in plot
litter&moss	continuous	average depth in cm of litter and moss (5 measures per sample location)
#class1trees	count	number of arboreal lichen class 1 trees in a plot
basal.area	continuous	basal area of all trees in a plot calculated from dbh measurements from each tree
SorSW.aspect	binomial	south and southwest aspect (157.6-247.5 degrees azimuth) versus any other aspect
%fir	continuous	percent of trees in plot that were subalpine fir

cover (to genus) to the nearest 1% in five, 240 cm^2 subplots in fixed corner locations of the plot. We also estimated cover of feathermoss (*Pleurozium* spp. or *Ptilium* spp.) and other moss genera (all other moss genera). In each subplot we also recorded moss and litter depth and depth from litter or moss surface to mineral soil. For the cover and depth estimates, we averaged the five subplot values to provide overall estimates for each sampling location. From the dominant canopy layer we selected three trees and took cores (at DBH) for aging. We used the highest ring count, as determined from these cores, as a conservative measure of minimum number of years since stand replacing fire at each site. We used the 20 m east-west line delineating the sides of the two quadrats as for line intercept sampling of the number of pieces of downed logs and had a 2 m by 2 m plot off the intersect point of the two quadrats in which we recorded the number and species of saplings (<5 cm diameter at 130 m height above ground). These variables and the model abbreviations are listed in Table 2.

We reduced the initial set of 49 habitat variables to 25 using univariate regression. Twenty candidate models derived from these 25 variables were constructed using data from all 192 field plots. We used AIC corrected for small sample sizes (AICc; Burnham & Anderson, 1998) to identify the most parsimonious model, and evaluated the top performing model using the Spearman rank, K-fold cross validation technique (Boyce *et al.*, 2002). We used a series of 10 random draws of 80% (154 plots) of our data for model training and the remaining 20% (38 plots) for validation. To ensure sufficient use locations per bin, with only 38 plots in our testing set, we used only 6 probability bins for the Spearman rank correlation test, and scaled the bins to correspond roughly with occurrence frequency (Boyce *et al.*, 2002), resulting in the following ranges: 0.00-0.25, 0.26-0.50, 0.51-0.70, 0.71-0.85, 0.85-0.95, and 0.96-1.00.

Results

Coarse-scale resource selection

The best coarse-scale model, in which all variables were significant, was the one incorporating all variables (Table 3). This model included: the linear form of slope in degrees (negative coefficient), elevation in meters (positive coefficient), the six (75-year) stand origin categories, the eight cardinal and semi-cardinal aspect categories, and a positive association for stands categorized as "closed conifer". Among predictor variables, elevation was most influential, explaining 74% of the variation, and forest closure the least (2%; Table 3). The model performed quite well, with significant and high Spearman Rank correlations (JNP: 0.950, BNP: 0.983; two tailed probability < 0.001).

At a landscape scale during winter, within the forested portion of BNP and JNP, caribou preferred higher elevations, less steep slopes, and closed conifer forest (*vs.* deciduous or open forest) (Table 3). Apparent preference for closed conifer forests supports our earlier assertion that accounting for habitat-induced bias was not necessary. Based on multiple comparison analysis of the six different fire categories, caribou preferred relatively older forest, showing the greatest preference for stands that were 226-300 years old and 75-150 years old. Caribou were least likely to select the youngest stands (<75 years old), but also avoided some older stands (151-225 years old and 301-375 years old) (Table 3). Multiple comparison analysis of aspect categories revealed that south and southwest aspects were avoided. "Fire" (stand origin date) was not a significant predictor for the training data set, while "fire.old" was not a consistent predictor variable between the training and testing data sets. "aspect.cat" with eight categories explained significantly more variation than "aspect.cat1" (south & southwest *vs.* all other aspects).

Fine-scale resource selection

At a fine scale, the best performing model included variables related to lichen abundance, along with several stand-structure variables. The model indicated a preference for locations with high terrestrial lichen cover (especially *Cladonia* spp.), that had older trees and more saplings (of which 75% were subalpine fir), with avoidance of areas with deeper litter and moss, more downed logs, more trees with low arboreal lichen abundance, and sites with Douglas-fir or deciduous trees as part of the canopy (see Table 4).

Validation runs of this model yielded average Spearman's rho values of 0.921 ($0.02<P<0.05$). Two of the 10 runs were not significant at $\alpha = 0.05$ (both were $0.10<P<0.20$); this is likely due to the relatively small sample size ($n=192$) that was partitioned for testing. There was only a slight decrease in AICc with the addition of either the binary aspect category (negative association with south or southwest aspects), or basal area (negative). All coefficients in our top model were significant (at $\alpha = 0.05$).

Discussion

Coarse-scale resource selection

At a coarse scale, caribou in BNP and JNP avoid areas with younger forest, preferring forest that was at least 75 years old. Research in Alaska (Joly *et al.*, 2003), the Northwest Territories (Thomas *et al.*, 1998) and west-central Alberta (Szkorupa, 2002;

Saher, 2005) has similarly shown that caribou avoid younger forest. Preference for older forest is most likely related to lichen forage availability (Rominger & Oldemeyer, 1989; Thomas *et al.*, 1996a). Shepherd (2006) found that *Cladonia* spp. cover in forest younger than 75 years was insufficient to attract caribou; other researchers report similar thresholds (Thomas & Armbruster, 1996; Thomas *et al.*, 1996a; Szkorupa, 2002). Caribou avoidance of 151-225 year old forest, while strongly selecting for 226-300 year old forest, was unexpected. The avoidance could be attributed to a decline in terrestrial lichen cover as forest floor mosses increase, which has been observed in forests older than 150 years (Coxson & Marsh

Table 3. Coefficients and 95% confidence intervals for variables included in the coarse scale model '*full1*'. The reference category for "firecat" (stand origin categories) was 1300 -1625 and the reference category for "aspectcat" (Aspect categories) was North (337.6°-22.5° azimuth). Beta coefficients and 95% confidence intervals are from a combined data set of all 3 years of caribou data (2001-2004). The percent of variation explained by each parameter is included.

Variable	β	CI upper	CI lower	*t* value	% of model variation explained
elev	0.007	0.0072	0.0068	55.49	74%
slope	-0.054	-0.049	-0.0590	-21.82	11%
closure	0.375	0.4690	0.2810	7.99	2%
fire.cat2 301-375yrs	-0.195	-0.0888	-0.3012	-4.72	
fire.cat3 226-300yrs	0.148	0.1922	0.1038	8.65	
fire.cat4 151-225yrs	-0.052	0.0030	-0.1070	-2.58	
fire.cat5 75-150yrs	0.052	0.0788	0.0252	5.57	
fire.cat6 < 75 yrs	-0.071	-0.0044	-0.1376	-2.49	Total= 4%
aspect.catNE	0.009	0.0786	-0.0606	0.24	
aspect.catE	0.001	0.0402	-0.0382	0.07	
aspect.catSE	-0.086	-0.0534	-0.1186	-5.28	
aspect.catS	-0.235	-0.2002	-0.2698	-13.5	
aspect.catSW	-0.067	-0.0484	-0.0856	-7.27	
aspect.catW	0.055	0.0706	0.0394	7.09	Total= 8%
aspect.catNW	0.029	0.0436	0.0144	4.00	

Table 4. Coefficients and 95% confidence intervals of variables included in the best fine scale model (*comb6*). Data were from all 192 plots sampled.

Variable	β	CI upper	CI lower	*t* value	% of model variation explained
all.lichen.cov	0.054	0.103	0.005	2.22	29%
cladonia.cov	0.129	0.226	0.032	2.65	14%
litter&moss	-0.226	-0.034	-0.418	-2.36	9%
#saplings	0.118	0.227	0.009	2.18	19%
#class1trees	-0.037	-0.010	-0.064	-2.72	9%
#logs	-0.147	-0.028	-0.266	-2.46	7%
max.core	0.008	0.014	0.002	2.42	6%
%not.Pl.Se.Fa	-4.392	-0.321	-8.463	-2.16	8%

2001). The selection for stands older than 225 years may reflect stand transition from lodgepole pine to Engelmann spruce and Subalpine fir, which begins to occur 150 years post-fire in JNP and BNP (La Roi & Hnatiuk, 1980). Caribou may be avoiding less mature, mixed Engelmann spruce/Subalpine fir/lodgepole pine stands (151-225 years) but selecting for the more mature spruce/fir stands (226-300 years) which tend to have greater amounts of arboreal lichen (Edwards *et al.*, 1960; Stevenson & Enns, 1992; Terry *et al.*, 2000). This corresponds to the observed selection for closed-conifer stands. The selection for higher elevation and avoidance of south and south-west aspects could also reflect effects of time-since-fire. High elevations tend to have older forest, while south-west aspects tend to have more frequent fire occurrence (Tande, 1979; Rogeau, 1996).

There are alternative explanations for the observed caribou habitat selection preferences. Preference for higher elevations and avoidance of southwest aspects would be likely to promote separation from predators, as research in JNP found wolves generally preferred low elevation and southwest aspects (Whittington *et al.*, 2005). Predator avoidance may also explain the preference for less steep slopes and for closed canopied forest over open areas. Flatter slopes may provide easier escape, while closed conifer forests likely offer greater hiding cover and at the same time confer a foraging benefit since snow interception by the canopy would reduce the cratering depth necessary to access terrestrial lichens (Terry *et al.*, 2000). Predator avoidance can deter selection of preferred forage (Bergerud & Luttich, 2003). The combined influence of predators, other prey, and fire on caribou habitat selection requires further investigation.

Fine-scale resource selection

Our fine scale model agrees with other fine-scale caribou selection research in suggesting preference for sites with greater lichen cover and older-forest characteristics (Johnson *et al.*, 2000; Szkorupa, 2002; Saher, 2005; Saher & Schmiegelow, 2005). Due to our initial frequentist approach, however, the fine scale model results should be viewed as suggestive rather than statistically definitive (Burnham & Anderson, 1998; Whittingham *et al.* 2006). At a fine scale, caribou preferred sites with high terrestrial lichen cover. Of the individual lichen genera examined, cover of *Cladonia* spp. was the strongest predictor of caribou use, and indeed was the strongest single predictor in univariate analyses. Interestingly, *Cladonia* spp. are not generally recorded as the primary terrestrial forage genus for caribou, with the possible exception of *Cladonia uncialis* or *C. arbuscula* (Szkorupa, 2002; Dunford, 2003; Saher, 2005; Saher & Schmiegelow, 2005). One study in northeastern British Columbia evaluated *C. uncialis* vs. *Cladonia* spp. and found only the latter to be a significant predictor of caribou habitat selection (Johnson *et al.*, 2000). In JNP, *Cladonia* spp. is the most abundant genera among the terrestrial forage lichens (Thomas & Armbruster, 1996; Shepherd, 2006), but overall, terrestrial lichen is relatively scarce in JNP and BNP as compared to northern Alberta, Alaska, or eastern Canada (Thomas *et al.*, 1996a, Arsenault *et al.*, 1997; Dunford, 2003, Joly *et al.*, 2003). Poole *et al.* (2000) and Johnson *et al.* (2001) found that in northern British Columbia, caribou selected for the species of lichen that was most abundant. The selection for areas with high cover of *Cladonia* spp. in this "lichen-impoverished" environment thus may represent a local foraging strategy.

Surprisingly, the number of heavily laden arboreal lichen bearing trees (Class 3 trees) was not an important predictor of caribou selection at the fine scale. While arboreal lichen has been identified as an important forage resource for caribou in west-central Alberta (Thomas & Armbruster, 1996; Szkorupa, 2002; Saher, 2005; Saher & Schmiegelow, 2005), this was not apparent from our analysis. However, arboreal lichens have been found to comprise only ~1% of caribou diet in BNP and JNP (Thomas *et al.*, 1996b). If areas with high abundance of arboreal lichens are important only during a relatively brief period of the winter season, our analysis may not have detected this as we included all early and late winter foraging (mid-October to mid-April). It is also possible that the short duration of our study did not capture a season in which heavy or long-lasting snow conditions necessitated a greater reliance on, and therefore noticeable selection for, areas with abundant arboreal lichen (Thomas *et al.*, 1996b). As mentioned previously, it is possible caribou are selecting for areas that would tend to have a higher likelihood of abundant arboreal lichen at the stand or coarse-scale, rather than at a foraging level. This is supported by avoidance of sites with Douglas-fir or aspen forest, and by avoidance of sites that had greater numbers of trees with little arboreal lichen (Class 1 trees).

Several lines of evidence point to selection for older stands at a fine scale. The strong positive influence of maximum tree core age (fine scale variable) indicates preference for sites with older trees. This is complementary to avoidance of sites with high numbers of Class 1 trees (< 5 grams of lichen /tree); these likely being younger, denser stands (Sillet & Goslin, 1999; Dettki *et al.*, 2000). Stand density itself, however, was not a significant predictor of caribou habitat selection. The positive influence of sapling density in the model is also suggestive of a preference for older forest, since 75% of the saplings found in the sample plots were subalpine fir, a late-successional, shade-tolerant, climax species that dominates under mature forest canopies in the subalpine (Johnson & Fryer, 1989; Callaway *et al.*, 2000). Selection for shallower duff could indicate favourable conditions occur on sites that had experienced a more recent fire event but that still have older trees present. This would have to be a low severity fire event, which is not considered the historic norm for the higher elevation sites preferred by caribou (Tande, 1979; Rogeau, 1996). In these areas, fire has been characterized as infrequent, severe, and stand replacing (Bessie & Johnson, 1995; Veblen, 2003). Determining the extent of low intensity fires in JNP and BNP would be required to assess this further.

Basal area, which increases with stand age, was not included in our top model, but it was a strong (positive) predictor of caribou selection in other candidate models. No other studies of woodland caribou in Alberta have reported basal area to be a significant predictor of habitat selection, but two studies in British Columbia's Selkirk Mountains found mountain caribou selected for habitat with greater basal area (Rominger & Oldemeyer, 1989; Terry *et al.*, 2000).

Avoidance of sites with increased numbers of downed logs could also reflect avoidance of younger sites, which would contain an abundance of fire-derived downed wood. A simpler explanation, however, is that this avoidance is related to logs being a physical barrier to travel (Schaefer & Pruitt, 1991). Areas with an abundance of downed wood may have been avoided to conserve energy, or to allow easier escape from predators.

Conclusions

Our selection models at both scales indicated a preference by caribou for older forest, or sites likely to have older forests. At a landscape scale, caribou selected older forest (75-150 yrs and 225-300 yrs), higher elevations and less steep slopes. Similarly, in the fine scale model there was selection for sites with older trees, and older forest characteristics. Terrestrial lichen abundance was a significant predictor of caribou habitat selection while arboreal lichen abundance was not. Nevertheless, harsher conditions than those encountered during the years of this study could increase the relative importance of arboreal lichens at a fine scale. It should also be emphasized that predator avoidance may be indirectly linked to several of the model variables. Information on the response of predators and their primary prey to stand age, as reflecting fire history, is critical for determining how to manage disturbances in caribou range. High disturbance levels in caribou ranges, with associated changes in habitat availability and distribution and shifts in predator and primary prey abundance and distribution, have been indentified as the ultimate cause of caribou decline throughout Alberta (Dzus, 2001; Alberta Woodland Caribou Recovery Team, 2005; Lessard *et al.*, 2005).

Our habitat selection models do not suggest that the lack of recent fire in JNP and BNP has been detrimental for caribou. Large prescribed burns within caribou habitat would create areas that caribou would be likely to avoid during the winter for up to 75 years. Caribou habitat would therefore benefit, at least in the short term, from exclusion of prescribed fires and wildfires from caribou range. Currently, only 9% of the study area includes stands in the <75 year category (Shepherd, unpublished data). While 9% is sufficient representation to ensure that caribou are not avoiding this age class due to scarcity, this proportion is negatively skewed from the expected negative exponential stand age distribution (Van Wagner *et al.*, 2006). To achieve fire management goals of restoring historic stand age distributions within the national parks, while avoiding negative impacts on caribou habitat, prescribed burning will need to be focused away from areas identified as critical caribou winter range.

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Arboreal forage lichen response to partial cutting of high elevation mountain caribou range in the Quesnel Highland of east-central British Columbia

Michaela J. Waterhouse[1*], Harold M. Armleder[1] & Amanda F. Linnell Nemec[2]

[1] Ministry of Forests and Range, Suite 200 – 640 Borland Street, Williams Lake, British Columbia, Canada V2G 4T1 (*corresponding author: Michaela.Waterhouse@gov.bc.ca).
[2] Box 496, Brentwood Bay, British Columbia, Canada V8M 1R3.

Abstract: Group selection silvicultural systems have been recommended for managing mountain caribou (*Rangifer tarandus caribou*) habitat in high elevation Engelmann spruce – subalpine fir forests in east-central British Columbia. We measured the response of arboreal lichen (a key winter forage) to harvesting of 30% of the forested area using three partial cutting treatments, which created small (0.03 ha), medium (0.13 ha), and large (1.0 ha) openings, and a no-harvest treatment. Treatments were replicated on four sites, and monitored over a ten year post-harvest period. The short-term loss of lichen associated with removal of approximately one third of the trees was partially offset by a significant (P=0.01) increase in lichen abundance on trees in the caribou feeding zone (up to 4.5 m) in the three partial cutting treatments relative to trees in the uncut forest. Differences among treatments in the change in lichen composition, as measured by the percentage of *Alectoria sarmentosa* and *Bryoria* spp., were marginally significant (P=0.10). The partial cutting treatments showing a greater likelihood of shifting towards more *Bryoria* spp. than no-harvest treatment (P=0.04). In the year of harvest (1993), larger trees were found to hold more lichen than smaller trees (P=0.04), and live trees supported more lichen than dead trees (P=0.01), but lichen loading was similar among tree species (P=0.51). Tree fall rates were similar among treatments, based on the ten year average (0.6–0.8% of sample trees per year). The results indicate that caribou foraging habitat is maintained in the residual forest when group selection systems that remove only 30% of the trees are applied. Information on the distribution of lichen is useful for developing stand level prescriptions. Providing lichen bearing habitat meets just one of the needs of caribou. A comprehensive approach that considers all factors and their interactions is essential to maintain and recover the threatened mountain caribou.

Key words: arboreal lichen, forest management, group selection silvicultural systems, *Rangifer tarandus caribou*.

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Introduction

Mountain caribou in the Southern Mountains National Ecological Area are designated as threatened by the Committee on Endangered Wildlife in Canada (COSEWIC) and qualify for protection and recovery under the federal Canadian *Species at Risk Act* (SARA). The British Columbia Conservation Data Centre (2007) describes mountain caribou as critically imperilled and have placed them on the endangered and threatened list of species (Red List). The population of mountain caribou was estimated at 1900 animals in 2006 in British Columbia (Hatter, 2006) and this represents 98% of the global population (British Columbia Conservation Data Centre, 2007). There are several planning processes in British Columbia addressing management of these caribou herds. The Cariboo-Chilcotin Land Use Plan (CCLUP), as early as 1995, recognized that mountain caribou were an important management issue in the central interior (Government of British Columbia, 1995). The Mountain Caribou Strategy component of the CCLUP (Youds *et al.*, 2000) delineated areas of no forest harvesting and over 53 000 ha for 'modified harvesting' across the caribou range in east-central British Columbia. This research trial was undertaken to test the hypothesis that group selection silvicultural systems (modified harvesting) are compatible with maintaining caribou habitat in a managed forest environment.

Within the Engelmann Spruce-Subalpine Fir (ESSF) and Interior Cedar Hemlock (ICH) biogeoclimatic zones (Steen & Coupé, 1997) in the central interior of British Columbia, clearcutting on short rotations does not maintain the old growth forest characteristics that caribou require (Mountain Caribou Technical Advisory Committee, 2002). Lichens are widely recognized as the major winter forage of woodland caribou throughout their range (Edwards *et al.*, 1960; Edwards & Ritcey, 1960; Scotter, 1962; Scotter, 1967). In mountainous areas of heavy snowfall in south eastern and east-central British Columbia, caribou eat arboreal (tree-dwelling) lichens almost exclusively during the winter (Terry *et al.*, 2000). Logging can have a drastic effect on available arboreal lichen biomass (Stevenson, 1979; Stevenson, 1985; Stevenson, 1988; Stevenson, 1990; Stevenson & Enns, 1992; Rominger *et al.*, 1994). Clearcutting is not compatible with maintaining mountain caribou habitat as it removes all arboreal lichen. It may take well over a century before the quantity of lichen within a clearcut is comparable to that found in old-growth stands because of the time it takes to develop stand attributes conducive to heavy lichen loading such as defoliated branches, stable environmental conditions and adequate ventilation (Goward & Campbell, 2005). Widespread application of clearcutting reduces the amount of usable caribou habitat, effectively shrinking their range. Large areas with sufficient forage are necessary so caribou can live at relatively low densities in order to successfully evade predators (Bergerud *et al.*, 1984; Seip, 1991).

The impacts of partial cutting on lichen biomass have been studied in Sweden (Esseen *et al.*, 1996) and in north-western North America (Rominger *et al.*, 1994; Stevenson, 2001; Coxson *et al.*, 2003; Stevenson & Coxson, 2003). In the central interior of British Columbia alternatives to clearcutting, specifically single-tree and group selection silvicultural systems are being tested as possible systems to maintain good quality foraging habitat, while allowing some timber harvesting (Armleder & Stevenson, 1996). Testing of partial cutting approaches is necessary to investigate three main concerns: potential increase in the rate of tree fall, potential loss of lichen through increased wind scouring in the residual stand (Terry, 1994), and potential change in the microclimate sufficient to affect lichen growth rates (Kershaw, 1985).

In their comprehensive study of lichen litterfall, growth and turnover, Stevenson and Coxson (2003) report, based on results from a single site, that group selection and single tree selection systems, removing 30% of the timber, maintained a satisfactory environment for continued lichen growth two years after logging. The Quesnel Highland trial described here was partially cut, in 1993, using a group selection silvicultural system based on 30% removal, with replication of the four treatments over four sites. The treatments varied by opening size: 0.03 ha, 0.13 ha, and 1.0 ha. Over the past ten years, we have measured the abundance of arboreal lichen (*Alectoria sarmentosa* and *Bryoria* spp.) in the residual forest in response to three opening size treatments and a no-harvest treatment. The longer term response includes the rate of tree fall and recruitment of new trees. Additionally, we describe the distribution of lichen by tree species, decay class and diameter class as well as the implications of tree fall and recruitment of new trees to lichen abundance.

Methods

Study area

The four study sites are located 12–28 km east of Likely in east-central British Columbia. Two of the sites, Upper and Lower Grain creeks (UGC and LGC), (52°41'29"N, 121°12'02"W and 52°40'45"N, 121°10'52"W, respectively) are located within the Grain Creek watershed. The other two sites (BBW and BBS) are adjacent to each other in the Blackbear Creek watershed (52°36'37"N, 121°24'30"W). All study sites are submesic to mesic within the Engelmann Spruce–Subalpine Fir wet, cold biogeoclimatic subzone variant (ESSFwc3) (Steen & Coupé, 1997). The elevation of the sites extends from 1440 to 1690 m. Above this elevation, the forest becomes subalpine parkland, then alpine. Slopes are similar at all sites ranging from 24 to 32%, while aspect is northeast at Blackbear Creek, northwest at Lower Grain Creek, and west at Upper Grain Creek.

The forest is dominated by subalpine fir (*Abies lasiocarpa*) and a lesser amount of Engelmann spruce (*Picea engelmannii*). The oldest trees are spruce aged 297 years on the Blackbear Creek site and from 426 to 446 years on the Grain Creek sites. Stands are multi-aged as the fire return intervals are very long; forest replacement typically occurs as individual or small groups of mature and old trees succumb to insects, disease, and tree fall (Steen *et al.*, 2005). Several small (<0.1 ha), wet subalpine meadows are scattered throughout the Lower and Upper Grain Creek study sites. Based on pre-harvest cruise data, gross timber volumes range from 300 to 387 m^3/ha (>17.5 cm diameter at breast height [dbh]). Stem densities are 357 to 736 stems/ha (>12.5 cm dbh), and averaged across the three sites, 29% of the subalpine fir and 12% of the spruce is dead (Steen *et al.*, 2005).

In the forest understory, the thick shrub layer is dominated by white-flowered rhododendron (*Rhododendron albiflorum*) (45% cover) and a lesser component of black huckleberry (*Vaccinium membranaceum*) (7%). The fairly abundant herb layer consists mostly of Sitka valerian (*Valeriana sitchensis*) (10%), oak fern

(*Gymnocarpium dryopteris*) (7%), mountain arnica (*Arnica latifolia*) (5%), rosy twistedstalk (*Streptopus roseus*) (4%), and foamflower (*Tiarella trifoliata*) (3%). The bryophyte layer is fairly continuous covering 40% of the ground.

Experimental design and treatments

The design is a randomized complete block with four sites representing the blocking factor. Each study site is approximately 40 ha and was divided into four - 10 ha treatment units. The four treatments were randomly assigned within each site. One treatment unit was no-harvest (control) while 30% of the area was harvested (including skid trails) in the other three units using one of three group selection treatments that differed by opening size: 0.03 ha (small), 0.13 ha (medium), and 1.0 ha (large). On average, the treatment units contained three - 1.0 ha openings, seventeen - 0.13 ha openings, or sixty - 0.01 ha openings. The partial cutting treatments were harvested using feller-bunchers and grapple skidders. On BBW, UGC and LGC sites harvesting was done on a snowpack of 0.5–1.5 m from December 1992 to January 1993 to minimize forest floor disturbance. The BBS site was cut in the summer of 1992. Permission was obtained from the Workers' Compensation Board of British Columbia to retain safe dead trees in the adjacent forest that would normally be felled during conventional ground-based harvesting.

Field methods

One or two permanent transect lines per treatment unit were set up immediately post-harvest in March of 1993. Transects were 4 m wide and were about 250 m long and were set across slope bisecting openings and residual forest. This captured about 80 trees per treatment unit. Based on four replicate blocks and four treatments, 1225 trees were permanently tagged, and assessed in 1993. Re-assessments were completed in 1997, 2001 and 2003 (10.5 years post-harvest). For each tree (> 10 cm diameter at breast height [dbh]) the following attributes were recorded: species, dbh, decay class (Backhouse 1993), any major breakage on the bole, and lichen abundance. In 2003, diameters of all the trees were re-measured and 30 new recruits were added to the dataset. Lichen abundance was visually rated in classes 0 to 5, and the percentage of *Alectoria* and *Bryoria* species on each sample tree was estimated to the closest 5% (Armleder *et al.*, 1992; Stevenson *et al.*, 1998). Visual estimations of quantity were made by comparing the observed amount of lichen on the tree in the caribou feeding zone (up to 4.5 m above ground) with a series of photographs with known quantities of lichen. Each class corresponds to a range of weights (g) that increases on an approximate logarithmic scale from the lower to the upper weight limit of the class. Similarly, a series of photographs with measured portions of *Alectoria* and *Bryoria* were used to estimate percent composition. All fallen trees were noted during each re-assessment, and the following data were recorded: year of fall, direction of fall, type of break, and decay class at the time of fall.

Data analysis

All data summaries and analyses were performed with SAS (SAS Institute Inc., 1999-2001). The 1993 data set (1225 trees) was used to compare the abundance of lichen among tree species (spruce, subalpine fir), decay classes (alive, dead), diameter classes (10-30 cm, 31-50 cm and > 50 cm) and sites (BBW, BBS, UGC, LGC). In order to estimate lichen loadings, the abundance class had to be converted to an approximate weight and averaged (or summed) over trees. Weights for individual trees were assumed to be equal to the exponential curve evaluated at the lichen class midpoint. The lichen load per tree was as follows for each class: class 0 = 0 g/tree, 1 = 1.25 g/tree, 2 = 16.25 g/tree, 3 = 126.00 g/tree and 4 = 425.00 g/tree). Annual rates of tree fall, and recruitment were tabulated by site and treatment. The percentage of trees by decay class, species, and diameter class, and lichen composition (% *Alectoria* for trees rated lichen class ≥ 2) were also summarized by site and treatment.

The 2003 dataset contains the original tree sample (including 87 fallen trees) and 30 new recruits. Fallen trees were assumed to have no lichen in 2003 unless an amount was recorded on a high stump, and recruits were assumed to have no lichen in 1993.

Logistic regression analyses were use to test for treatment effects immediately after application (in 1993) and by comparing the changes that occurred between the 1993 and 2003 measurement periods. Analysis of the difference between 1993 and 2003 is a type of repeated measures analysis, which accounts for slight variability between the treatments in 1993 and reduces bias due to changes in observers from year to year.

The statistical significance of apparent treatment effects on the amount and composition of arboreal lichen was determined by fitting logistic models that relate lichen response to treatment and site, as well as allowing for the potentially confounding effects of species, live/dead decay class, and tree diameter:

$$\log\left(\frac{p_i(t, s, u, v, dbh)}{p_3(t, s, u, v, dbh)}\right)=\alpha_{it}+\beta_{is}+\alpha\beta_{its}+\gamma_{iu}+\delta_{iv}+(\phi_i+\gamma\phi_{ui})\times dbh$$

where $p_i(t, s, u, v, dbh)$ is the probability that a tree in the plot receiving Treatment t at Site s falls into one of three levels i (=1, 2, or 3), when the tree is Species u, is in Decay Class v, and has Diameter dbh.

For the purpose of analysis, responses were coded as one of three levels. In particular, the five classes used to rate the abundance of lichen in the field were pooled as follows: Level 1= Lichen Classes 0 and 1, Level 2 = Lichen Class 2, and Level 3 = Lichen Classes 3 and 4. Similarly, the relative abundance of *Alectoria* was classified as 0%-10%, 11%-50%, > 50%, and changes between 1993 and 2003 (in lichen or % *Alectoria*) were classified as an increase, decrease, or no change. Only trees with rated Class 2 and greater were included in the analysis of the proportion of *Alectoria* in response to the harvesting treatments.

The parameter α_{it} is the fixed effect (log-odds) of treatment relative to the control (no-harvest) (i.e., $\alpha_i = 0$ for the control); γ_{iu}, δ_{iv}, $\phi_{i,}$ and $\gamma\phi_{iu}$ are respectively the fixed effects (log-odds) of subalpine fir compared with spruce (i.e., $\gamma_{iu} = 0$ for spruce), a live tree compared with a dead tree (i.e., $\delta_{iv} = 0$ for a dead tree), and a diameter increase of 1 cm ($\phi_{i,}$ is the slope for spruce and $\phi_{i,+}$ $\gamma\phi_{iu}$ is the slope for subalpine fir); and β_{is}, $\beta\alpha_{its}$ are the random effects of site and treatment plot (i.e., site × treatment interaction). All random effects were assumed to be independent and normally distributed; variability among lines in the same plot was assumed to be negligible compared with variability among trees, plots, and sites. Model parameters were estimated by the method (Poisson log-linear model) described by Chen & Kuo (2001), using the SAS macro GLIMMIX (Littell *et al.*, 1996). Both a simplified model that excluded species, alive/dead status, and diameter (Model 1: Equation 1 with $\gamma_{iu} = 0$, $\delta_{iv} = 0$, $\phi_i = 0$, $\gamma\phi_{iu} = 0$) and the model that included these effects (Model 2) were fitted to the data. Results were considered significant at $\alpha = 0.05$.

Results

Distribution of lichen by tree species, decay class and diameter class

Analysis of the distribution of lichen immediately after harvest (1993) showed no significant treatment ($P = 0.20$) or species ($P = 0.51$) effects, while decay class (live / dead) ($P = 0.01$) and diameter ($P = 0.04$) were significant factors (Table 1). The proportion of spruce trees (> 10 cm dbh) in the forest was 17.5% and they held 18.9% of the total lichen biomass, while subalpine fir, the dominant species, held 81.1% of the lichen. Dead trees (17.7% of the sample) contained 12.2% of the lichen while live trees held 87.8%. Small (10-30 cm dbh) subalpine fir trees were the most common size and species of tree in the sample (Fig. 1), and collectively with live medium size subalpine fir (30-50 cm dbh) contain the majority of lichen from all trees sampled (Fig. 2). However, on a per tree basis the small, live subalpine fir trees held about half the amount of lichen as found on the two larger size classes (Fig. 3). The amount of lichen on live spruce trees also increased with size class (Fig. 3). There appeared to be no relationship with species or size class for the amount of lichen per dead tree (Fig. 3). The amount of lichen per tree was substantially lower at the UGC site than the other three sites (Fig. 4). Analysis (Table 2) showed that there was a marginally significant ($P = 0.08$) difference among partial cutting treatments and no-harvest treatment in the proportion of *Alectoria* immediately post-harvest. The trees in the partial cutting treatment with medium-size (0.13 ha) openings were more likely to have more *Bryoria* than those trees in the no-harvest or other two partial cutting treatments. Decay class (live / dead) was highly significant ($P < 0.0001$) (Table 2) with dead trees having more A*lectoria*. (56.3%) than live trees (41.5%) (Fig. 5).

Tree fall and recruitment

A total of 87 trees fell from the original sample of 1225, over 10.5 years. Tree fall rates averaged 0.7% per year of standing trees across all sites and treatments. It ranged from 0.6% to 0.8% per year by treatment (Table 3) and 0.3% to 0.9% among sites. The rate of fall was higher for subalpine fir (0.7%) than for spruce (0.5%). Before falling, the majority of trees were dead (73.5%) compared to live (26.5%). Of the 227 dead standing trees in the sample, 23.4% fell in 10.5 years at a rate of 2.2% per year. The live trees had a much lower fall rate (0.2% per year). Thirty new recruits were recorded in 2003 (27 subalpine fir and 3 spruce).

Response to partial cutting

Results of the logistic analysis of changes in lichen abundance for the whole time period 1993 to 2003 (Table 4) show that there were significant differences among treatments ($P = 0.03$ for Model 2 which included tree species, diameter and decay class). Trees in the residual forest in either small (0.03 ha), medium (0.13 ha), or large (1.0 ha) opening treatments showed more of a shift towards higher lichen classes than did trees in the no-harvest treatments (Fig. 6). Decay class ($P < 0.0001$) and species ($P = 0.02$) exhibited significant relationships with change in lichen class (Table 4). However, ignoring these factors (Model 1) appeared to have little impact on the significance of the treatment effect ($P = 0.05$). Logistic analysis of changes in lichen composition from 1993 - 2003 suggested that there were marginally significant differences among treatments after ten years ($P = 0.06$ for Model 1 and $P = 0.10$ for Model 2); partial cuts showed a greater tendency than the no-harvest treatment to shift towards more *Bryoria* and less *Alectoria* ($P = 0.04$) (Table 5, Fig. 7).

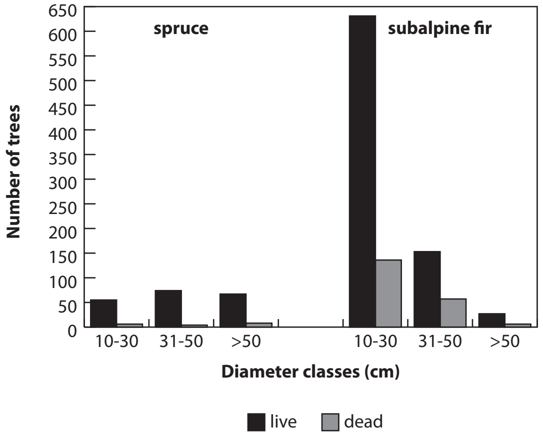

Fig. 1. Distribution of sample trees (n=1225) by species, decay class, and dbh class (1993).

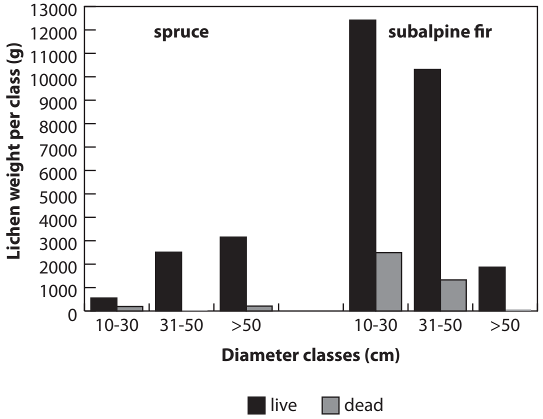

Fig. 2. Total weight of lichen in each combination of species, decay class and diameter class based on 1225 sample trees from all sites and treatments (1993).

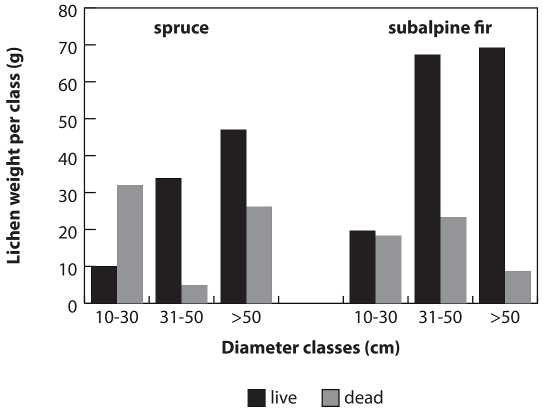

Fig. 3. Mean weight of lichen per tree in each combination of species, decay class and diameter class.

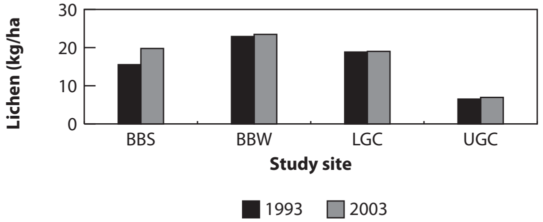

Fig. 4. Estimate of quantity of lichen per site (kg/ha) in the caribou feeding zone (up to 4.5 m) in 1993 and 2003.

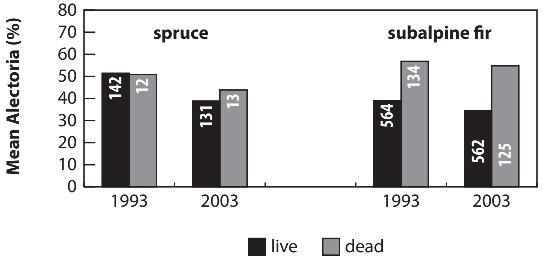

Fig. 5. Composition of lichen (average percentage of *Alectoria*) on dead and live subalpine fir and spruce trees in 1993 and 2003 for trees rated class 2 and higher. Sample size (number of trees) is noted in each bar.

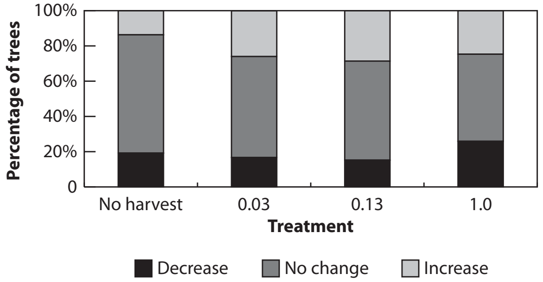

Fig. 6. The percentage of sample trees that showed an increase or decrease or no change in lichen abundance from 1993 to 2003 (percentages differed significantly among treatments, P=0.03).

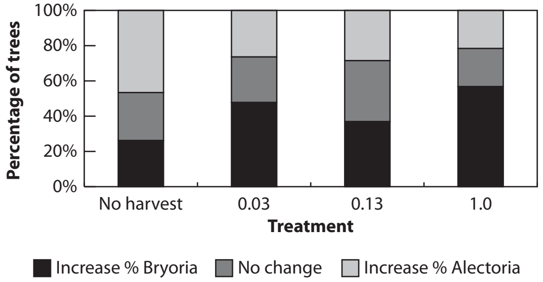

Fig.7. The percentage of sample trees that showed a change in composition (% *Alectoria* / *Bryoria*) from 1993 to 2003 (differences among treatments were marginally significant, P=0.10)

Discussion and management implications

Forests at high elevations are dominated by subalpine fir, have many sizes of trees, and contain numerous dead trees in various stages of decay. Each component contributes to the lichen loading in the forest as a whole. The small subalpine fir trees hold a large quantity of the total lichen but in small amounts per tree. The larger trees in our study tended to hold a larger quantity of lichen in the caribou feeding zone. Campbell & Coxson (2001) also found the lichen load to increase with the size of whole subalpine fir and Engelmann spruce trees. Snow trailing studies have shown that caribou select trees with higher lichen ratings for foraging (Terry, 2000; Kinley *et al.*, 2003); therefore, retention of a portion of the larger trees is vital.

Dead trees are an important component of the stand due to their large number (17.7% of stems in this study) and the total amount of lichen they hold (12.2%). Dead trees hold a somewhat larger proportion of *Alectoria* and lower amounts of *Bryoria* than live trees. Campbell & Coxson (2001) found *Alectoria* to be most abundant in the lower canopy and to utilize summer rainfall events to a greater extent than *Bryoria* to sustain thallus hydration. Perhaps, exposure to summer rainfall events is accentuated in dead trees thus favouring *Alectoria*. Although caribou prefer foraging on *Bryoria* (Rominger *et al.*, 1996), it is important to retain both genera in the stand. In particular during forest operations, safe dead trees should be kept, while ones in advanced stages of decay (unsafe) should be cut. In any case, unsafe ones are likely to fall out of the stand quickly.

Table 1. Logistic regression models of lichen abundance distribution immediately post-harvest (1993). The reference value in the analysis is Lichen Classes 3, 4. A) Parameter estimates (± estimated standard error). B) Tests of significance.

A	Model 1		Model 2	
	Lichen Classes 0,1	Lichen Class 2	Lichen Classes 0,1	Lichen Class 2
α (Large)	0.18 ± 0.23	0.07 ± 0.22	0.31 ± 0.24	0.17 ± 0.22
α (Medium)	0.68 ± 0.24	0.45 ± 0.23	0.68 ± 0.24	0.44 ± 0.23
α (Small)	-0.08 ± 0.23	-0.02 ± 0.21	0.09 ± 0.23	0.09 ± 0.22
γ (Subalpine fir)			0.44 ± 0.40	0.39 ± 0.37
δ (Live)			-0.73 ± 0.25	-0.75 ± 0.24
ϕ (Dbh)			-0.015 ± 0.006	-0.011 ± 0.006
$\gamma\ \phi$ (Subalpine fir x Dbh)			0.005 ± 0.012	0.001 ± 0.011

B	Model 1			Model 2		
Effect	Degrees of freedom	*F* ratio	Prob *F*	Degrees of freedom	*F* ratio	Prob *F*
Treatment	6	2.03	0.1000	6	1.56	0.1989
No-harvest *vs* Large	2	0.34	0.7156	2	0.85	0.4374
No-harvest *vs* Medium	2	4.06	0.0303	2	3.93	0.0330
No-harvest *vs* Small	2	0.08	0.9191	2	0.10	0.9029
Large *vs* Medium	2	2.10	0.1442	2	1.12	0.3424
Large *vs* Small	2	0.75	0.4813	2	0.50	0.6098
Medium *vs* Small	2	5.20	0.0134	2	3.00	0.0677
No-harvest *vs* Partial Cut	2	0.96	0.3972	2	1.76	0.1921
Species				2	0.68	0.5089
Live/Dead				2	4.86	0.0078
Dbh				2	3.26	0.0387
Dbh x Species				2	0.11	0.8987

Table 2. Logistic regression models of lichen composition (% *Alectoria*) immediately post-harvest (1993). The reference value in the analysis is *Alectoria* > 50%. A) Parameter estimates (± estimated standard error). B) Tests of significance.

A	Model 1		Model 2	
	0%-10% *Alectoria*	11%-50% *Alectoria*	0%-10% *Alectoria*	11%-50% *Alectoria*
α (Large)	-0.35 ± 0.58	-0.11 ± 0.54	-0.34 ± 0.60	-0.09 ± 0.56
α (Medium)	1.43 ± 0.56	0.63 ± 0.55	1.50 ± 0.58	0.66 ± 0.57
α (Small)	-0.16 ± 0.57	-0.26 ± 0.55	-0.18 ± 0.59	-0.27 ± 0.56
γ (Subalpine fir)			-0.09 ± 0.45	0.02 ± 0.36
δ (Live)			1.14 ± 0.21	0.55 ± 0.17
ϕ (Dbh)			-0.005 ± 0.007	-0.007 ± 0.006
$\gamma\,\phi$ (Subalpine fir x Dbh)			0.001 ± 0.014	-0.002 ± 0.011

B	Model 1			Model 2		
Effect	Degrees of freedom	*F* ratio	Prob *F*	Degrees of freedom	*F* ratio	Prob *F*
Treatment	6	2.12	0.0918	6	2.19	0.0821
No-harvest vs Large	2	0.19	0.8302	2	0.17	0.8411
No-harvest vs Medium	2	3.22	0.0600	2	3.37	0.0533
No-harvest vs Small	2	0.11	0.8943	2	0.12	0.8889
Large vs Medium	2	4.87	0.0177	2	4.97	0.0163
Large vs Small	2	0.17	0.8484	2	0.17	0.8433
Medium vs Small	2	3.94	0.0347	2	4.12	0.0300
No-harvest vs Partial Cut	2	0.22	0.8008	2	0.24	0.7869
Species				2	0.03	0.9713
Live/Dead				2	16.37	<.0001
Dbh				2	0.85	0.4296
Dbh x Species				2	0.02	0.9757

Table 3. Number of tree falls and recruits per treatment as a percentage of standing trees.

		No-harvest	Small	Medium	Large	Total
Tree falls	1993-1997	7	10	13	11	41
	1997-2001	8	9	14	5	36
	2002-2003	4	2	1	3	10
	Sum 1993-2003	19	21	28	19	87
	Total trees 1993	305	314	318	290	1225
	1993-2003 % of total	6.23	6.69	8.81	6.55	7.09
	% per year	0.59	0.64	0.84	0.62	0.68
Recruits	Sum 1993- 2003	9	6	12	3	30
	Total trees 2003	295	299	302	274	1170

Our results are consistent with those of Coxson *et al.* (2003), who found that the abundance of lichen in the caribou feeding zone (4.5 m) did not vary with tree species. However, Campbell & Coxson (2001) also found by sampling branches throughout whole trees, in uncut forest, that subalpine fir did hold more lichen than Engelmann spruce and the natural clumpy arrangement of subalpine fir was a factor that increased lichen abundance. Trees with higher lichen loading throughout would contribute more potential forage as litterfall or on tree falls. There is a temptation to reforest the harvested openings with spruce that has higher commercial value. However, until more research is available, the recommended regeneration strategy is to plant or acquire natural regeneration, in small groups (with reduced inter-tree distance) with a species mix similar to that found at the site before harvest (Youds *et al.*, 2000).

The removal of one third of the trees, through group selection harvesting, resulted in an immediate loss of lichen. The amount of time required for trees in these openings to develop with sufficient quantities of lichen for forage in the future is not known. However, the sites at Blackbear Creek which originated about 297 years ago, through natural regeneration following wildfire (Steen *et al.*, 2005), have similar lichen abundance to Lower Grain Creek established about 446 years ago and much more lichen than Upper Grain Creek (426 years old). The elapsed time since tree removal is just one of many factors that determine the lichen holding capacity of the forest. Goward & Campbell (2005) describe three important

Table 4. Logistic regression models for the change in lichen abundance from 1993 to 2003, including fallen and recruited sample trees. The reference value in the analysis is the increase. A) Parameter estimates (± estimated standard error). B) Tests of significance.

A	Model 1		Model 2	
	Decrease	No change	Decrease	No change
α (Large)	-0.86 ± 0.38	-0.81 ± 0.35	-0.84 ± 0.37	-0.81 ± 0.34
α (Medium)	-0.93 ± 0.37	-0.90 ± 0.35	-1.11 ± 0.36	-0.99 ± 0.34
α (Small)	-0.23 ± 0.37	-0.84 ± 0.35	-0.34 ± 0.36	-0.90 ± 0.34
γ (Subalpine fir)			-1.08 ± 0.41	-0.78 ± 0.34
δ (Live)			-2.19 ± 0.23	-1.23 ± 0.22
ϕ (Dbh)			0.000 ± 0.006	-0.005 ± 0.005
γ ϕ (Subalpine fir x Dbh)			0.004 ± 0.012	0.007 ± 0.010

B	Model 1			Model 2		
Effect	Degrees of freedom	*F* ratio	Prob *F*	Degrees of freedom	*F* ratio	Prob *F*
Treatment	6	2.55	0.0484	6	2.96	0.0277
No-harvest *vs* Large	2	3.50	0.0461	2	3.60	0.0432
No-harvest *vs* Medium	2	4.25	0.0265	2	5.91	0.0084
No-harvest *vs* Small	2	3.22	0.0587	2	3.68	0.0413
Large *vs* Medium	2	0.03	0.9684	2	0.31	0.7396
Large *vs* Small	2	2.12	0.1436	2	1.64	0.2172
Medium *vs* Small	2	2.37	0.1169	2	2.90	0.0768
No-harvest *vs* Partial Cut	2	4.61	0.0202	2	5.60	0.0102
Species				2	3.79	0.0227
Live/Dead				2	50.44	<.0001
Dbh				2	0.69	0.5041
Dbh x Species				2	0.21	0.8130

factors for development of an abundant lichen community which generally increase over time: availability of defoliated branches (attachment sites), stable environmental conditions and openness of the forest (increased ventilation). Other factors such as aspect, slope, slope position, presence of open water, and distance from inoculation source are also important.

The re-establishment of trees and the subsequent inoculation with lichen after a large wildfire may be comparatively slow compared with a group selection system. The openings (particularly those greater than 0.1 ha) can be successfully regenerated through planting (Lajzerowicz *et al.*, 2006) or by natural regeneration, over a somewhat longer period (Steen *et al.*, 2006). Close proximity to the uncut forest should ensure inoculation with lichen fragments that will establish when substrate and climate conditions are conducive for attachment and growth. The recommended cutting cycle of 80 years means that trees will have 240 years to grow and accumulate forage lichen before being harvested again (Youds *et al.*, 2000; Stevenson *et al.*, 2001).

Loss of lichen bearing trees over the entire ten year period has been low and there was little difference in tree fall rates among the treatments (0.6 – 0.8% of the standing trees per year). The subalpine fir trees that died some years ago (decay class 4), perhaps due to western balsam bark beetle (*Ceratocystis dryocoetidis*) (Steen *et al.*, 2005), are now falling out of the stand. The relatively low rates are consistent with other British Columbia studies (Coates, 1997; Huggard *et al.*, 1999; Waterhouse & Armleder, 2004). Typically,

Table 5 Logistic regression models for the change in lichen composition (% *Alectoria*) from 1993 to 2003, including fallen and recruited sample trees. The reference value in the analysis is the increase. A) Parameter estimates (± estimated standard error). B) Tests of significance.

A	Model 1		Model 2	
	Decrease	No change	Decrease	No change
α (Large)	1.03 ± 0.41	0.38 ± 0.42	0.92 ± 0.41	0.36 ± 0.42
α (Medium)	0.62 ± 0.41	0.68 ± 0.41	0.63 ± 0.40	0.70 ± 0.41
α (Small)	1.31 ± 0.41	0.44 ± 0.43	1.16 ± 0.41	0.40 ± 0.43
γ (Subalpine fir)			-1.10 ± 0.44	-0.02 ± 0.54
δ (Live)			0.45 ± 0.22	0.14 ± 0.23
ϕ (Dbh)			0.007 ± 0.007	0.013 ± 0.008
γ ϕ (Subalpine fir x Dbh)			0.015 ± 0.013	-0.010 ± 0.016

B	Model 1			Model 2		
Effect	Degrees of freedom	*F* ratio	Prob *F*	Degrees of freedom	*F* ratio	Prob *F*
Treatment	6	2.46	0.0564	6	2.06	0.1008
No-harvest *vs* Large	2	3.22	0.0597	2	2.62	0.0957
No-harvest *vs* Medium	2	1.68	0.2101	2	1.82	0.1862
No-harvest *vs* Small	2	5.26	0.0134	2	4.22	0.0278
Large *vs* Medium	2	1.46	0.2551	2	1.19	0.3220
Large *vs* Small	2	0.26	0.7715	2	0.21	0.8127
Medium *vs* Small	2	2.74	0.0863	2	2.15	0.1400
No-harvest *vs* Partial Cut	2	4.37	0.0256	2	3.77	0.0396
Species				2	4.61	0.0101
Live / Dead				2	2.03	0.1311
Dbh				2	1.22	0.2944
Dbh x Species				2	2.00	0.1352

the first few years following harvest are the most susceptible to endemic wind throw (Stathers *et al.*, 1994). Coates (1997) and Huggard *et al.* (1999) found increased rates overall in partial cuts relative to uncut forests within the first couple of years post-harvest. In a longer term study of five years, Waterhouse & Armleder (2004) found no treatment differences between uncut and partially cut forest. In our study, the high proportion of dead fallen trees (73.5%) and much higher rate of tree fall for standing dead compared to standing live (10 times) is similar to that reported by Waterhouse & Armleder (2004). Huggard *et al.* (1999) found the rate of fall for subalpine fir was higher than that of Engelmann spruce. Veblen (1986) notes the greater stability of Engelmann spruce leads to its long-term presence in ESSF forests.

Although a certain amount of arboreal lichen in the stand is lost through tree fall, in the short-term it provides a concentrated supply of lichen which is actively sought out by caribou (Rominger & Oldemeyer, 1989; Rominger & Oldemeyer, 1991; Terry *et al.*, 2000; Kinley *et al.*, 2003). This important source of forage should be encouraged by maintaining a high proportion of subalpine fir in the stand, retaining the standing dead where safe during harvesting operations and using long cutting cycles to recruit live and dead lichen bearing trees over time.

Over the ten year study period, partial cutting using any of the opening sizes increased the frequency of a higher abundance rating for arboreal lichen relative to the no-harvest treatment ($P=0.03$). Therefore, losses through in situ decomposition, fragmentation and foraging are being exceeded by growth rate gains to a greater extent in the partial cut treatments. Using the same lichen estimation technique, Coxson *et al.* (2003) found no differences in lichen loading two years post-harvest among no-harvest, single tree and group selection (30% cut) treatments on one site in the Cariboo Mountains to the northeast of our study site. Rominger *et al.* (1994) reported no difference in quantity of lichen on branches taken from two pairs of partial cuts and no-harvest blocks, 8 -10 years after cutting. In *Picea abies* dominated Scandinavian forest, Esseen & Renhorn (1998) reported wind scouring of *Alectoria sarmentosa* up to two tree lengths from newly created edges. At distances of 20-30 m from edges the lichen biomass recovered and ultimately reached higher levels of abundance than those in forest interior sites. Greater post-harvest light exposure while being protected from the winds at the immediate edge may explain this increase (Esseen & Renhorn, 1998). Coxson *et al.* (2003) reported higher light levels in the group selection treatment compared to uncut forest. This may also explain the trend we recorded of increased frequency of higher lichen ratings in our partial cutting relative to the uncut forest. The edge effect was also expected to be greater in the boreal forest study where harvest openings were much larger (Esseen & Renhorn, 1998) allowing greater wind fetch resulting in further wind penetration into the uncut forest.

In addition to light availability, lichens are sensitive to wetting and drying cycles (Kershaw, 1985) and degree of ventilation in the stand (Goward & Campbell, 2005). In our study, Stathers *et al.* (2001) measured canopy wetness, relative humidity and air temperature (1.5 m above ground) in one opening of each size (0.03 ha, 0.13 ha and 1.0 ha) and the no-harvest treatment on the Blackbear winter block. These variables were very similar among treatments so were considered to be a function of the overlying air mass. In a more refined study, Coxson *et al.* (2003) measured lichen thallus temperature and hydration and found the cumulative duration of thallus hydration (required for photosynthetic activity) to be greater in the uncut forest than in a group selection treatment (especially on south aspect branches). This finding was supported in a companion study (Stevenson & Coxson, 2003) that found growth rates of *A. sarmentosa* and *Bryoria fuscenscens* were higher in a no-harvest treatment compared to the edges of a group selection cut. If this trend is happening on our study area, the effect must be spatially limited and not reflective of the entire residual stand. It is possible that the group selection treatments have increased the overall ventilation of the stands enabling species of *Bryoria* normally occurring higher in the canopy to colonize and grow in the lower portions of the canopy (Goward & Campbell, 2005).

Coxson *et al.* (2003) hypothesize that the lichen community could shift on the group selection edges to greater abundance of *Bryoria* and reduction in *Alectoria* over a longer period of time. Studies by Rominger *et al.* (1994) and Stevenson (2001) suggest a possible shift to *Bryoria* in partially harvested stands. Our findings are consistent with this hypothesis. After ten years, we found, based on samples throughout the residual forest, a marginally significant difference among treatments ($P=0.10$), with partial cutting treatments showing a greater likelihood of an increase in the proportion of *Bryoria* than the no-harvest treatment ($P=0.04$).

Terry *et al.* (2000) studied winter habitat selection by mountain caribou including foraging strategies. They concluded that 400-500 stems ha-1 should be maintained in managed forests to provide adequate lichen forage. The stem density in the residual forest (Steen *et al.*, 2005) after the first entry in our low volume removal group selection meets this recommendation and in time more lichen bearing trees will recruit as the openings regenerate. Also, the lichen bearing capacity of the residual forest has not been negatively affected by any of the partial cutting treatments. Therefore, application of group selection silvicultural systems on long cutting cycles (80 years) and with low levels of removal (30%) as tested in this study and recommended for 'modified harvesting' areas (Youds *et al.*, 2000) should maintain enough lichen for foraging caribou.

Removal of one-third of the forest, even if tempered by increased abundance in the residual portion, may diminish the attractiveness of the habitat for caribou. This concern fostered development of an adaptive management trial, involving a 1200 ha of partial cutting area and a 2000 ha unharvested area, to determine whether caribou would utilize habitat changed by group selection (Armleder *et al.*, 2002). Providing lichen bearing habitat meets just one of the needs of caribou. Other potentially adverse factors that need to be managed include: habitat fragmentation in conjunction with creation of early seral range for other ungulate species (Seip, 1992), predation (Bergerud *et al.*, 1984; Bergerud & Elliot, 1986; Seip, 1992) and motorized winter recreation (Kinley, 2003; Powell, 2004). Some of these factors are inter-related. For example, while partial cutting may retain sufficient forage lichen, the access created by timber harvesting could lead to increased snowmobile use and consequently increased detection, encounter and kill rates of caribou by wolves (Powell, 2004). A comprehensive approach that considers all factors and their interactions is essential to maintain and recover the threatened mountain caribou.

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Arboreal forage lichens in partial cuts – a synthesis of research results from British Columbia, Canada

Susan K. Stevenson[*] **& Darwyn S. Coxson**

University of Northern British Columbia,Ecosystem Science and Management Program, 3333 University Way, Prince George, B.C. V2N 4Z9, Canada.
[*]Corresponding author. Address for correspondence: Silvifauna Research, 101 Burden St., Prince George, B.C. V2M 2G8 (sksteven@telus.net).

Abstract: The mountain ecotype of the woodland caribou (*Rangifer tarandus caribou*) is highly dependent on the arboreal hair lichens *Bryoria* spp. and *Alectoria sarmentosa* during winter. In parts of British Columbia, partial-cutting silvicultural systems have been used in an effort to provide continuously usable winter habitat for mountain caribou, while allowing some timber removal. We reviewed available information about the changes in hair lichens after partial cutting in Engelmann spruce (*Picea engelmannii*) – subalpine fir *(Abies lasiocarpa*) forests of British Columbian and Idaho. Generally, abundance of *Bryoria* spp. in the lower canopy of individual residual trees increases with increased exposure after partial cutting, until the new regeneration begins to shelter the lower canopy of the residuals. Heavy basal area removal, however, results in low lichen availability at the stand level for many years. Abundance of *Bryoria* on the regeneration is low, and appears to be limited largely by the structure of the young trees, not by lichen dispersal, although dispersal capability may be limiting in *Alectoria*. Both distributional and physiological data suggest that *Bryoria* is intolerant of prolonged wetting, and that increased ventilation, rather than increased light, accounts for enhanced *Bryoria* abundance in the partial cuts. *Alectoria sarmentosa* reaches its physiological optimum in the lower canopy of unharvested stands; its growth rates are somewhat reduced in the more exposed environment of partial cuts. Both genera are capable of rapid growth: over a 7-year period, individual thalli of *A. sarmentosa* and *Bryoria* spp. (excluding those with a net biomass loss due to fragmentation) in an unlogged stand more than tripled their biomass. Calculated growth rates, as well as dispersal potential, are influenced by fragmentation. *Bryoria* produces more abundant, but smaller, fragments than *Alectoria*, and fragmentation in both genera increases in partial cuts. In subalpine mountain caribou habitat, partial-cutting prescriptions that enhance exposure of residual trees while keeping basal area removal low will maintain forage best. Regeneration management should focus on maintaining ventilation in the lower canopy of the residual stand.

Key words: *Alectoria, Bryoria,* hair lichens, mountain caribou, *Rangifer tarandus caribou*, silvicultural systems.

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Introduction

In British Columbia, Canada, the range of the mountain ecotype of the woodland caribou (*Rangifer tarandus caribou*) is closely associated with the Interior Wetbelt (Stevenson *et al.*, 2001; Apps & McLellan, 2006), an area of high precipitation located on the western slopes of the Rocky Mountains. Mountain caribou spend all or part of the winter in high-elevation subalpine fir (*Abies lasiocarpa*) – Engelmann spruce (*Picea engelmannii*) forests, where they forage almost exclusively on the arboreal hair lichens *Bryoria* spp. and *Alectoria sarmentosa*. Where both genera are available, *Bryoria* is preferred (Rominger *et al.*, 1996). A settled snowpack of 2-4 m increases the caribou's access to the lichens on the lower branches of trees. As well, the caribou remove lichens from freshly fallen trees, and consume lichen litterfall when it is available on top of the snowpack.

Mountain caribou have been red-listed by the British Columbia Conservation Data Centre, and designated as threatened under the Canadian *Species at Risk Act*. Even before they were formally considered to be at risk, the mountain caribou were a species of management concern because of their declining numbers and their apparent sensitivity to resource development and human activity within their range (Stevenson & Hatler, 1985). Clearcut forest harvesting was thought to be incompatible with the conservation of mountain caribou, which were known to be closely associated with old-growth forests. Recommendations for the use of partial cutting, rather than clearcutting, within the range of mountain caribou were developed (Stevenson *et al.*, 1994; 2001), and a number of experimental and operational partial cuts were implemented. These have included group retention, in which trees are removed in patches up to 1 ha, and single-tree retention, in which trees are removed in a dispersed pattern from throughout the harvest block.

Part of the rationale for using partial cutting rather than clearcutting methods in mountain caribou range is that partial-cutting prescriptions can be designed to maintain substantial numbers of lichen-bearing trees, and may provide continuously usable winter habitat for mountain caribou. Partial cutting may affect mountain caribou in many ways: by altering abundance of forage for other ungulates; by altering abundance or efficiency of predators; by increasing road access and the potential for human disturbance; by modifying snowpack characteristics; and by changing the amount of available forage for the caribou. This paper addresses only the question of how partial cutting affects the abundance and dynamics of the hair lichens *Bryoria* spp. and *Alectoria sarmentosa*.

Partial cutting results in immediate loss of the lichen substrate on felled trees. It creates growing space for new regeneration, and over time, increasing amounts of substrate on young trees become available. The residual trees are exposed to a different microclimatic regime, characterized by greater insolation, more wind exposure, lower humidity, and more exposure to precipitation. Hair lichens in subalpine spruce-fir stands exhibit a marked vertical zonation, with *Bryoria* peaking in abundance in the mid to upper canopy, and *Alectoria sarmentosa* reaching its greatest abundance in the lower canopy (Campbell & Coxson, 2001). For some time after partial cutting, the light environment in the canopy of the residual stand resembles that in the mid canopy of an unlogged stand (Coxson *et al.*, 2003), but as the regeneration develops it will begin to shade the lower branches of the residuals. As well, partial cutting, like any forest harvesting, alters the spatial relationships among trees, increasing the distance between large old residual trees and the new regeneration. These changes in spatial relationships raise the question of the effectiveness of dispersal in promoting the colonization of the new regeneration by lichens.

The objective of this paper is to synthesize what is known about the changes in hair lichens (*Bryoria* spp. and *Alectoria sarmentosa*) after partial cutting in subalpine fir-spruce forests of British Columbia and adjacent Idaho. We review studies of lichen abundance at the tree level and at the stand level in mountain caribou habitat after partial cutting, and studies of the dispersal capability of *Bryoria* spp. and *Alectoria sarmentosa*. We then draw on studies of the physiology and growth rates of these lichens to try to elucidate the mechanisms that might explain the abundance patterns that have been observed. We conclude with the implications of our findings to the management of partial cuts in mountain caribou habitat.

Abundance of hair lichens on residual trees after partial cutting

The impact of partial cutting on the abundance and genus composition of arboreal lichens is expected to change over time. The first partial cuts in mountain caribou habitat that have been consistently monitored were established in the early 1990s. In some parts of the range of mountain caribou, however, partial cuts dating back to the late 1960s have been examined in retrospective studies. We reviewed both types of studies to evaluate long-term patterns in the abundance and genus composition of arboreal forage lichens. All studies but one used the photo guide of Armleder *et al.* (1992) to classify each tree into a lichen abundance class, using photographs of trees with known quantities of lichen below 4.5 m for reference. The study of Rominger *et al.* (1994) was based on biomass sampling in the 2- to 6-m range.

Rominger *et al.* (1994) found no difference between tree-level lichen abundance in partial cuts and unlogged stands in two study areas (Table 1). In northeastern Washington, estimated lichen abundance at the tree level declined between 7 and 15 years after partial cutting; this decline may have been due a windstorm that resulted in significant blowdown in the study area (T. Layser, Idaho Panhandle National Forests, pers. comm., 29 March 2006). All other studies (Table 1) reported an increase in forage lichen abundance in the lower canopy of individual trees after partial cutting.

The studies were consistent in reporting an increase in the proportion of total forage lichens composed of *Bryoria* spp. Based on a retrospective study of 26 partial cuts and 37 unlogged stands, Lewis (2004) reported that in partial cuts, tree-level *Bryoria* biomass increased rapidly for the first 20 years, then appeared to stabilize. The rate of *Bryoria* accumulation on residual trees was greatest in partial cuts with low levels of green tree retention (basal area <10 m^2/ha).

Alectoria biomass increased linearly with increasing basal area of the residual stand, regardless of time since logging. The proportion of total forage lichens composed of *Alectoria* decreased with time since logging to about 20 years, then showed a slight increase in partial cuts older than about 30 years, especially the ones with higher basal area (>20 m^2/ha). This shift in genus composition in the oldest partial cuts probably occurred because tree growth was beginning to alter the lower canopy environment to favor development of *Alectoria.* The findings of Lewis (2004), in combination with the other studies (Table 1), strongly suggest that the increased exposure associated with partial cutting promotes the growth of *Bryoria* on the residual trees, at least for the first 30 years. *Alectoria* remains present on residual trees in the partial cuts, but does not appear to benefit from the increased exposure.

Table 1. Summary of effects of partial cutting on abundance and genus composition of arboreal forage lichens on residual trees.

Reference; local population[1]	Partial cuts	Unlogged comparison	Time since harvest	Tree-level effect on lichen abundance	Tree-level effect on genus composition
Delong *et al.*, 1999; South Selkirks	15 operational bark beetle salvage blocks	known caribou foraging areas in Revelstoke and N. Cariboo Mtns.	14-23 years	Significantly more trees with high lichen abundance in partial cuts	Significantly more trees dominated by Bryoria rather than Alectoria in partial cuts
Rominger *et al.*, 1994; South Selkirks and adjacent Idaho	1 high-volume removal cut (density 33% of unlogged stand and 1 low-volume removal cut (density 81% of unlogged stand)	adjacent stands	12-15 years	No difference between partial cuts and unlogged stands	Slightly higher proportion of Bryoria in partial cuts
Stevenson, 2001 and unpubl. data; North Cariboo Mtns.	1 block with dispersed retention ranging from 51-31% of initial basal area	adjacent stand	measured in Years 0, 4, 8, & 13	Decrease in Year 4 followed by increase	Percent Bryoria increased
Lewis, 2004; Wells Gray South	26 partial cuts with various levels of dispersed retention	37 unlogged stands of various ages	0-38 years	Lichen biomass increased after logging due to increased rate of Bryoria accumulation.	Percent Bryoria increased with time since logging to about 20 years, then decreased slightly in the oldest partial cuts
Waterhouse *et al.*, 2007; Wells Gray North	4 replicates; group selection harvesting w/ 3 opening sizes; 30% volume removal	adjacent stands	10 years	More trees in partial cuts than uncut stands shifted toward higher lichen classes	Slightly higher proportion of Bryoria in partial cuts
Layser, unpubl. data[2]; NE Washington	1 block w/40% crown closure retention	adjacent stand	measured after 7 & 15 years	Apparent loss between Years 7 and 15; may have been due to major windthrow event	Percent Bryoria increased

[1] Local populations as defined by Mountain Caribou Technical Advisory Committee (2002).

[2] T. Layser, Idaho Panhandle National Forests, pers. comm., 29 March 2006.

Effects of partial cutting on forage lichen biomass at the stand level may differ substantially from effects at the tree level. DeLong *et al.* (1999) found that the average density of trees >12.5 cm dbh in the partial cuts they studied was 50-60% lower than the density in known mountain caribou foraging areas. They concluded that the partial cutting maintained suitable trees, but perhaps not enough of them to maintain suitable habitat. Lewis (2004) reported that stand-level lichen biomass was low (<12 kg/ha) in older partial cuts with basal area <10 m^2/ha, even though tree-level lichen biomass was high. Older partial cuts with basal area >15 m^2/ha supported up to 10 times as much stand-level biomass, sometimes exceeding that in unlogged stands, even though stem density was lower.

Abundance of hair lichens on young trees after partial cutting

Most of the available forage lichen biomass in partial cuts is present on the residual trees, not on the trees that have regenerated after harvesting. Although few studies have documented lichen biomass on young trees in partial cuts, research from a variety of forest types has documented low biomass of hair lichens in young stands in general (McCune, 1993; Price & Hochachka, 2001; Campbell & Fredeen, 2004). Within mountain caribou range, Lewis (2004) reported that biomass of both *Bryoria* and *Alectoria* was low in stands younger than 50 years and the proportion of the biomass composed of *Alectoria* decreased as stand age decreased. Seventy-five years after wildfire, hair lichen biomass in a regenerating Engelmann spruce-subalpine fir stand was low compared to old-growth stands, and *A. sarmentosa* was particularly sparse (Goward & Campbell, 2005). In a western larch seed tree block, none of the 20- to 40-year-old trees sampled by Bunnell *et al.* (2007) reached Lichen Abundance Class 3 of Armleder *et al.* (1992), the threshold for potential caribou feeding sites identified by field researchers (Stevenson *et al.*, 1998).

There has been considerable discussion in the literature of the extent to which the low abundance of hair lichens in young stands is attributable to dispersal limitations, to slow growth rates, to microclimatic variables, or to structural limitations of young trees (e.g., Esseen *et al.*, 1996; Peck & McCune, 1997; Peterson & McCune, 2001; Goward & Campbell, 2005). Dispersal studies in a variety of locations have consistently shown that *Bryoria* spp. disperse more effectively than *Alectoria sarmentosa* (Stevenson, 1988; Dettki, 1998; Dettki *et al.*, 2000; Quesnel & Waters, 2001; Stevenson & Coxson, 2003). Within mountain caribou range, Goward (2003) reported that *Bryoria* fragment densities on snow in subalpine meadows were greatest near the forest edge but still substantial at 1 and 2 km from the edge. In a larch stand in the East Kootenay region of British Columbia, abundance of *Bryoria* spp. on the regenerating trees was not associated with proximity to the larch seed trees (Bunnell *et al.*, 2007). It appears that, at least at the scale of a partial cut, dispersal does not limit the colonization of regeneration by *Bryoria* spp. in high-elevation mountain caribou range.

There is more evidence for dispersal as a limiting factor for *A. sarmentosa*. In addition to studies cited above that showed limited dispersal distances of *A. sarmentosa*, abundance of *A. sarmentosa* in managed stands has been associated with the presence of remnant old trees (Neitlich & McCune, 1997; Peterson & McCune, 2001). The limited dispersal capability of *A. sarmentosa* is probably associated with both large fragment size and, in many forest types, its characteristic location in the lower canopy that results in a low release height of fragments.

There is mounting evidence that the abundance of *Bryoria* spp. in young stands is limited primarily by the structural attributes of young trees. Goward (1998) hypothesized, based on the distributional patterns of *Bryoria* spp. in Engelmann spruce-subalpine fir forests, that *Bryoria* is intolerant of prolonged wetting, especially as a result of snowmelt. He observed that *Bryoria* biomass is invariably much greater on defoliated portions of branches than in the foliated zone, except where foliated branches are exposed to high ventilation. He ascribed the low abundance of *Bryoria* on foliated branch portions primarily to greater accumulation and retention of snow, resulting in prolonged wetting and periodic dieback of *Bryoria*. *Bryoria* does not become abundant until trees are old enough – usually 100-150 years – to develop a substantial defoliated zone. In their study of a regenerating stand 75 years after wildfire, Goward & Campbell (2005) attributed the low *Bryoria* biomass in the upper canopy to substrate limitations – the availability of defoliated branches and the stable environmental conditions that develop once crown growth has slowed. They attributed the low *Bryoria* biomass in the lower canopy (above the snowpack) to sheltered conditions producing humidity levels that are too high for many *Bryoria* species.

Physiology and growth rates of hair lichens

The studies of hair lichen abundance in high-elevation mountain caribou range discussed in the previous sections revealed that *Alectoria sarmentosa* is often abundant in the lower canopy of old stands, and sparse or absent in the upper canopy. It remains present on residual trees after partial cutting, but does not exhibit a conspicuous increase in biomass. It is extremely sparse or absent on young regeneration after partial cutting.

These studies also showed that *Bryoria* spp. are present throughout the canopy in old Engelmann spruce-subalpine fir stands, but reach their highest abundance in the mid to upper canopy. After partial cutting, the abundance of *Bryoria* on residual trees increases. *Bryoria* spp. are consistently present on regenerating trees in young stands and partial cuts, but do not attain high biomass until later in stand development. The distribution pattern of *Bryoria* spp. suggests that many species do not tolerate prolonged wetting, and are excluded from locations that are poorly ventilated or subject to prolonged hydration.

Studies of the physiology and growth rates of lichens can help to elucidate the mechanisms behind observed patterns of abundance. Coxson & Coyle (2003) examined the hypothesis that height-related niche partitioning of *Alectoria* and *Bryoria* reflects differential growth responses to gradients in canopy microclimate. If that hypothesis was supported, it would also help to explain changes in abundance patterns in partial cuts, where increased exposure alters the canopy microclimate profile. Coxson & Coyle (2003) measured microclimate variables at two heights in an old Engelmann spruce-subalpine fir stand: at 4 m, in the zone where *A. sarmentosa* is abundant, and at 15 m, in the lower portion of the zone dominated by *Bryoria* spp. In the laboratory, they measured photosynthetic and respiratory activity of *A. sarmentosa* and *Bryoria* spp. at a range of temperatures, moisture levels, and light intensities. Combining the two data sets, they estimated net assimilation by month for *A. sarmentosa* and *Bryoria* spp. at the 4- and 15-m level over a 20-month period.

Both genera were capable of maintaining positive net assimilation during most of the year, experiencing negative assimilation only during early winter (Fig. 1). Lichen thalli were hydrated from snowmelt events 26-29% of the time during the winter, though 75% of the time hydration occurred in the dark. During summer, the lichens were hydrated by rainfall 16% of the time, 45% of this in the dark. During both winter and summer, the single largest limitation on net assimilation in both genera was thallus moisture content (Coxson & Coyle, 2003). *A. sarmentosa* showed consistently higher rates of net assimilation at 4 m than at 12 m. These results would predict reduced biomass accumulation in upper canopy positions, though perhaps not as abrupt a decline as is observed in the field. This may reflect the relatively small gradients in moisture availability observed with height in the canopy profile, due to the quite open canopy structure in ESSF. Other factors, such as breakage of the long, relatively heavy thalli of *A. sarmentosa* when subjected to loads of ice or snow, may be more important in excluding *Alectoria* from the upper canopy positions in these high-snowfall ecosystems.

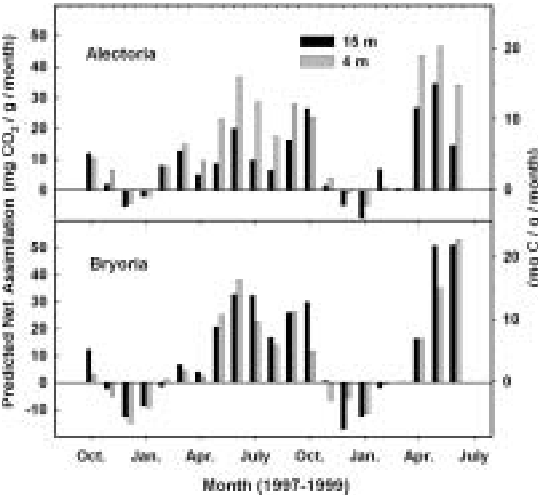

Fig. 1. Predicted net assimilation (mg $CO_2 \cdot g^{-1} \cdot month^{-1}$ and mg $C^{-1} \cdot g^{-1} \cdot month^{-1}$) in *Alectoria sarmentosa* and *Bryoria* spp. (*B. fremontii* and *B. fuscescens*) at heights of 4 and 15 m within the canopy. Measurements are for the period October 1997 to June 1999 (reproduced from Coxson & Coyle, 2003).

In contrast, Coxson & Coyle (2003) found no consistent relationship between canopy position and net assimilation for *Bryoria* spp Their results predict that *Bryoria* would occur with equal abundance in upper and lower canopy positions. As that is not the case, Coxson & Coyle (2003) also examined the possibility that some *Bryoria* spp. are excluded from the lower canopy by their response to prolonged wetting. They measured rates of gas exchange of thalli of *Bryoria* spp. and *A. sarmentosa* that were kept fully saturated for 12 days. Although rates of net photosynthesis of saturated thalli declined over time in both genera (Fig. 2), *Bryoria* spp. showed a more abrupt decline after six days of continuous hydration, whereas *A. sarmentosa* declined more gradually. It should be noted that this decline appears mainly to be one of the algal biont's physiological response, as rates of dark respiration (predominantly from the fungal biont) show little change over this time period. These results, though not conclusive, tend to support Goward's (1998) hypothesis that some *Bryoria* species do not persist in canopy positions where they experience prolonged wetting, either from summer rainfall events or from wet snowpack held on branches within the canopy. Although a more open stand structure will most immediately reduce the duration of periods when lichens can grow, with evaporation rates increasing as exposure to wind and solar insolation increase, these same trends will limit respiratory loss of lichen biomass during extended wetting events (and subsequent dieback events). Further, the sloughing of accumulated snow from canopy branches during high wind gusts may reduce *in-situ* decomposition of thalli within lower canopy positions.

It is reasonable to expect that differences in net assimilation will be reflected in the growth rates of individual lichen thalli. On the basis of physiological studies, we would predict higher growth rates for *Alectoria* in sheltered locations, such as the lower canopy or a more closed stand, than in exposed locations, such as the upper canopy or a more open stand. Physiological studies do not suggest any difference in *Bryoria* growth rates between more sheltered and more exposed locations, although there does appear to be a physiological basis for the exclusion of *Bryoria* from sheltered locations. The lichen abundance studies, however, suggest that individual thalli of *Bryoria* might grow faster in more exposed locations.

Growth rates of individual lichen thalli

At three silvicultural systems study areas in Engelmann spruce-subalpine fir stands (Table 2), we have measured growth rates of arboreal lichens by repeatedly weighing lichen thalli that were attached to an artificial substrate and grown in the field. Although methods varied slightly among study areas, the general approach was the same: we weighed composite samples of 2-4 individual specimens of either *Alectoria sarmentosa* or *Bryoria* spp. in a laboratory in which temperature and humidity were controlled, and then attached the samples to glass tubes with silicone seal. After the silicone seal dried, we reweighed the lichen/tube assemblies, fitted them into mesh-covered enclosures, and suspended them from the branches of trees. In spring and fall of each year, we reweighed the lichen/tube assemblies and returned them to the field. Lichen fragments found on the floor of the enclosure were weighed and discarded, but some loss of sample fragments as well as gain of non-sample fragments occurred. These methods were described in more detail by Stevenson (2001) and Stevenson & Coxson (2003).

In all treatments except the Group Selection treatment (Table 2), the enclosures were placed on randomly selected trees located along transects. In the Group Selection treatment at Pinkerton CP377, enclosures were placed on randomly selected trees along the edges of the openings (Stevenson & Coxson 2003).

We expressed the results of these three studies as relative growth (RG) over the entire measurement period (Fig. 3), or

$$RG = (W_2 - W_1)/ W_1 * 100$$

where W_1 is lichen weight at the beginning of the study and W_2 is lichen weight at the end of the study. Thus, relative growth of 100% indicates that the

Table 2. Summary of lichen growth rate study areas

Study area	References	Monitoring period	Treatments	Treatment description	Number of growth rate samples
Pinkerton CP 376	Stevenson *et al*., 2001; S. Stevenson, unpubl. data	1992-1994	Single-tree selection (STS)	61% basal area removal with dispersed retention	17 Bryoria 16 Alectoria
			Unlogged control (UN)		19 Bryoria 19 Alectoria
Lucille Mountain	Stevenson, 2001; S. Stevenson, unpubl. data	1993-2000	Irregular shelterwood (ISW)	50% basal area removal with dispersed retention	11 Bryoria 12 Alectoria
			Group retention (GR)	69% basal area removal with clumped retention	13 Bryoria 14 Alectoria
			Unlogged control (UN)		17 Bryoria 16 Alectoria
Pinkerton CP 377	Stevenson & Coxson, 2003	1999-2000	Single-tree selection (STS)	30% basal area removal with dispersed retention	39 Bryoria 46 Alectoria
			Group selection (GS)	30% basal area removal in openings of 0.1-0.4 ha	36 Bryoria 32 Alectoria
			Unlogged control (UN)		41 Bryoria 39 Alectoria

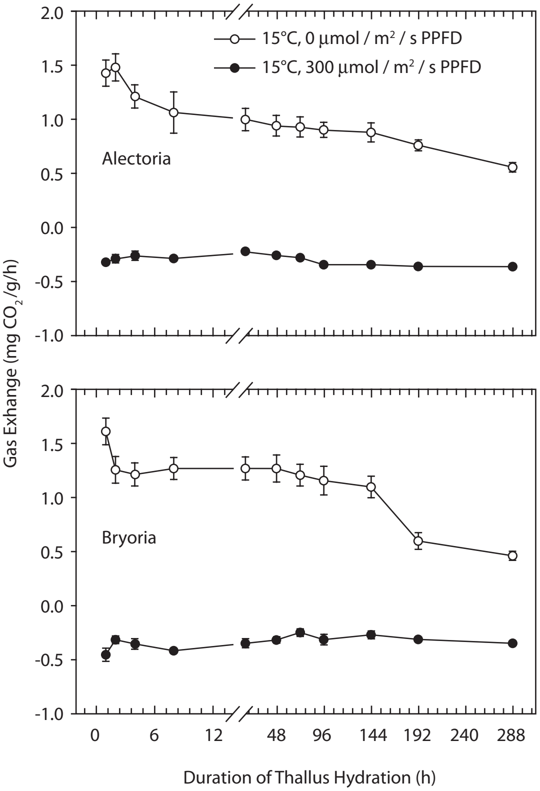

Fig. 2. Mean rates of gas exchange (mg $CO_2 \cdot g^{-1} \cdot h^{-1}$) in summer-collected thalli of *Alectoria sarmentosa* and *Bryoria* spp. held at full thallus saturation for up to 288 h. Gas exchange measurements took place at 15ºC, and each of 0 and 300 µmol · $g^{-1} \cdot m^{-2} \cdot s^{-1}$ photosynthetic photon flux density (PPFD) (reproduced from Coxson & Coyle, 2003).

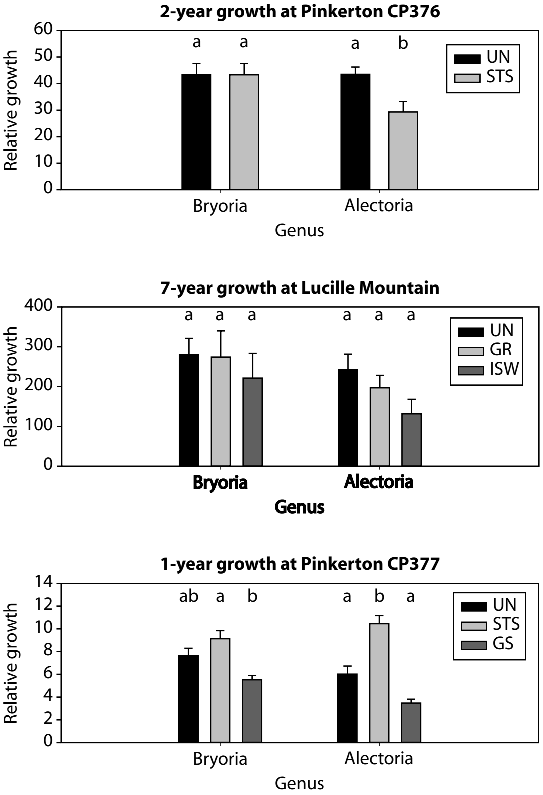

Fig. 3. Relative growth (per cent) and standard error of *Bryoria* spp. and *Alectoria sarmentosa* thalli at three silvicultural systems study areas: Pinkerton CP376 (adapted from Stevenson *et al.*, 2001), Lucille Mountain (S. Stevenson, unpubl. data; methods in Stevenson, 2001), and Pinkerton CP377 (adapted from Stevenson & Coxson, 2003). Within species, means sharing the same letter were not significantly different (*P* >0.05; Bonferroni adjustment for multiple comparisons).

thalli doubled their mass; the relative growth rates of approximately 250% observed in the unlogged treatment unit at Lucille Mountain indicate that the thalli more than tripled their mass over a 7-year period. Thalli that failed to gain mass during the study period – generally because of mortality, loss of large fragments, or damage to the enclosures – are excluded; the resulting sample sizes are shown in Table 2. Data were arcsine transformed for statistical analysis. Significant differences shown in Figure 3 are based on *t*-tests (Pinkerton CP376) and analysis of variance with Bonferroni adjustments for multiple comparisons (Lucille Mountain; Pinkerton CP377).

In general, growth rates of *Alectoria* were lower in the partially cut areas than in the unlogged control areas. At Lucille Mountain, *Alectoria* growth rates appeared to be lower in the more evenly dispersed retention of the irregular shelterwood treatment than in the clumpier retention of the group retention treatment, even though basal area removal was higher in the group retention treatment (Table 2). These trends were not statistically significant at the 0.05 level, perhaps because attrition over the seven-year study period resulted in small sample sizes. The single exception to this pattern occurred in the single-tree selection treatment unit at Pinkerton CP377, which represented the smallest increase in canopy exposure of any of the treatments studied. Thus, the *Alectoria* growth rates observed in the growth rate studies are generally consistent with the physiological studies and with the abundance patterns observed in partial cuts.

On the basis of the lichen abundance studies reviewed above, we would expect that growth rates of individual *Bryoria* thalli would be elevated in partial cuts. Physiology studies, which found no relationship

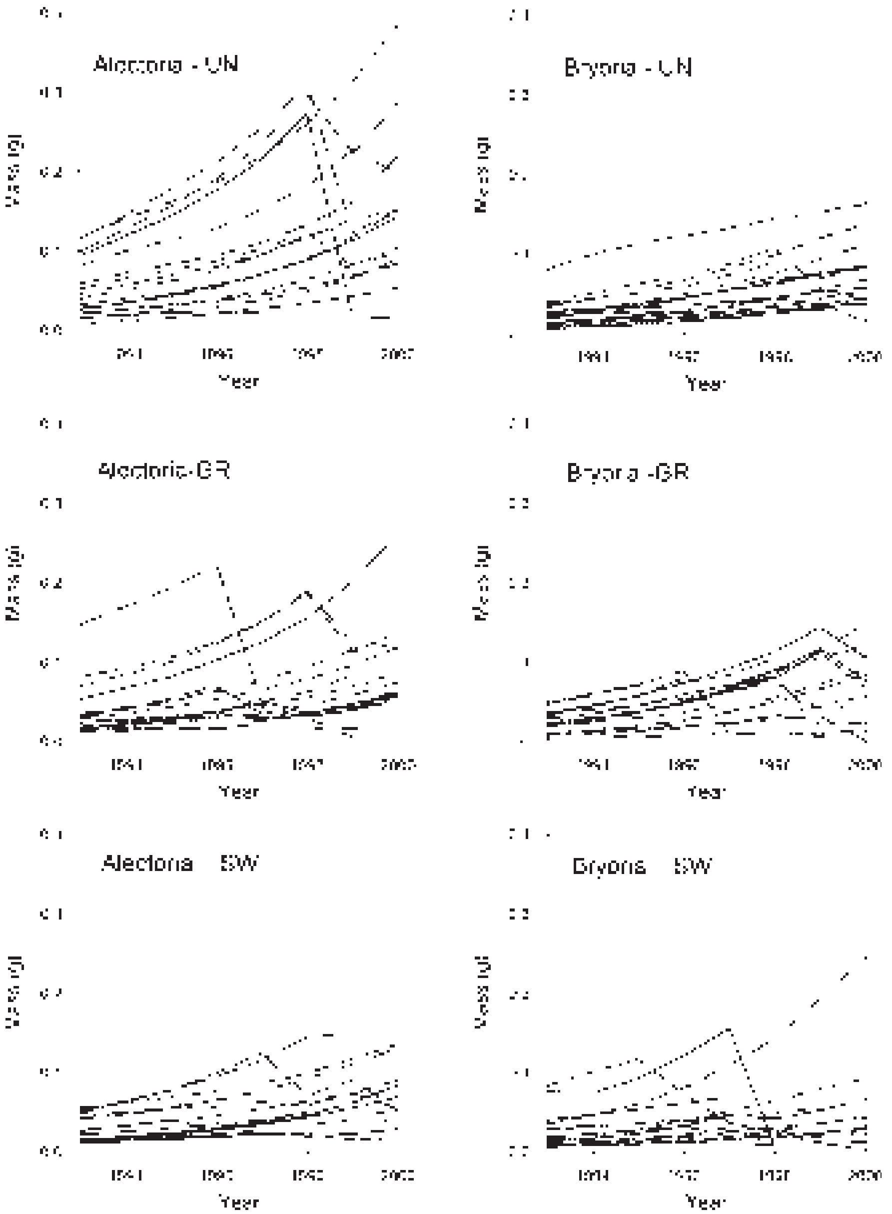

Fig. 4. Mass (g) of individual growth-rate replicates of *Alectoria sarmentosa* and *Bryoria* spp. in the unlogged control area (UN), group retention area (GR), and irregular shelterwood area (ISW) at Lucille Mountain, fall 1993-fall 2000 (S. Stevenson, unpubl. data; methods and site description in Jull & Stevenson, 2001).

between net assimilation in *Bryoria* and canopy position, would predict that growth rates of *Bryoria* in partial cuts would not differ from those in an unlogged stand. Our results (Fig. 3) show few significant differences in *Bryoria* growth rates between the unlogged control areas and the partial cuts. Only on trees at the edges of group selection openings at Pinkerton CP377 were growth rates of *Bryoria* spp. significantly lower than growth rates in the unlogged control area. Stevenson & Coxson (2003) suggested that the reduced growth rates reflected reduced duration of lichen hydration at the edge of the group selection openings, as described by Coxson *et al.* (2003). As well, substantial fragmentation of both *Alectoria* and *Bryoria* growth rate samples was documented at Pinkerton CP377 (Stevenson & Coxson 2003). Although samples that lost biomass were not included in the growth-rate analysis (Fig. 3), calculated growth rates may still have been affected by the loss of smaller fragments.

The role of fragmentation

Changes in the biomass (standing crop) of canopy lichens depend on their net carbon assimilation (growth), but also on several other factors: losses through consumption by herbivores, losses through in situ decomposition, losses through fragmentation, and gains through colonization. Consumption by caribou in these ecosystems is relatively low because there are few caribou, and most of the lichens in the forest canopy are out of their reach. In situ decomposition probably is a significant factor in subalpine forests (Goward, 1998; Stevenson & Coxson, 2003), but it tends to differentially affect lichens in low-exposure habitats. As the growth-rate samples were small clumps isolated within mesh enclosures, they were well ventilated and unlikely to be subject to the dieback described by Goward (1998). Fragmentation, however, is an important factor in the ecology of hair lichens, and is the major source of the propagules that are responsible for colonization.

The seven-year growth rate data set from Lucille Mountain described above (Table 2) allows us to examine biomass accumulation of individual lichen thalli from fall 1993 until fall 2000, or until samples were lost due to enclosure damage or breakage of the entire specimen (Fig. 4). The data reveal a pattern of exponential growth, interrupted by deviations from the pattern. About half of the thalli that experienced a precipitous decline in biomass resumed exponential growth, while the remainder continued to decline. Thalli such as these, which lost large fragments, would have been excluded from the results shown in Fig. 3, because of their net loss of biomass over the 7-year period. Other thalli leveled off or declined slightly in biomass, and then resumed exponential growth. These individuals, which presumably lost smaller fragments, would have been included in the data summarized in Fig. 3. Overall, the results reveal a dynamic system in which fragmentation has a major influence on calculated growth rates.

Fragmentation does not affect calculated growth rates equally, however, in all lichen groups. The tendency of *Alectoria sarmentosa* to produce fewer but larger fragments than *Bryoria* spp. has been documented in several studies (Stevenson, 1988; Renhorn & Esseen, 1995; Dettki, 1998). Using the Lucille Mountain growth rate data set, we calculated the mass of each fragment found on the floor of the enclosure as a percent of the mass of the growth rate sample at the beginning of the measurement period, and graphed the results by 10% intervals. More small fragments of *Bryoria* spp. than *Alectoria* were found in the bottoms of cages (Fig. 5). These results actually understate the effect because the smallest fragments (< about 1% of the mass of the growth rate sample), which were overwhelmingly *Bryoria* spp., were not collected and weighed. As well, fragmentation occurs more commonly in partial cuts than in unlogged stands. Over the course of the Lucille Mountain study, the occurrence of fragments at the bottoms of cages in the partial cuts was about twice that in the unlogged control area (unpublished data).

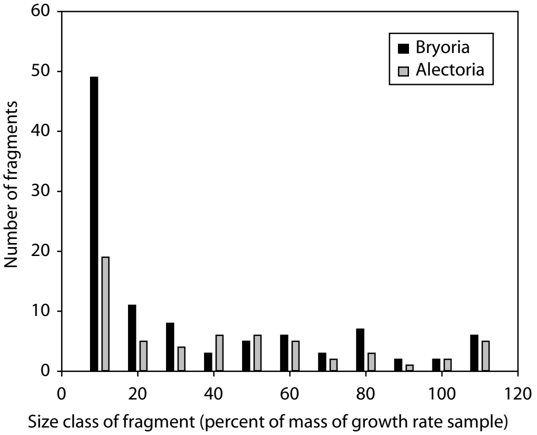

Fig. 5. Size-class distribution of *Bryoria* and *Alectoria* fragments collected from the bottoms of enclosures at Lucille Mountain, 1993-2000. Size classes represent the mass of the fragment as a percentage of the mass of the sample at the beginning of the measurement period (S. Stevenson, unpubl. data; methods in Stevenson, 2001).

We agree with the contention of Goward (1998) that ventilation has an important role in the ecology of *Bryoria* spp. Although a more exposed microclimate does not appear to enhance the capacity of *Bryoria* spp. for net assimilation (at least within the microclimatic range we studied), it probably helps to prevent the dieback phenomenon described by Goward (1998) in less open stands. As well, it increases the amount of substrate available for colonization by *Bryoria*, because increased ventilation enables *Bryoria* to survive on the foliated portions of branches. Finally, we suggest that a windier environment increases fragmentation rates. Although continuous production of small fragments in *Bryoria* may have somewhat reduced calculated growth rates, the dispersal and colonization of copious amounts of small fragments probably enhanced the overall levels of biomass accumulation in partial cuts.

The evaluation of lower canopy environments and their ability to support lichen growth after harvesting can be assessed using measurements of light availability and/or canopy openness from a fish-eye lens or canopy densiometer (see Coxson & Stevenson 2007 for an outline of relevant methodologies). Although it is unlikely that light availability by itself is an important parameter controlling net assimilation in *Alectoria* or *Bryoria* (Coxson & Coyle, 2003), it provides a valuable surrogate for the assessment of convective exchange and associated ventilation of lichen thalli. Vertical profiling of convective exchange within forest stands, using cup- or hot-wire anemometers, provides a more direct assessment of canopy ventilation, though installation costs can be high. Direct measurements of lichen hydration status using impedance measurements may provide the most cost-effective approach for assessing lichen growth environments (Coxson, 1991), though care must be taken to ensure sufficient replication to capture what can be quite high levels of variability between adjacent branches.

Management implications

The development of partial-cutting prescriptions that will maintain adequate availability of forage lichens for mountain caribou in Engelmann spruce-subalpine fir forests requires a balance between increasing the level of exposure of retained trees to enhance tree-level *Bryoria* accumulation, and retaining enough trees that stand-level lichen biomass is adequate. It is now clear that over time, partial cutting not only increases the relative proportion of *Bryoria* to *Alectoria*, but also increases the total amount of forage lichen available on individual trees. Prescriptions that enhance exposure while keeping basal area removal low will maintain forage best. Naturally clumped groups of trees in old stands have been found to support significantly more forage lichens per branch than solitary trees (Campbell & Coxson, 2001), and are prime candidates for retention in partial cutting prescriptions.

Maintaining a continuous supply of forage lichen at the stand level is critical to meet the objective of maintaining large, unfragmented areas of habitat for mountain caribou. Because lichen colonization on regenerating trees is slow – despite abundant propagules for colonization – prescriptions should be designed to maintain adequate lichen biomass at the stand level on residual trees. Stands with high basal area removal may show continued low lichen availability at the stand level over much of the rotation age of the stand. We recommend that managers continue to restrict basal area removal to 30% or less in partial cuts planned to maintain habitat for mountain caribou, as recommended by Stevenson *et al.* (2001).

As the regeneration develops after partial cutting, it begins to reduce ventilation in the lower canopy of residual trees, and if the regeneration is dense, it may trigger dieback of *Bryoria* spp. At this stage, spacing of the regeneration may help maintain lichen availability on the residuals. Planting or spacing prescriptions that encourage a clumped distribution of the regeneration may help maintain ventilation, and also enhance the future ability of the young trees to support forage lichens. Nevertheless, managers who seek to maintain a continuous source of lichen using selection-harvesting systems in mountain caribou range should not expect a second harvest entry in less than 80 years.

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Caribou nursery site habitat characteristics in two northern Ontario parks

Natasha L. Carr[1*], Arthur R. Rodgers[2] & Shannon C. Walshe[1]

[1] Ontario Ministry of Natural Resources, Ontario Parks, Thunder Bay, ON P7E 6S8, Canada (*corresponding author: natasha.carr@ontario.ca).

[2] Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, ON P7B 5E1, Canada.

Abstract: To prevent further range recession, habitat features essential to the life-history requisites of woodland caribou (*Rangifer tarandus caribou*) such as calving and nursery sites need to be protected for the persistence of the species. Woodland caribou may minimize predation risk during calving by either spacing out or spacing away from predators in the forest to calve on islands, wetlands, or shorelines. Our objective was to determine the characteristics of shoreline habitats used as calving and nursery sites by female woodland caribou in northern Ontario. Detailed vegetation and other site characteristics were measured at nursery sites used by cow-calf pairs in Wabakimi and Woodland Caribou Provincial Parks for comparison with shoreline sites that were not used by caribou within each park. Differences in habitat variables selected by female caribou in the two study areas reflect broad ecoregional differences in vegetation and topography. In Wabakimi Provincial Park, understorey tree density and ground detection distance played key roles in distinguishing nursery sites from sites that were not used. In Woodland Caribou Provincial Park, groundcover vegetation and shrub density were important in the selection of nursery sites by female caribou. Generally, female caribou in both parks selected nursery sites with greater slope, lower shrub density but thicker groundcover vegetation, including greater lichen abundance, and higher densities of mature trees than shoreline sites that were not used. The identification of these important features for caribou nursery sites provides a basis for improving their protection in future management policies and legislation.

Key words: calving sites, forest-dwelling woodland caribou, nursery sites, predator avoidance, protected areas, *Rangifer tarandus caribou*, resource selection, Wabakimi Provincial Park, Woodland Caribou Provincial Park.

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Introduction

In Ontario, woodland caribou (*Rangifer tarandus caribou*) range of continuous occupancy has receded further north since the late 1800s (Racey & Armstrong, 2000). This recession is mainly attributed to habitat loss through anthropogenic disturbance and Schaefer (2003) estimates that, at the current rate, forest-dwelling woodland caribou will be extirpated from Ontario in 90 years. Increased predation, especially on calves, may result from habitat alteration and corridor development (e.g., roads, seismic lines) that facilitate ingress and movements of predators and alternative prey (James & Stuart-Smith, 2000). Caribou have evolved space-use strategies to avoid predation (Bergerud *et al.*, 1990; Rettie and Messier, 2001), which is considered the main proximate factor of population limitation of woodland caribou across North America (Bergerud, 1974; Seip, 1992; Ouellet *et al.*, 1996; Stuart-Smith *et al.*, 1997; Rettie & Messier, 1998). When forest disturbance (i.e., timber harvest) takes place, it reduces the available space for caribou, thereby increasing caribou densities elsewhere and forfeiting the advantage of space (Bergerud, 1985; Bergerud & Page, 1987). Predators can kill more than 50% of young ungulates in free-ranging populations (Bergerud, 1971). Ungulates appear to be particularly vulnerable when they are old enough to flush from hiding, but are still too young to outrun predators (Fitzgibbon, 1990). Studies of caribou report that calves are most vulnerable to wolf (*Canis lupus*) (Bergerud & Page, 1987) and black bear (*Ursus americanus*) (Ballard, 1994) predation in their initial weeks of life.

Female woodland caribou have distinct summer and winter ranges (Edmonds, 1988) and exhibit selectivity and fidelity for specific calving and summer ranges (Brown *et al.*, 1986). If islands and shorelines are available, female caribou scatter to these relatively safe habitats to calve (Bergerud, 1985). Woodland caribou may spatially separate themselves from other ungulates that provide prey for wolves and bears, such as moose, by using lakeshores and islands (Bergerud, 1985; Cumming & Beange, 1987) or bog complexes (Valkenburg *et al.*, 1996; Stuart-Smith *et al.*, 1997) to calve in the spring.

Ferguson & Elkie (2004) suggest that fine-scale attributes of preferred caribou calving and nursery sites, such as those found along shorelines, need to be examined further in Ontario. Disturbances caused by landscape exploitation surrounding parks and protected areas (e.g., forestry activities) and human recreational activities (e.g., outpost camps, shore lunch areas, camping) both outside and within protected area boundaries, may prevent female caribou from returning to previously used calving sites on shorelines or in bog complexes. As a result, female caribou may be forced to use less suitable habitats, which can lead to greater predation and reduced population viability. To ensure caribou persistence across northern Ontario and impede further range recession, it is critical to identify potential nursery sites and ensure that adequate protection is given to these sites (Morrill *et al.*, 2005).

We describe fine-scale habitat characteristics of caribou nursery sites in two protected areas, not directly disturbed by forestry activity, to provide baseline information that may be used to predict locations of potential caribou nursery sites both outside and within protected area boundaries across northern Ontario. Vegetation and topographic characteristics were measured at nursery sites along shorelines used by cow-calf pairs in Wabakimi and Woodland Caribou Provincial Parks for comparison with shoreline sites that were not used by caribou within each park. These surveys focused on lakes, rather than bog complexes, because of the high recreational use of these areas and the known importance of these types of areas to caribou cow-calf pairs (Bergerud, 1985; Cumming & Beange, 1987). Important characteristics were used to develop and evaluate Resource Selection Functions (Boyce *et al.*, 2002; Manly *et al.*, 2002) for calving woodland caribou in northern Ontario. Critical habitat characteristics selected at nursery sites were hypothesized to reflect predator avoidance strategies and thus their protection in future management policies and legislation would have the greatest impact on population persistence.

Study areas

Wabakimi Provincial Park

This park is located in northern Ontario about 200 km north of Thunder Bay (Fig. 1). In 1983, Wabakimi Provincial Park was established at 155 000 ha in size and in 1997, the park was expanded to roughly 892 000 ha (Duinker *et al.*, 1996). The average July temperature in Wabakimi Provincial Park is 16 °C, while the average January temperature is -17 to -20 °C (Chapman & Thomas, 1968). Total annual precipitation is approximately 750 mm, which is considered moderate relative to other parts of the province, with approximately two-thirds falling from May to September (Chapman & Thomas, 1968). Tree species (Harris & Foster, 2005) include white spruce (*Picea glauca*), black spruce (*Picea mariana)*, jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), white pine (*Pinus strobus*), and red pine (*Pinus resinosa*). Mosses are a conspicuous cover over much of the forest floor, while patches of ground lichen (*Cladina* spp.) are common on jack pine-dominated sand flats and under open spruce stands on bedrock (Harris & Foster, 2005). The fire regime of this ecoregion is characterized by numerous small fires (<1040 ha) and few large fires (>5000 ha), but most of the total area burned is in large, intense fires (Beverly, 1998). Beverly (1998) found that the total area burned in the park decreased steadily from the 1930s to the 1960s but increased in the 1990s. The estimated fire cycle range for Wabakimi Provincial Park is 65-250 years (Ride *et al.*, 2004).

Woodland Caribou Provincial Park

Woodland Caribou Provincial Park is 450 000 ha in size and is located between Red Lake and the Manitoba border in northwestern Ontario, about 500 km northwest of Thunder Bay (Fig. 1). The average July temperature in Woodland Caribou Provincial Park is 18.4 °C while the average January temperature is -20.4 °C (OMNR, 2004). Average annual precipitation is approximately 609 mm; the second lowest in Ontario (Brunton, 1986). Approximately two-thirds of the total precipitation falls from May to September (OMNR, 2004). Vegetation of the area consists of typical boreal tree species such as jack pine, black spruce, balsam fir, and trembling aspen dominating

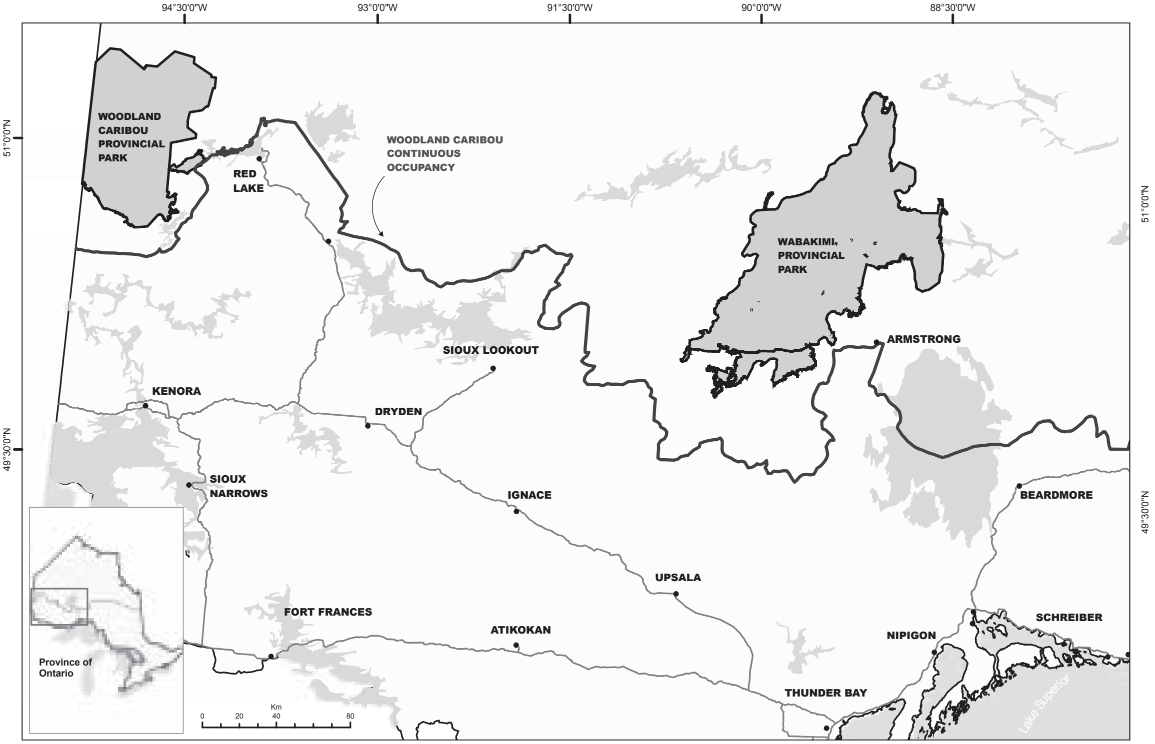

Fig. 1. Locations of Wabakimi and Woodland Caribou Provincial Parks in relation to the southern limit of continuous range occupancy of woodland caribou (*Rangifer tarandus caribou*) in northern Ontario.

upland sites, with black spruce and larch (*Larix laricina*) characterizing the wet, organic deposits commonly found in bedrock depressions (OMNR, 2004). The park is situated on a relatively flat plateau and soils are thin when present at all (Brunton, 1986). The slightly elevated position of the park area has resulted in a greater than normal incidence of dry upland forest, so jack pine is more dominant than black spruce (Brunton, 1986). Ground lichen is dominant in older jack pine forests and a dense ground cover of feather moss is common in black spruce forests (Brunton, 1986). This park is significantly affected by its proximity to the Prairie Provinces, resulting in a dry, hot growing season creating "boreal prairie" forests that experience a greater frequency of naturally occurring forest fires, in contrast with the more moist boreal forests further east (OMNR, 2004). The wilderness landscapes of this park have been strongly influenced by wildfire (Harris *et al.*, 2001). Brunton (1986) noted that most of the park had been burned between 1956 and 1986 and frequent and repeated burns appear to be representative of the area's natural cycle of burning since deglaciation. The estimated fire cycle range for Woodland Caribou Provincial Park is 40-110 years (Ride *et al.*, 2004).

Methods

Study sites

Caribou calves are generally born between the last week of May and first week of June in northern Ontario (Bergerud, 1975; Ferguson & Elkie, 2004). Based on systematic surveys (Timmermann, 1998) and anecdotal observations of caribou cow-calf activity in late May and early June in previous years, lakes ranging in size from 127 ha to 11 420 ha were selected for detailed study within each park; 4 lakes in Wabakimi Provincial Park (mean size 6 828 ha) and 10 lakes in Woodland Caribou Provincial Park (mean size 1193 ha). Systematic transect surveys for physical evidence (i.e., calf beds, pellets or tracks) of use (Timmermann, 1998) were then applied to identify nursery and "absence" sites associated with these lakes.

Calving sites are generally taken to be locations at which parturition occurs, whereas nursery sites are areas occupied by cow-calf pairs during the post-partum period (Lent, 1974; Addison *et al.*, 1990; Schaefer *et al.*, 2000). Calving and nursery sites cannot be readily distinguished from one another by physical evidence in transect surveys, and direct observations of parturition or cow-calf pairs were not made in this study. Therefore, all cow-calf sites identified in this study were classified as nursery sites, even

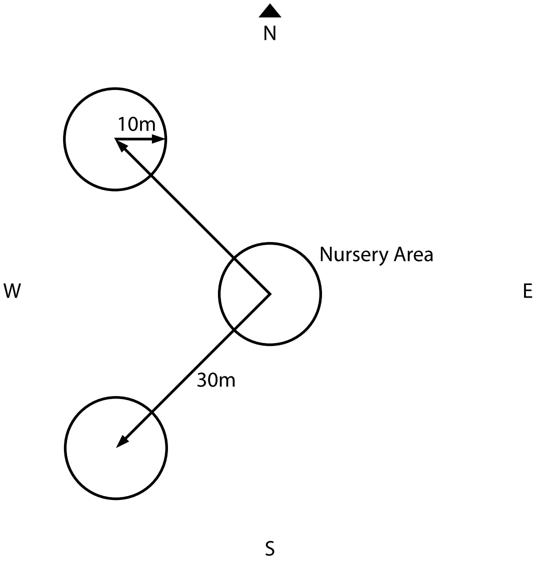

Fig. 2. Schematic of the three 10 m-radius sampling plots used to collect detailed vegetation data and other site characteristics at caribou nursery sites and randomly chosen absence sites on lakes in Wabakimi and Woodland Caribou Provincial Parks, northern Ontario.

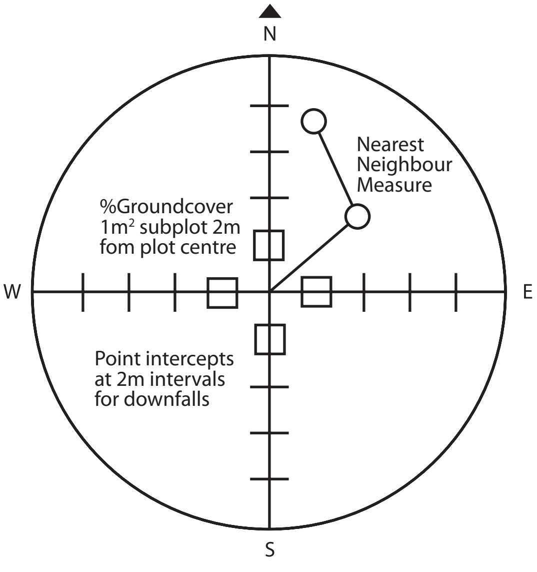

Fig. 3. Schematic of detailed vegetation measurements made within 10 m-radius sampling plots at caribou nursery sites and randomly chosen absence sites on lakes in Wabakimi and Woodland Caribou Provincial Parks, northern Ontario.

though birthing activity may have taken place as well. Absence sites were defined as areas with no physical evidence of use by caribou.

To limit the potential effects of human disturbance on the behaviour of calving caribou or physical disruption of nursery sites (e.g., by walking systematic transects, using motorboats, canoeing), surveys started in the middle of June each year (2001-2003) and most finished by the end of July. Along the shorelines of lakes and islands larger than 500 m in width or length, 100 m transects perpendicular to the shoreline were set every 1-2 km and surveyed for physical evidence of use (Timmermann, 1998). Islands less than 500 m in width or length were surveyed for nursery sites by walking transects, set perpendicular to the shoreline at 1 km intervals, across the entire island. Island and mainland transects were re-surveyed in subsequent years to determine whether or not nursery sites were used in the second and third year of the study. Absence sites were then identified as transects that were surveyed in at least two consecutive years without finding any physical evidence of caribou activity.

The transect surveys resulted in the identification of numerous nursery and absence sites from which 15 nursery sites in each park were selected for site measurements on the basis of accessibility. Fifteen absence sites in each park, on the same lakes as the nursery sites, were selected at random for comparisons.

Site measurements

Detailed vegetation data and other site characteristics were collected at three 10 m-radius plots established at each nursery site and each randomly chosen absence site (Fig. 2). Table 1 provides a list of the interval scale variables measured at each site (Leptich and Gilbert, 1986; Addison *et al.*, 1990; Langley & Pletscher, 1994; Welch, 2000).

At nursery sites, the centre point of the first plot was established along the original transect where the most evidence of cow-calf activity was found. At absence sites, the centre of the first plot was established at the midpoint of the transect that had been walked at least twice without finding physical evidence of caribou activity. The geographic coordinates and elevation of the centre point of the first plot were determined with a handheld GPS unit (Garmin eTrex, Olathe, Kansas, USA). The slope was recorded using a clinometer and the direction of "downhill" (i.e., aspect) was also noted in 45-degree intervals (i.e., N, NE, etc.) relative to the evidence of cow-calf activity. Two additional 10 m-radius plots were established 30 m from the centre point of the first plot, both at a random compass direction, as long as there was no open water and no overlap between plots. Measurements from the three plots were averaged to obtain overall values for a site (Langley & Pletscher, 1994).

Measurements in each 10 m-radius plot

In each 10 m-radius plot, overstorey and understorey canopy cover were estimated occularly at plot centre and at points 30 m from plot centre in each of the four cardinal compass directions. These five cover estimates were later averaged to obtain a single percent cover estimate for each plot (Welch, 2000).

Ground detection distances were used as a means of quantifying the horizontal density of vegetation surrounding the centre of each plot. The minimum distance at which a red card measuring 0.5 m wide and 1 m high was completely hidden from view to an observer moving away from plot centre along each of the four cardinal compass directions was recorded (Welch, 2000). The observer used a 1 m-high pole to standardize the heights at which the card was viewed. This procedure was repeated with the bottom edge of the card on the ground. An average of the four measurements was used as an index of ground detection distances for 0-1 m and 1-2 m high views through the vegetation surrounding the site (adapted from Addison *et al.*, 1990).

The total number of standing dead trees (>1 m in height, ≥5 cm dbh, and >30 degrees up from the plane of the ground) and the number of stumps (<1 m in height) in each 10 m-radius plot were recorded (Rodgers *et al.*, 1997).

Each 10 m-radius plot was subdivided into four quadrants to measure tree density and species composition (Fig. 3). The dominant species of overstorey (woody vegetation ≥5 m in height and ≥5 cm dbh) and understorey (woody vegetation >2 m and <5 m in height and <5 cm dbh) trees (Rodgers *et al.*, 1997) within each quadrant were recorded, and a T-square nearest neighbour method was used to estimate density (Hays *et al.*, 1981). Two trees in each category were selected for density measurements in each quadrant. The first overstorey or understorey tree selected was the tree nearest to plot centre in each quadrant and the second tree was the nearest neighbour from the first tree within a 180° arc perpendicular to the line from plot centre to the first tree. Distances from plot centre to the base of the first tree and from the base of the first to the base of the second tree were used to estimate density of overstorey and understorey trees in each quadrant. Diameter at breast height was also recorded for overstorey trees used in density estimates and these measurements were averaged to determine the mean dbh of overstorey trees on each 10 m-radius plot.

One 20 m transect line, bisecting the centre of each plot (north-south), was used to determine the density and species of shrubs, consisting of woody vegetation >0.4 m and <2 m in height (Rodgers *et al.*, 1997). A 1 m ruler was centred over the transect line (protruding 0.5 m on each side) and the number of shrubs contacting the ruler (counting only the base not the branches) by walking with it along the length of the line was recorded (Rodgers *et al.*, 1997).

Line intercept methods (Hays *et al.*, 1981) were also used to quantify downfalls and browse (herbaceous and woody shrubs). At 2 m intervals along the intersecting (diameter) transect lines (Fig. 3), the number of downfalls and stumps crossing the line were recorded, along with their height from the ground and their diameter. Downfalls were distinguished as logs/trees ≥1 m in length and ≥5 cm in diameter (Rodgers *et al.*, 1997), lying horizontally along the ground or at an angle of ≤30 degrees up from the plane of the ground. The diameter of the log was determined at its maximum along its length. Total height from the ground was measured as the distance from the ground surface to the top of the fallen log or logs, if there were several overlying layers, and the number of layers was recorded.

One 30 m transect was walked that started at the centre of each plot and ran in the direction that had the most uniform ground distribution of lichens. At every one meter, at the tip of the right toe (2 cm spot), presence or absence of lichens was recorded (Lance & Eastland, 2000).

Square-metre sub-plots

Quadrats of 1 square metre were placed 2 m from the centre point of each 10 m-radius plot, along each of the four cardinal compass directions (Fig. 3). The dominant (most abundant) herbaceous species and woody plant species (<0.4 m in height) were recorded (Rodgers *et al.*, 1997) along with an estimate of their percent cover in each of the square metre plots. Percent ground cover, consisting of bare rock, gravel, soil/litter, wood, grass, rushes, sedges, herbs, shrubs, ferns/allies, fungi, moss/liverworts, and lichen were estimated within each quadrat. The percent ground cover data from the 4 quadrats were averaged for each of the 10 m-radius plots.

Statistical analyses

Prior to statistical analyses and model development, we examined the variance and normality of all interval scale variables and determined that the groundcover percent coverage variables were highly variant, in spite of transformations, relative to the other variables. Since caribou eat opportunistically and quite broadly with regard to vegetation types in the summer months (Ahti & Hepburn, 1967), groundcover variables were grouped into open (i.e., bare rock, gravel, soil/litter, and wood) or vegetation (i.e., grass, rushes, sedges, herbs, shrubs, ferns/allies, fungi, moss/liverworts,

Table 1. Means ± standard errors of interval scale variables measured in sample plots at caribou nursery sites and randomly chosen absence sites on lakes in Wabakimi (W.P.P.) and Woodland Caribou Provincial Parks (W.C.P.P.), northern Ontario. Variables that showed significant differences in the MANOVA, individual park DFA results used to identify and determine variables most important in distinguishing nursery sites from absence sites, and variables used in the development and evaluation of Resource Selection Functions for calving caribou in each park are indicated by superscripts.

Measurement	W.C.P.P. Absence sites (*n*=15)	W.C.P.P. Nursery sites (*n*=15)	W.P.P. Absence sites (*n*=15)	W.P.P. Nursery sites (*n*=15)
Slope$^{2\ 3}$ (degrees)	13.4 ± 2.5	18.0 ± 1.2	6.4 ± 1.7	10.6 ± 2.7
Elevation$^{1\ 2}$ (m)	364.9 ± 94.2	364.8 ± 94.2	364.5 ± 94.1	360.9 ± 93.2
# Standing Dead Trees^{3}	6.7 ± 1.7	6.9 ± 1.8	4.5 ± 1.2	4.0 ± 1.0
# Stumps	3.1 ± 0.8	3.6 ± 0.9	3.0 ± 0.78	2.7 ± 0.70
Ground Detection Distance1 2 3 5 (0-1 m)	19.5 ± 5.0	21.7 ± 5.6	28.0 ± 7.2	23.5 ± 6.1
Ground Detection Distance (1-2 m)	23.5 ± 6.1	25.9 ± 6.7	30.8 ± 8.0	26.1 ± 6.7
Shrub Density$^{1\ 2\ 5}$ (stems/m^2)	0.39 ± 0.10	0.25 ± 0.07	0.39 ± 0.10	0.22 ± 0.06
Lichen Transect Occurrence$^{1\ 2\ 3\ 6}$ (%)	31.1 ± 8.0	38.9 ± 10.0	9.6 ± 2.5	20.0 ± 5.2
Open Groundcover$^{1\ 4\ 6}$ (Rock, Wood, Soil/Litter) (%)	37.01 ± 9.6	18 ± 4.7	38.9 ± 10.0	22.7 ± 5.9
Vegetation Groundcover$^{2\ 4}$ (Moss, Lichen, Herbs, Shrubs, Fungi, Ferns) (%)	75.5 ± 19.5	93.6 ± 24.2	77.9 ± 20.1	83.0 ± 21.4
# Downed Trees^{3}	0.75 ± 0.19	0.71 ± 0.18	0.13 ± 0.03	0.13 ± 0.03
Maximum Height of Downfall (cm)	30.0 ± 7.8	27.8 ± 7.18	34.2 ± 8.8	32.2 ± 8.3
Diameter of Downfall$^{1\ 2\ 6}$ (cm)	10.6 ± 2.8	11.2 ± 2.9	10.8 ± 2.8	12.3 ± 3.2
Overstorey Cover$^{1\ 2}$ (%)	19.9 ± 5.1	24.9 ± 6.4	14.3 ± 3.7	22.0 ± 5.7
Understorey Cover^{1} (%)	7.5 ± 1.9	5.1 ± 1.3	3.0 ± 0.78	5.3 ± 1.4
Dbh (cm)	14.6 ± 3.8	13.8 ± 3.6	14.3 ± 3.7	13.5 ± 3.5
Overstorey Woody Vegetation Density^{1} (stems/m^2)	0.58 ± 0.15	0.73 ± 0.19	0.68 ± 0.18	1.1 ± 0.28
Understorey Woody Vegetation Density$^{2\ 4\ 5}$ (stems/m^2)	0.87 ± 0.23	0.66 ± 0.17	0.41 ± 0.11	0.63 ± 0.16

[1] Variables included in Woodland Caribou Provincial Park models.

[2] Variables included in Wabakimi Provincial Park models.

[3] Variables that had significant differences between the two parks (MANOVA).

[4] Variables that had significant differences between nursery and absence sites (MANOVA).

[5] Variables marked as important from DFA standardized canonical discriminant functions in Wabakimi Provincial Park.

[6] Variables marked as important from DFA standardized canonical discriminant functions in Woodland Caribou Provincial Park.

and lichen) groundcover categories, leaving a total of 18 interval scale variables for analysis (Table 1). Subsequent statistical tests were completed using the Statistical Package for the Social Sciences (Version 14.0, SPSS Inc., Chicago, Illinois).

We tested for differences in aspect between nursery and absence sites within each park using a chi-square test but did not find any statistically significant differences in either Wabakimi Provincial Park (χ^2 = 5.717, d.f. = 4, P = 0.221) or Woodland Caribou Provincial Park (χ^2 = 7.671, d.f. = 4, P = 0.104), so this categorical variable was removed from further consideration.

To determine if the measured interval scale variables differed between the two parks, and between caribou nursery and absence sites, we used multivariate analysis of variance (MANOVA). Following the MANOVA, Discriminant Function Analysis (DFA) was used to determine how well the variables were able to distinguish among nursery and absence sites in both Wabakimi and Woodland Caribou Provincial Parks.

The variables for ground detection distance at the 0-1 m and 1-2 m level were highly correlated, as might be expected. An individual DFA for each park demonstrated the importance of the 0-1 m ground detection distance variable in distinguishing between nursery sites and unused absence sites in Wabakimi Provincial Park, but not in Woodland Caribou Provincial Park. Thus, we removed the 1-2 m ground detection distance variable from both models and used the remaining 17 variables for further DFA analyses.

The results of both the MANOVA and DFA suggested there were greater differences between the two parks than between nursery and absence sites within each, so we developed separate Resource Selection Functions (Boyce *et al*., 2002) for each park following the model selection procedure suggested by Shtatland *et al*. (2003). This procedure maximizes variable selection strengths of stepwise regression in predictive and exploratory studies (Menard, 1995) while avoiding arbitrary alpha values by using an information-theoretic approach (Burnham & Anderson, 1998; Vander Wal, 2004). Models were evaluated using a combination of Akaike Information Criteria (AIC; Burnham & Anderson, 2002), Receiver Operating Curves (ROCs; Pearce and Ferrier, 2000) and k-fold cross-validation (Fielding & Bell, 1997).

Variable reduction

Because of potential statistical biases caused by the large number of independent variables (18) we measured relative to the sample sizes (15 nursery sites and 15 absence sites) in each park (Peduzzi *et al*., 1996), we sought to reduce the number of variables used for model development. Initially, data for all 18 variables were combined for nursery and absence sites within each park and included in multivariate linear regressions. We followed this with a series of steps (Shtatland *et al*., 2003) to remove variables that demonstrated multicollinearity with other independent predictors by examination of variance inflation factors (VIFs) in linear regression analysis, average linkages in hierarchical cluster analysis, and condition numbers in principal components analysis (PCA).

VIFs were obtained from multivariate linear regressions of all 18 variables in each park and were subsequently related by dendrograms in hierarchical cluster analyses. To remove potential multicollinearity, variables with VIFs > 2.5 (Allison, 1999) that were strongly linked in dendrograms were removed from further analyses. This procedure left 9 different potential variables in each park for further model development and evaluation. To validate the non-multicollinearity assumption in the VIF approach, condition numbers (k) were calculated using a PCA (Williams, 2005). As all condition numbers for the 9 remaining variables in each park were less than 15, multicollinearity among variables was apparently removed by the VIF approach (Williams, 2005) and no further variables were removed prior to model development and evaluation. The 9 different variables used for each park in predictive model development are identified in Table 1.

Model development and evaluation

Predictive model development using forward conditional logistic regression and automatic selection procedures were applied following variable reduction (Menard, 1995; Simonoff, 2000; Shtatland *et al*., 2003). The data set was randomly subdivided into a model building subset and a model validation subset for Woodland Caribou and Wabakimi Provincial Parks. Two-thirds (n=20 sites) of the data from each park were dedicated to model development and the remaining one third (n=10 sites) were used to evaluate the resulting models for each park.

Stepwise logistic regression of the 9 variables associated with two-thirds of the caribou nursery and absence sites in each park was used to produce subsets of models with different combinations of predictor variables. Akaike's Information Criterion for small sample size (AIC_c) and associated evidence ratios were used to select the "best" and most parsimonious model from among the models with statistically significant coefficients produced by stepwise logistic regression (Burnham & Anderson, 1998; 2002). Candidate models were then evaluated using ROC curves. These curves allow evaluation of the predictive power of the logistic regression models and reflect how accurately and robustly models classify the data (Pearce & Ferrier, 2000; Boyce *et al*., 2002). Validation data, representing the remaining one-third of the caribou nursery and absence sites in each park, were substituted into their respective models and tested by examining the predictive probabilities of each model (i.e., proportions of sites correctly or incorrectly classified as nursery or absence sites).

Results

The MANOVA indicated there were overall significant differences both between Wabakimi and Woodland Caribou Provincial Parks (F=14.23, d.f.= 18, 39, P = 0.000) and between caribou nursery and absence sites (F=2.04, d.f.= 18, 39, P = 0.031) in relation to some of the variables measured (Table 1). These overall differences suggested development and evaluation of separate Resource Selection Functions for calving caribou in each park.

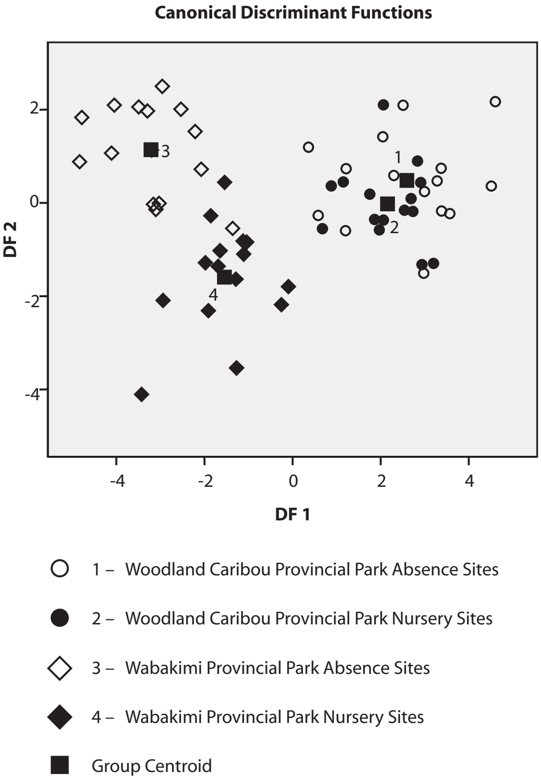

Fig. 4. Canonical Discriminant Functions of 17 variables measured at 30 caribou nursery sites and 30 randomly chosen absence sites on lakes in Wabakimi and Woodland Caribou Provincial Parks, northern Ontario. The *x*-axis (DF 1) indicates differences between the parks and the y-axis (DF 2) indicates differences between caribou nursery and unused absence sites.

The DFA results including all 4 groups indicated overall successful classification results of 87% (Fig. 4). Both the DF1 and DF2 tests were significant. DF1 explained 81.2% of the total model variance based on park differences and DF2 explained 13.7% of the total model variance in nursery versus absence sites. The variables important in differentiating between parks were primarily the number of downed trees and density of understorey woody vegetation. The variable most important in differentiating nursery from absence sites was groundcover vegetation.

Stepwise logistic regression of the 9 variables associated with caribou nursery and absence sites (Table 1) resulted in 3 candidate models with statistically significant coefficients ($P < 0.01$) for each park (Table 2). In Wabakimi Provincial Park, density of understorey woody vegetation, ground detection distance at 0-1 m, and vegetation groundcover were included in the models, whereas open groundcover, shrub density, and overstorey canopy cover were included in models for Woodland Caribou Provincial Park. Evidence ratios, based on AIC_c weights, indicated that the most parsimonious model for each park included all 3 of their respective variables. Further evaluation using ROC curves also indicated that the 3-variable model for each park had the highest predictive power in each case. However, examination of the predictive probabilities of candidate models, using the remaining one-third of the nursery and absence site data from each park, suggested the 3-variable models did not perform as well as the 2-variable models (Table 3).

The 2-variable Resource Selection Function model for calving caribou in Wabakimi Provincial Park, based on density of understorey woody vegetation and ground detection distance at 0-1 m, successfully classified caribou nursery and absence sites for 80% of the test data, while the 3-variable model, which also included vegetation groundcover, had a 60% success rate (Table 3). Although the 3-variable model performed better than the 2-variable model based on the logistic regressions, AIC_C, and ROC values using two-thirds (n=20) of the nursery and absence site data (Table 2), the 2-variable model had an R^2 of 0.74, a 90% correct classification rate, and an area under the ROC curve of 0.96. Given the small sample size relative to the number of variables in the models, the 3-variable model may overparameterize the data, leading to perfect separation as indicated by an area of 1.0 under the ROC curve (Pearce & Ferrier, 2000; Boyce *et al.*, 2002). Thus, we suggest the 2-variable model may better represent the Resource Selection Functions of calving caribou in Wabakimi Provincial Park.

The 2-variable Resource Selection Function model for calving caribou in Woodland Caribou Provincial Park, based on open groundcover and shrub density, successfully classified caribou nursery and absence sites for 80% of the test data, while the 3-variable model, which also included overstorey canopy cover, had a 60% success rate (Table 3). Similar to the Wabakimi Provincial Park models, the 3-variable model for calving caribou in Woodland Caribou Provincial Park performed better than the 2-variable model based on the logistic regressions, AIC_C, and ROC values using two-thirds (n=20) of the nursery and absence site data (Table 2), but the 2-variable model also provided good results; an R^2 of 0.85, an 85% correct classification rate, and an area under the ROC curve of 0.98. As before, given the small sample size relative to the number of variables in the models, the 3-variable model may overparameterize the data and the 2-variable model may also better represent the Resource Selection Functions of calving caribou in Woodland Caribou Provincial Park.

Table 2. Candidate Resource Selection Function models resulting from stepwise logistic regression of 9 variables associated with two-thirds (n=20) of the caribou nursery and randomly chosen absence sites sampled in Wabakimi Provincial Park and two-thirds (n=20) of the caribou nursery and randomly chosen absence sites sampled in Woodland Caribou Provincial Park, along with their evaluations by Akaike Information Criterion for small sample size (AIC_c) and Receiver Operating Characteristic curves (ROCs).

Park	Variables in Model	-2log likelihood	Nagelkerke R Square	% Correct	AIC_c	AIC_c Evidence Ratio	Area Under ROC Curve
Wabakimi Provincial Park	Understorey Woody Vegetation Density	20.777	0.39	75	49.055	>10	0.80
	Understorey Woody Vegetation Density, Ground Detection Distance (0-1m)	11.389	0.74	90	33.444	>10	0.96
	Understorey Woody Vegetation Density, Ground Detection Distance (0-1m), Vegetation Groundcover	1.52E-06	1.00	100	14.286	1	1.00
Woodland Caribou Provincial Park	Open Groundcover	16.878	0.56	65	41.256	>10	0.85
	Open Groundcover, Shrub Density	7.597	0.85	85	25.861	>10	0.98
	Open Groundcover, Shrub Density, Overstorey Cover	2.45E-06	1.00	100	14.286	1	1.00

Table 3. Predictive probabilities (i.e., proportions of sites correctly or incorrectly classified) of candidate Resource Selection Function models (Table 2) based on one-third (n=10) of the data from caribou nursery and randomly chosen absence sites sampled in Wabakimi Provincial Park and one-third (n=10) of the data from caribou nursery and randomly chosen absence sites sampled in Woodland Caribou Provincial Park.

Park	Variables in Model	Absence Sites		Nursery Sites	
		% Correctly Predicted	% False Positives	% Correctly Predicted	% False Positives
Wabakimi Provincial Park	Understorey Woody Vegetation Density	60	40	60	40
	Understorey Woody Vegetation Density, Ground Detection Distance (0-1m)	80	20	80	20
	Understorey Woody Vegetation Density, Ground Detection Distance (0-1m), Vegetation Groundcover	60	40	60	40
Woodland Caribou Provincial Park	Open Groundcover	80	20	80	20
	Open Groundcover, Shrub Density	80	20	80	20
	Open Groundcover, Shrub Density, Overstorey Cover	60	40	60	40

Discussion

In Woodland Caribou Provincial Park the slope, lichen occurrence, and number of standing and downed trees were higher, while ground detection distances at 0-1 m were lower, than at sites in Wabakimi Provincial Park. These small-scale differences between the parks are likely the result of large-scale geographic variation in weather, topography, soil productivity, and dominant vegetation across the two different ecoregions in which they are situated (Hills, 1959; Crins & Uhlig, 2000). Woodland Caribou Provincial Park falls in more of a "boreal prairie" area, being on the east Manitoba border, whereas Wabakimi Provincial Park falls in more of a "true boreal" region in north-central Ontario. Although not statistically different, the density of overstorey trees and canopy cover were higher at nursery sites than unused absence sites in both Woodland Caribou and Wabakimi Provincial Parks, suggesting selection of nursery sites in older-growth forests of both ecoregions.

Many of the characteristics associated with caribou nursery sites in Wabakimi and Woodland Caribou Provincial Parks, particularly those identified for inclusion in 2-variable Resource Selection Functions (Tables 1 and 2), were related to forage abundance and predator avoidance strategies. Female caribou in Woodland Caribou Provincial Park used nursery sites with less open groundcover, and thus more vegetative groundcover including higher lichen abundance, and lower shrub density than randomly chosen absence sites (Table 1). In Wabakimi Provincial Park, density of understorey woody vegetation and ground detection distance at 0-1 m were the two most important variables differentiating nursery sites from absence sites. The density of understorey woody vegetation was higher at nursery sites than absence sites (Table 1), although unused absence sites were generally in shrub-rich areas while nursery sites were in old-growth areas of spruce. Deciduous tree species such as white birch and trembling aspen were noted more often at absence sites than nursery sites. Due to differences in deciduous versus coniferous growth forms, particularly foliage density, ground detection distances at 0-1 m were higher at absence sites than nursery sites in Wabakimi Provincial Park. In both parks, nursery sites had higher densities of mature trees and lower shrub densities than unused absence sites (Table 1), providing concealment for calves and potentially greater sensory detection of approaching predators. As well, higher vegetative groundcover, including greater lichen abundance, was found at nursery sites compared to absence sites in the two parks (Table 1). All of these characteristics suggest female caribou in both parks were selecting nursery sites that may reduce predation risk while providing abundant forage.

Lent (1974) described the "hiding" and "following" responses of ungulate neonates as anti-predator strategies and Fitzgibbon (1990) described the tactics used by woodland caribou to be those of a "follower". In dense vegetation, a caribou calf may drop down out of sight and take a prone position, keeping the head low to the ground and remaining motionless if spotted by a predator (Fitzgibbon, 1990). Upon closer approach by a predator, the cow may take flight and the calf follows closely, rather than attempting to remain hidden in the vegetation as is the typical hiding behaviour of other ungulates such as white-tailed deer (*Odocoileus virginianus*: Lesage *et al.*, 2002). Caribou nursery site selection and response to predators is thus more similar to that of moose (*Alces alces*). Bowyer *et al.* (1999) identified greater forage abundance, a south-easterly aspect and better visibility as being the key variables at Alaskan moose birth sites. Although we did not find any relationship between aspect and nursery site selection, greater forage abundance and visibility were also important to female caribou nursery site selection in our study. In a manipulative habitat study, Bowyer *et al.* (2001) found that female moose were willing to trade off better foraging opportunities by choosing sites with more concealment cover. Food in the summer months for caribou consists of forbs, shrubs, fungi, grasses and sedges (Darby and Pruitt, 1984) but lichens, even though they have lower nutritional value, may also comprise a high proportion of their diet (Ahti & Hepburn, 1967). As vegetative ground cover, including greater lichen abundance, was found at nursery sites compared to absence sites in the two parks we studied, it does not appear that caribou necessarily trade off forage availability for greater concealment cover but they may be willing to accept lower forage quality (i.e., lichens rather than other summer foods) in exchange for a reduction in predation risk.

Protective cover inhibits prey detection, facilitates escape, and reduces the capture efficiency of visually oriented predators (White & Berger, 2001). There are variations in these findings and predators can use lateral cover to avoid being detected by prey (Moreno *et al.*, 1996). This same lateral cover may also obstruct the flight escape of prey (Lima, 1992). Bergerud (1985) and Ferguson *et al.* (1988) suggested woodland caribou maternal cows should take actions to reduce the success rates of wolves and bears in encountering, detecting and capturing calves by reducing movement and using shorelines with slopes, especially on islands, such as those in Pukaskwa National Park and Neys Provincial Park. Although not statistically different, the higher slopes at caribou nursery sites than absence sites that we found in both parks are consistent with this strategy. Similarly, Wilton & Garner (1991) found that moose calving sites were most often situated at high points, and on knolls, on islands, and Addison *et al.* (1990) determined these were usually within 200 m of water. A higher slope at nursery sites may help caribou detect oncoming predators more easily and facilitate escape. These locations may minimize encounters with mobile predators that will need to use more energy to get to islands and slopes will further increase their searching time for caribou with calves (Bergerud, 1985).

In Ontario, forest management guidelines for the conservation of woodland caribou, give special consideration to calving areas by providing a 1,000 m buffer around sites (Racey *et al.*, 1999). Given the potential for disturbance from attempting to directly observe parturition in calving caribou and the difficulties in distinguishing calving sites from postpartum nursery sites, protection should be extended to nursery sites in general. Moreover, as forestry activities generally increase the number of roads around parks and protected areas, allowing easy access for predators, roads need to be limited in number and use. The impact of recreational use on calving caribou within parks and protected areas also needs to be minimized. Travel and recreational use of lakes or areas of lakes, particularly near nursery sites that are reused by female caribou, should be restricted at least during the calving and nursery periods.

This study provides a preliminary basis for identifying caribou nursery sites both outside and within protected area boundaries across northern Ontario. Although logistically challenging, future studies should attempt to identify a larger number of nursery sites for assessment, but we do not suggest that all variables we initially collected be measured. Rather, the 12 variables we used for development of models (Table 1), particularly those related to overstorey and understorey cover and woody vegetation density, groundcover, especially lichen abundance, shrub density, slope, and ground detection distance at 0-1 m, may provide a more suitable starting point. As remote sensing information improves, it may be possible to correlate some of these variables with spectral data to decrease the logistic/financial problems associated with the identification of caribou nursery sites in remote locations, thereby improving their protection in future management policies and legislation. Ultimately, future studies need to relate caribou fitness to nursery site selection.

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The effects of human land use on the winter habitat of the recovering Carcross woodland caribou herd in suburban Yukon Territory, Canada

Rob Florkiewicz[1], Ramona Maraj[1], Troy Hegel[2] & Marcus Waterreus[1]

[1] Environment Yukon, Fish and Wildlife Branch, Box 2703, Whitehorse, Yukon, Canada, Y1A2C6. (rob.florkiewicz@gov.yk.ca).

[2] Institute of Arctic Biology, Biology and Wildlife Department, University of Alaska Fairbanks, Fairbanks AK, USA, 99775.

Abstract: Carcross woodland caribou (*Rangifer tarandus caribou*) numbers are increasing as a result of an intensive management and recovery program initiated in 1993. In the last 13 years, three overlapping First Nation land claim agreements were settled resulting in a complicated array of private and public land management authorities on this winter range, situated in the Whitehorse periphery. Twelve years of VHF radio-collar data (1994-2005) and 5 years of GPS radio-collar data (2000-2005) for female caribou were assessed to determine winter concentration areas and important winter habitats. We contrasted locations from 11 GPS radio-collared caribou with land cover classes, derived from classified Landsat 7 imagery, to evaluate the distribution and abundance of preferred habitats within this winter range. We found significant use of Open Needle Leaf lichen vegetation classes and avoidance of the relatively more abundant Closed Needle Leaf class. Our resource selection function model validated the preference for Open Needle Leaf Lichen and determined that caribou were spaced significantly further from an estimate of the human Zone of Influence (ZOI) than was expected from random locations. While our assessment determined that 64% of the winter range was located outside of either private lands or land influenced by human activity, key winter vegetation classes were under-represented within this area. If caribou are to successfully recover on this landscape and persist through time it is essential to manage, through meaningful participation among land management authorities, the remaining caribou habitat for environmental rather than human consumptive values.

Key words: Landsat imagery, northern mountain population, RSF model, radio-collars, zone of influence.

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Introduction

Caribou (*Rangifer tarandus caribou*) from the Carcross herd, and the people that rely on them, have persisted for centuries on the landscape of what is now the southwest Yukon Territory, Canada (Yukon). Cryo-preserved caribou dung and associated hunting artifacts date to 8330 years bp (Farnell *et al.*, 2004; Hare *et al.*, 2004). Market hunting associated with the Klondike gold rush, White Pass rail line and early riverboat travel (McCandless, 1985) was likely an important source of mortality to the Carcross and possibly other Yukon caribou herds. McCandless (1977) suggested the gold rush had a "crippling effect" on game and their habitat and that the RCMP were unable to prevent widespread slaughter. Resident meat hunting and non-resident sport hunting popular through the early 1920s (McCandless, 1985) likely kept numbers from increasing. Finally, construction of the Alaska Highway through the Carcross herd winter range in 1942 brought thousands of soldiers followed by an influx of new residents to the area. Even a modest harvest on this range likely maintained low caribou numbers through the latter half of the 20th century.

Since 1993 the Southern Lakes Caribou Recovery Program, a partnership between First Nations, non-government organizations, communities, and governments, has worked to increase two herds (Carcross and Ibex) to a common recovery objective of 2000 animals (Egli *et al.*, 2000) likely achievable within a few years. From 1994 to 2003, the Carcross herd increased from an estimated 300 to 850 animals (O'Donoghue, 1996; Farnell *et al.*, 1998; Yukon Government, unpublished data) and is expected to constitute 1400 of the 2000 caribou objective. Caribou from the adjacent Ibex herd make up the balance of the final recovery objective. Given the national trend of declining woodland caribou herds (Thomas & Gray, 2002) growth of these herds is noteworthy and could only have been achieved through a collaborative effort among recovery partners and the cessation of all hunting The recovery focus for the Ibex range is management of harvest and recreational activity on their sub-alpine winter range (Powell, 2004). Prior to and throughout the recovery period, the Carcross winter range has experienced increasing levels of linear development and landscape change associated with timber harvest, residential growth and industrial development in addition to increasing recreational use.

Carcross caribou habitually winter in close proximity to the heavily populated Southern Lakes area presenting a management challenge uncommon to most Yukon caribou herds and many other herds in the Northern Mountain Population (NMP; Thomas & Gray, 2002). The area is also home to 80% of the territory's 30 000 human residents, primarily in the Yukon's capital of Whitehorse, but also in five outlying communities. Yukon Government land policies evaluate disposition of public lands for residential and industrial use on a case by case basis (Yukon Government, 2006). In recent years applications for rural land have dramatically increased (Yukon Government, unpublished data) due to an apparent shortage of readily available residential building lots, agricultural properties and the attractiveness of a rural lifestyle. Much of this activity has been directed to the Whitehorse periphery and frequently to the winter range of the Carcross caribou. While the physical extent of each successive land disposition, timber harvest or land use activity may be small relative to existing dispositions, they should be evaluated in the context of cumulative habitat loss and/or displacement of caribou from important winter habitats.

Yukon woodland caribou are of the mountain terrestrial ecotype (Edmonds, 1991) and most of the 22 herds concentrate onto lichen dominated forested winter ranges (Farnell *et al.*, 1998). For the Carcross herd, terrestrial lichens constituted 76% of the estimated winter diet based on fecal fragment analysis from pellets collected between 1994 and 1997 (Yukon Government, unpublished data) and is consistent with other Yukon herds (Farnell & McDonald, 1989; Farnell & McDonald, 1990; Farnell *et al.*, 1991, Yukon Government, unpublished data). In southern Yukon, caribou winter in conifer forest types with low or poor quality soils, often glacial in origin, characterized by open forest canopies (25-50% crown closure) and well established lichen groundcover (Frid, 1998, Florkiewicz *et al.*, 2003). Similar relationships have been noted for woodland caribou in other jurisdictions (Cichowski & Banner, 1993, Wood, 1996). Caribou are frequently associated with mature and old forest cover types because of their reliance on slow growing lichen. Forest stands over 80 years of age were found to support terrestrial lichen cover (Thomas *et al.*, 1996; Szkorupa, 2002; Szkorupa & Schmiegelow, 2003); however, older stands are considered to be more productive. In some cases lichen can remain productive in pine stands up to 300 years old (Brulisauer *et al.*, 1996).

Integrity of winter range is fundamental to ensure both the availability of lichen and the ability of caribou to access it. How winter range integrity is maintained has become the subject of considerable research and management effort in the last decade, largely around the threatened Boreal (BP) and Southern Mountain Populations (SMP) (Thomas & Gray, 2002; McLoughlin *et al.*, 2003). Forest and wildlife managers are increasingly concerned as caribou numbers have declined in the face of significant landscape changes. These are associated with timber harvest (Smith *et al.*, 2000; Mahoney & Virgil, 2003; Morgantini & Schmiegelow, 2004; Saher & Schmiegelow, 2005) and the proliferation of linear corridors usually associated with the oil and gas and forest industries (James, 1999, James & Stuart-Smith, 2000; Dyer *et al.*, 2001). The mechanisms for change in caribou numbers, recently reviewed by Adamczewski *et al.* (2003), include factors that influence caribou directly such as habitat loss, increased road kill, and illegal harvest, and indirectly such as displacement into poorer habitats, increased prey biomass supporting higher predator populations, and increased predator efficiency. In their review of human factors contributing to the declining trend in other caribou populations, Thomas & Gray (2002) reasoned that many of these were also influencing NMP caribou and therefore a recent status assessment elevated this population to "Special Concern" (COSEWIC, 2002).

Winter ranges are considered "key areas" within the Yukon Wildlife Key Area inventory program. This designation indicates part of a species range considered essential to its life function (Yukon Government, 2005). This program serves to provide an early alert to potential wildlife issues where land development is being considered. However, for the Carcross winter range, land management decisions are being made at a much finer scale than the winter range, frequently measured in 10s of hectares. In addition, neither the

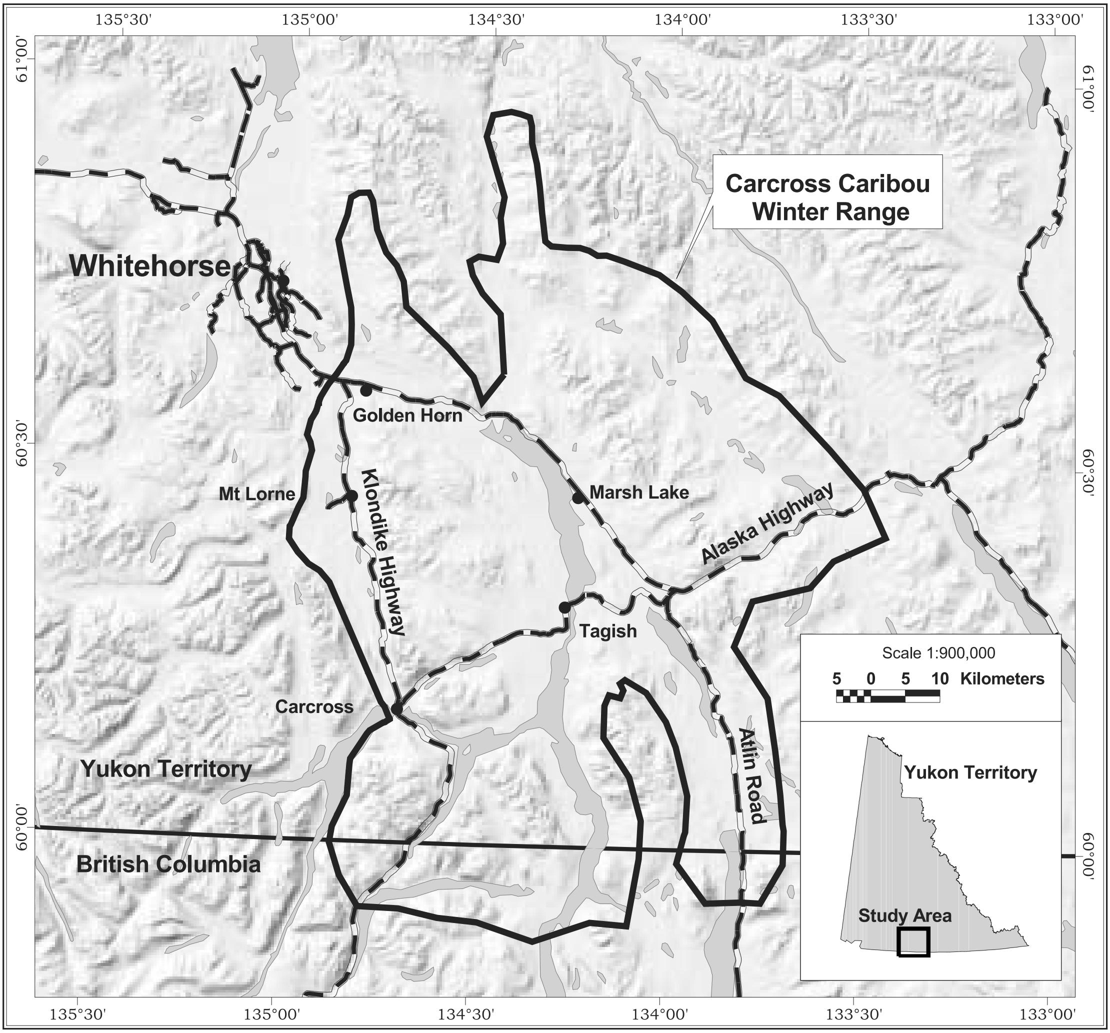

Fig. 1. Location of Whitehorse, outlying communities and major highway corridors relative to the Carcross caribou winter range.

key area program nor designation as a winter range advise sufficiently well on land use practices as they cover large areas and include substantial proportions of what could be considered non-habitat for wintering caribou.

To further our understanding of the Carcross caribou herd, of challenges to achieving the recovery objective for this herd on this landscape, and our ability to advise land use processes, we evaluated 12 years of data from radio-collared caribou using a satellite based land cover classification and a detailed assessment of human land use on this range. Our specific objectives were:

1: To empirically assess winter range and to define a core winter range based on radio-collared caribou and habitat values within them; and,
2: To evaluate the relative influence of human activity on winter habitat important to this herd.

This assessment can then be used to support decision making on the disposition and/or retention of land in the Whitehorse periphery. If the Carcross herd is to persist, it is essential to develop a management program based on a clear understanding of how caribou use the landscape and the potential risks from existing and future development.

Study area

The Carcross caribou winter range is located in south-central Yukon and straddles the Yukon-British Columbia border (Fig. 1). The area lies within the Southern Lakes Ecoregion (Yukon Ecoregions Working Group, 2004) which is characterized by large lakes, broad valleys and a number of mountain peaks over 2000 m asl. It is strongly influenced by the most recent (McConnell) glaciation and fluvial processes associated with water impounded behind retreating glaciers. The landscape is dominated by glacio-fluvial gravels overlain with lacustrine clays and silts. Soils are predominantly Eutric Brunisols overlying a variety of glacial parent materials, some of which are influenced by scattered discontinuous permafrost. The area is within the heart of the Coast Mountain rain shadow where precipitation varies between 200 and 325 mm annually, one third to one half as rain. Snow depth, measured at the Whitehorse airport, at the end of March averaged 31 cm, (Environment Canada; http://www.climate.weatheroffice.ec.gc.ca/climate-normals). Annual mean temperatures range between -1 °C and -2 °C. Forests are largely open coniferous and mixedwood, dominated by pine (*Pinus contorta*) or mixed pine/spruce (*Picea* spp.) on glaciofluvial and morainal deposits. White spruce forest stands are scattered in lowland habitats and shrub birch (*Betula glandulosa*) dominated stands underlain by lichen and forbs occur at higher elevations.

Material and methods

Animal capture and monitoring

From 1994 to 2005, 30 very high frequency (VHF) radio-collars (Telonics Inc., Mesa, AZ, USA) were placed on adult female caribou on the Carcross caribou range. Between 1999 and 2004, 11 adult female caribou were fitted with Global Positioning System (GPS) radio-collars (Lotek Engineering, Newmarket, ON, Canada; Models GPS_2200 & GPS_3300). All animals were captured using aerial net gun techniques (Barrett *et al*., 1982). VHF radio-collar locations were gathered seasonally using fixed and rotary wing aircraft, at least five times per year to coincide with calving and post-calving, rut, early and late winter periods. We used individual GPS radio-collared caribou positions as VHF locations when they were located on routine telemetry flights. GPS radio-collars were programmed to gather locations at intervals ranging from one to six hours. Locations with dilution of precision (DOP) values greater than 8 were removed from the sample (British Columbia Standards, 2001). For the purposes of this study, the winter period was considered to be November 15 through April 15.

Characterization of winter range

A generalized winter range boundary (Fig. 1), established as part of the management initiative for the Carcross caribou herd (O'Donoghue, 1996; Smith & McDonald 1996) was revised in 2003. The revision included new information for caribou range use (from local observations and updated survey information) and on habitats near the range periphery considered valuable caribou habitat. To refine the winter range configuration and to identify concentration areas within the winter range, we generated home range estimates by the adaptive kernel method (Worton, 1989; Worton, 1995). We used the Animal Movement Extension (Hooge & Eichenlaub, 1997) for ArcView 3.3 (ESRI, 2002), with least-squares cross-validation to estimate the smoothing parameter, on VHF caribou locations between 1994 and 2005. This method takes advantage of the large number and relative density of caribou locations in generating concentration areas within the winter range with a limited bias (Seaman & Powell, 1996). This contributes added rigour over "expert opinion" approaches to mapping animal range. We objectively identified a core area using a utilization plot (Kenward, 2001). Range area estimates were calculated at 5% increments from the 20% to 95% isopleths. Range area generally increases linearly with increasing isopleth level. Range area was plotted against isopleth level and a core area (isopleth) identified at the first discontinuity in this linearly increasing trend. Caribou locations were entered as either Garmin GPS waypoints (WGS 84 datum) or, for earlier surveys, were digitized from locations recorded on 1:250 000 scale topographic maps.

A Landsat 7-derived land cover classification of the Southern Lakes Region (Ducks Unlimited *et al*., 2002) was used to describe caribou winter range. Analysis of this classification was done using PCI Geomatica v. 9.1.5 (PCI, 2004). A 3x3 mode filter was applied to the classification to remove "noise" associated with isolated pixels. Spatial/statistical overlays were performed on the filtered classification with coverages representing human land use, land ownership, and winter locations of GPS-collared caribou (see Bechtel *et al*., 2004). Overlays were performed for the generalized winter range and subsequently contrasted with the kernel home range estimates. Vegetative characteristics from aerial plot data gathered through the initial Landsat mapping initiative (Ducks Unlimited *et al*., 2002) were summarized to evaluate important lichen supporting classes.

Human use on the landscape was established through comprehensive mapping of all discernable land uses within the generalized winter range boundary (Applied Ecosystem Management, 2004). Each feature identified from digital topographic data (Natural Resources Canada, 2003), digital orthophotos, and cadastral layers was classified by land use type and mapped as a polygon layer within ArcGIS (ESRI, 2005). To approximate the influence of human activity within human use areas, we applied a buffered polygon around each feature to represent a "Zone of Influence" (ZOI). Values for the extent of the ZOI were derived from existing literature where appropriate, from the UNEP (2001) Globio standards, or were otherwise developed by a

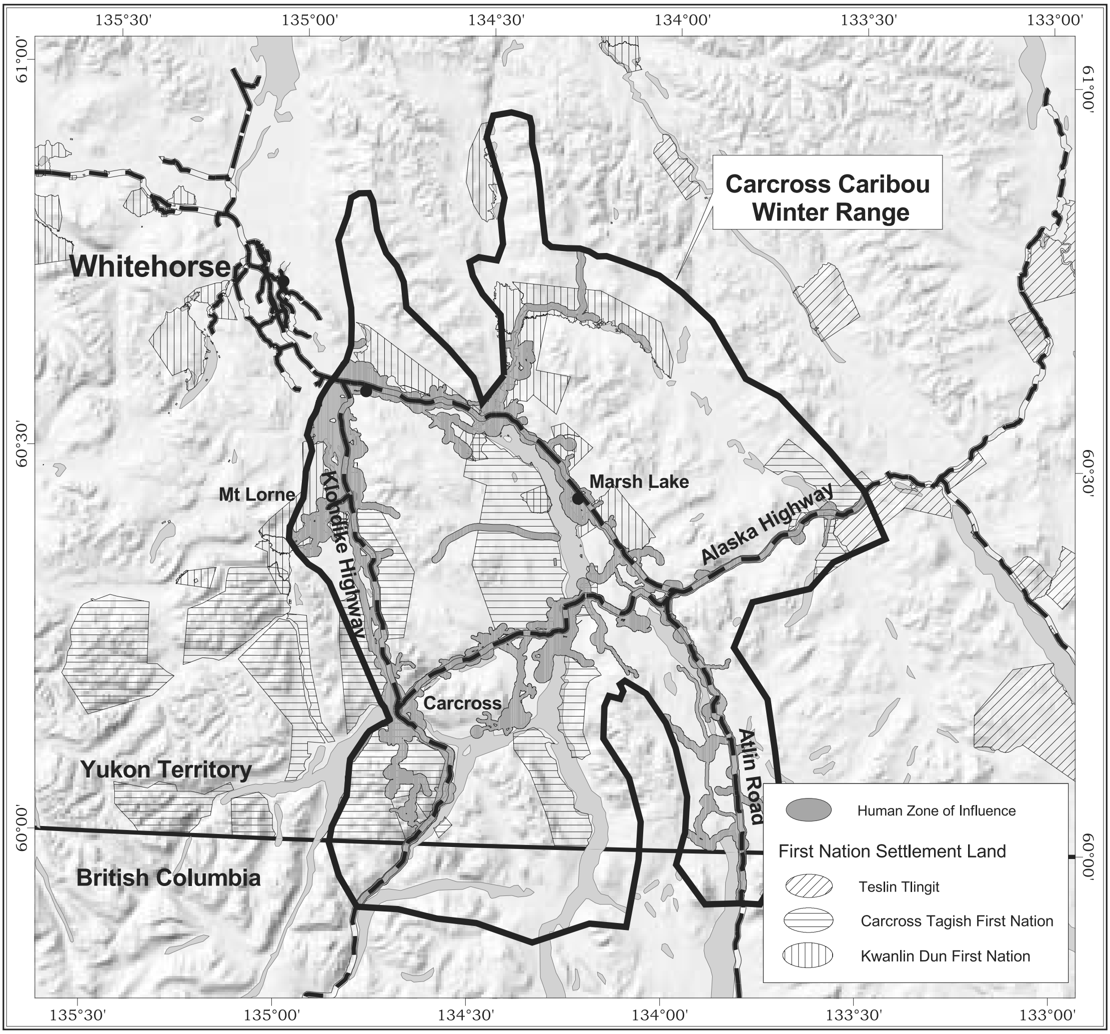

Fig. 2. Distribution of First Nation land selections, private land and estimated human Zone of Influence (ZOI) around development in the Carcross caribou winter range.

group of local experts (Applied Ecosystem Management, 2004; Appendix 1).

Caribou winter range influenced by land use was evaluated by intersecting the human land use (ZOI) coverage with the Landsat derived classes. We also included First Nation land selections as human land use within the winter range (Fig. 2) as they are not within the "public" domain for possible development. We assume, in the short term, that First Nation partners will direct development on settlement land away from important winter habitats.

We assessed type I, or first order selection (Johnson, 1980) by GPS radio-collared caribou over the entire landscape. Using Bonferonni confidence intervals (Neu *et al*., 1974), we evaluated the relative frequency of caribou use for each land cover class (Ducks Unlimited *et al*., 2002) (see Bechtel *et al*., 2004).

Human Impact on Caribou Winter Habitat

To assess the impact of the human footprint on caribou winter habitat we developed a resource selection function (RSF; Manly *et al*., 2002). RSFs are statistical models that calculate values proportional to the actual probability of use of resource units on the landscape (Manly *et al*., 2002; Johnson *et al*., 2006). This provides a framework to assess and quantify the impact of certain landscape changes, such as human infrastructure, on habitat (e.g., Johnson *et al*., 2005). We modelled third-order selection patterns (Johnson, 1980) of adult female caribou during winter following a use - availability sampling protocol (Manly *et al*., 2002) whereby a sample of locations used by GPS radio-collared caribou was compared to a random sample of points on the available landscape. We adopted a design 4 strategy (Thomas & Taylor,

2006) in which used locations were paired with available locations for the analysis.

The full relocation dataset consisted of 20 833 relocations from 11 individuals. To reduce autocorrelation in the relocations (Nielsen *et al.*, 2002) and to create a balanced sample of used points among individuals, we randomly selected 325 locations for each individual for inclusion in the analysis. Around each of these used locations we generated a buffer (Johnson *et al.*, 2005) of radius 1.1 km which was equal to the median daily distance moved by the GPS radio-collared caribou. Within each buffer, five random points were generated to represent availability using Hawth's Tools (Beyer, 2004) for ArcGIS 9.1 (ESRI, 2005). Five random points were chosen because the addition of more available points would not provide any additional information (King & Zeng, 2001).

To generate the RSF we modelled the binary response variable (used vs. available) with eight spatially explicit covariates mapped within a GIS (ArcGIS 9.1; ESRI, 2005). All covariates were mapped at a 30-meter pixel resolution. Covariates were selected based on previous research and our observations of caribou behaviour during winter in the study area. We collapsed the existing landcover map (Ducks Unlimited *et al.*, 2002) from 31 classes to 12 to increase parameter certainty. Original cover types were grouped into what we felt were biologically meaningful functional classes. Each new cover class was treated as a binary indicator variable. Elevation (meters) was calculated from an existing digital elevation model (DEM) of the study area. Slope (degrees), aspect, and hillshade were derived from the DEM using Spatial Analyst for ArcGIS 9.1 (ESRI, 2005). Aspect was classified into five classes based on the cardinal direction (east, west, north, or south) of the pixel or flat (reference category) if the slope of the pixel was less then five degrees. The Euclidean distance (meters) to the nearest water body was calculated in ArcGIS 9.1 using an existing hydrographic database. A topographic position index (TPI; Jenness, 2005) was calculated using the DEM and a 300-meter circular window and provides an indication of slope position. Negative TPI values indicate valley bottoms while positive values indicate ridge or hill tops. Values near zero indicate flat areas. The final predictor, human zone of influence (ZOI), represents the area on the landscape affected by human infrastructure (Applied Ecosystem Management, 2004). We rasterized the initial vector-based ZOI to a 30-meter pixel resolution, providing a binary variable indicating whether the location was in or out of the ZOI. The value, or category, of each covariate was extracted for all used and available locations. We assessed for collinearity by calculating the Pearson correlation between variables and used $|r| > 0.6$ as the threshold for removing one of the covariates.

We used conditional fixed-effects logistic regression (Long & Freese, 2003) to estimate the model coefficients. Analyses were carried out in Stata/SE 9.2 (StataCorp, 2005). We followed an information-theoretic approach (e.g., AIC) for identifying the most parsimonious model (Burnham & Anderson, 2002). This model was determined using a forward-looking stepwise-AIC (SWAIC) approach (Nielsen *et al.*, 2003), in which covariates were added to the model until parsimony was reached. To account for possible lack of independence of locations from the same individual we used a modified sandwich estimator to calculate robust standard errors (Nielsen *et al.*, 2002). To assess the model's predictive ability we used a *k*-fold cross-validation procedure (Boyce *et al.*, 2002) to calculate a Spearman rank correlation coefficient (r_s).

From the final selected model we applied the RSF to the landscape to generate a relative distribution map of caribou occurrence. We used the quantile function in ArcGIS 9.1 to classify the map into ten quantiles. This map represented the habitat effectiveness of the current winter range. Habitat effectiveness is an estimate of the percentage of habitat available to caribou after subtracting habitat alienated by human influences. We reapplied the RSF to the landscape removing the ZOI from the landscape (i.e., no human influence in the study area). Again we classified the map into ten quantiles representing the habitat potential of the study area. Habitat potential theoretically reflects the inherent ability of the landscape to support caribou without human activity. Thus, pixels in both maps were classified from one through ten, where one indicated low habitat quality and ten represented the highest habitat quality. To both quantify, and visualize, the reduction in habitat quality due to the influence of human activity we subtracted the habitat effectiveness map from the habitat potential map in the GIS. We then generated a difference map indicating the difference between the habitat potential and effectiveness maps. The possible minimum and maximum differences between the two maps were zero and nine, respectively. To quantify habitat quality reduction we calculated the proportion of this difference map that was made up of each of the ten possible values. High difference values indicate relatively large reductions in habitat quality whereas small or no differences indicate a negligible loss.

Results

Winter range and core area

We generated an adaptive kernel winter range estimate based on 434 winter VHF locations (November 15-April15) from the total sample of 741 locations over all seasons and years. Estimates of winter range

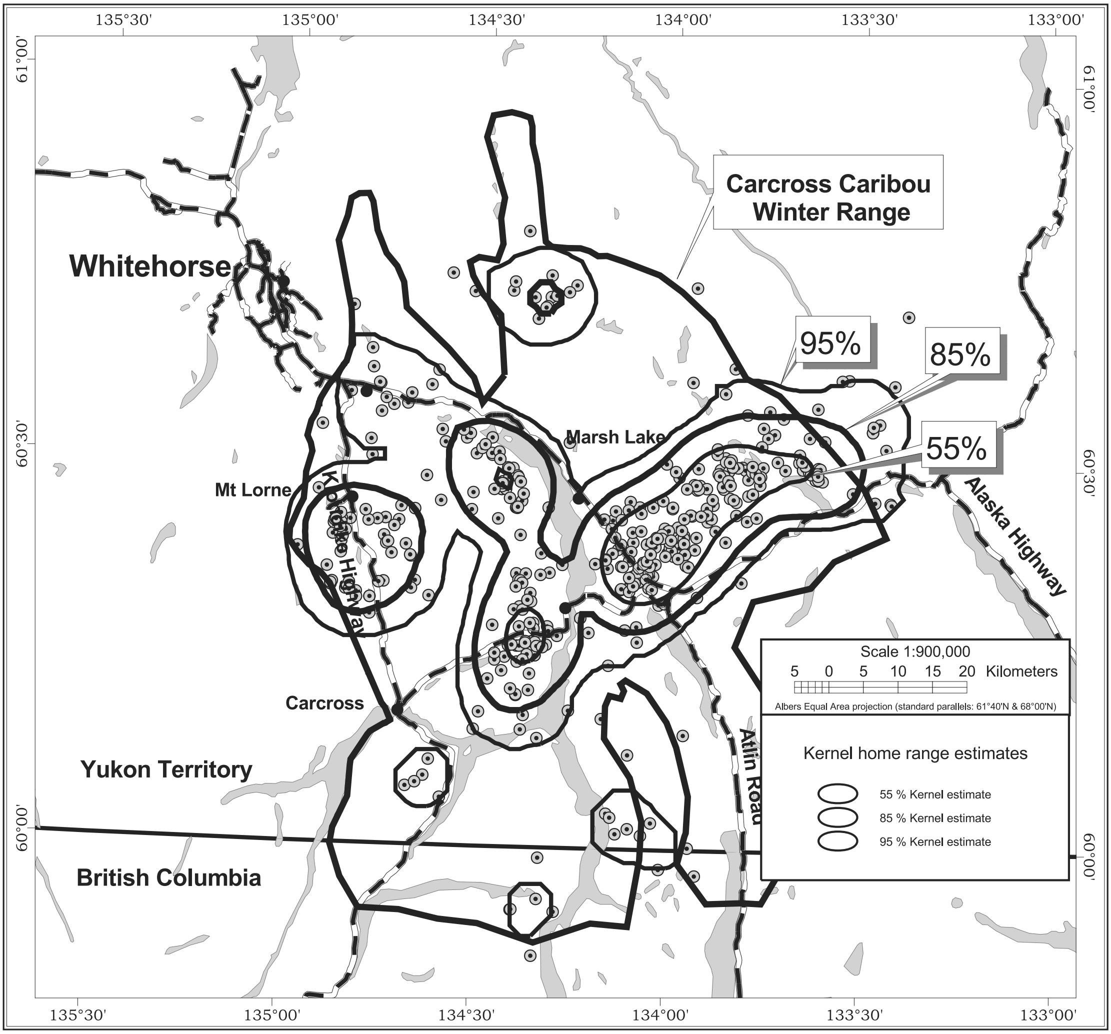

Fig. 3. Kernel home range estimate for 41 radio collared caribou in the Carcross caribou winter range.

represented 6.3%, 26.8% and 53% of the Carcross winter range area for the 55%, 85% and 95% kernel isopleths respectively (Fig. 3; Applied Ecosystem Management Ltd., 2004). The utilization plot indicated a core area at the 85% isopleth.

Habitat assessment

Vegetation characteristics for 401 aerial sample plots gathered through the satellite land cover classification were summarized into principle forage categories for each of the 25 land cover types identified (Table 1). Of these, 11 forested classes represented 73.6%, and 8 shrub classes an additional 15.3% of the winter range. The remaining area was dominated by water (6.2%), sparsely vegetated, rock-gravel, lichen or forb classes. With the exception of the Closed Needleleaf (CN) and Open Pine (OP) classes, no cover type contributed more than 10% to the total winter land cover (Table 2). Only the Open Needleleaf Lichen (ONLi; 33.5% lichen cover) and Woodland Other (WOt; 17.9% lichen cover) classes supported substantial lichen cover. The WOt class is an open canopy class of conifer-dominated forest type of which 5 of the 9 plots sampled were classified as Woodland Needleleaf/Lichen. Shrub lichen classes were associated with subalpine parts of the range.

Habitat availability

The influence of human activity through direct loss of habitat, including private, public, and recreational features (Table 3) was estimated to be 3.3% of the winter range (Applied Ecosystem Management, 2004). The estimated indirect influence or ZOI after applying the buffers to these features (Appendix 1) increased the estimate of human influence to 16.7% of the winter range (Fig. 2).

Table 1. Vegetation characteristics for 25 land cover classes found in the Carcross caribou winter range as outlined in Fig. 1.

				Mean % Cover							
Cover Type	ID	Symbol	Plots	Tree	Shrub	Forb	Graminoid	Lichen	Moss/Fern	Litter	Other[1]
Closed Needleleaf	1	CN	28	65.2	15.9	2.7	0.5	1.6	5.5	7.0	1.6
Open Mixed Needleleaf	2	OXN	6	43.3	19.2	6.7	1.7	2.5	10.0	15.0	1.7
Open Needleleaf Lichen	3	ONLi	10	34.5	12.5	0.5	0.0	33.5	1.0	14.0	4.0
Open Spruce	4	OS	24	34.8	35.0	3.1	0.4	7.9	7.7	7.5	3.5
Open Pine	5	OP	25	41.6	19.8	4.8	0.6	7.0	1.8	22.6	1.8
Closed Mixed Needleleaf Deciduous	6	CXND	1	70.0	5.0	5.0	0.0	0.0	10.0	10.0	0.0
Open Mixed Needleleaf Deciduous	7	OXND	12	39.2	32.9	6.3	3.3	0.8	0.4	15.8	1.3
Woodland Shrub	8	WSh	28	14.5	51.8	3.8	3.2	6.1	8.0	10.4	2.3
Woodland Other	9	WOt	9	17.2	27.2	2.8	5.6	17.8	4.4	12.8	11.7
Closed Deciduous	10	CD	10	68.5	14.0	9.5	2.5	0.0	0.5	4.5	0.5
Open Deciduous	11	OD	16	44.4	30.6	8.4	4.4	0.3	0.0	7.5	4.4
Tall Shrub	12	OCTSh	28	2.5	62.9	7.0	9.5	2.1	2.5	9.6	3.0
Closed Low Shrub	13	CLSh	19	1.1	76.8	2.1	4.2	8.4	2.9	3.2	1.3
Open Low Shrub	14	OLSh	28	1.4	62.3	5.7	8.4	5.9	2.0	8.0	6.1
Open Low Shrub Herb	15	OLShHb	15	2.0	46.7	9.3	25.3	2.7	2.7	7.7	2.7
Open Low Shrub Lichen	16	OLShLi	12	0.8	50.4	2.5	5.0	26.7	1.7	3.3	9.6
Dwarf Shrub Other	17	DsOt	28	0.7	40.9	16.8	7.9	8.0	1.8	5.7	17.9
Dwarf Shrub Lichen	18	DsLi	27	0.4	33.1	20.0	6.7	24.1	0.4	2.4	13.0
Dwarf Shrub Herb	19	DsHb	14	0.7	22.5	20.0	23.6	11.4	0.7	9.3	10.7
Mesic Dry Forb	20	MYFb	2	2.5	10.0	25.0	10.0	0.0	10.0	17.5	25.0
Lichen	21	Li	2	0.0	5.0	17.5	22.5	32.5	0.0	10.0	12.5
Clear Water	24	Wc	4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.0
Rock – Gravel	27	Rg	28	0.0	1.3	2.0	0.2	0.8	0.4	0.4	95.0
Sparse Vegetation	28	Sv	15	0.3	7.3	9.0	4.3	4.7	3.0	3.3	68.0
No data[2]	32	Ot	10	1.0	4.5	13.0	24.5	0.0	2.0	4.5	9.0

[1] Other composition category is the combined classes including Algae, Bare ground, Snag and Snow.

[2] No data Type given to plots that did not fall into any other class (Ducks Unlimited *et al.*, 2002).

Table 2. Distribution (area and %) of land cover classes (Ducks Unlimited, 2002) over the Carcross caribou herd winter range, within the human Zone Of Influence, and the 85% Adaptive Kernel.

Landcover class	Total winter range Area (ha)	Total winter range Proportion of total (%)	Human ZOI Area (ha)	Human ZOI Proportion of human ZOI (%)	85% Adaptive kernel Area (ha)	85% Adaptive kernel Proportion of total (%)
CN	134205	24.2	15309	16.5	36326	24.6
OXN	16992	3.1	3523	3.8	5331	3.6
ONLi	25073	4.5	8764	9.5	12481	8.4
OS	54291	9.8	10969	11.9	15069	10.2
OP	59468	10.7	13661	14.8	19816	13.4
CXND	9920	1.8	372	0.4	1893	1.3
OXND	33652	6.1	4780	5.2	8595	5.8
WSh	7946	1.4	1020	1.1	1412	1.0
WOt	8767	1.6	1977	2.1	1462	1.0
CD	51995	9.4	7789	8.4	15494	10.5
OD	5473	1.0	1296	1.4	1470	1.0
OCTSh	11879	2.1	1127	1.2	2470	1.7
CLSh	19775	3.6	1577	1.7	3896	2.6
OLSh	16853	3.0	1192	1.3	2818	1.9
OLShHb	7236	1.3	763	0.8	1354	0.9
OLShLi	12978	2.3	2203	2.4	2749	1.9
DsOt	9205	1.7	1052	1.1	1078	0.7
DsLi	5388	1.0	891	1.0	265	0.2
DsHb	1551	0.3	281	0.3	77	0.1
MYFb	560	0.1	71	0.1	73	< 0.1
Li	754	0.1	43	0.1	32	< 0.1
Wc	34199	6.2	5869	6.3	8900	6.0
Rg	2818	0.5	257	0.3	98	0.1
Sv	9391	1.7	1255	1.4	661	0.4
Other	15071	2.7	6551	7.1	4030	2.7
Total	555448	100	92594	100	147851	100

Table 3. Contribution of anthropogenic feature classes to the total human footprint within the Carcross caribou winter range.

Feature Class Description	Contribution of each feature class to total human footprint Area (ha) Direct[1]	Indirect[2]	% study area Direct	Indirect
Agricultural	2811.5	3439.7	0.48	0.59
Industrial	1438.4	7759.3	0.25	1.33
Recreation	8177.0	19800.6	1.40	3.39
Transportation	4646.6	43628.5	0.79	7.46
Urban	2343.0	22763.2	0.40	3.89
Total	97391.2	19416.5	3.3	16.7

[1] Direct pertains to the actual area covered by a land disposition.

[2] Indirect pertains to an area beneath the Zone of Influence buffers applied to each feature class.

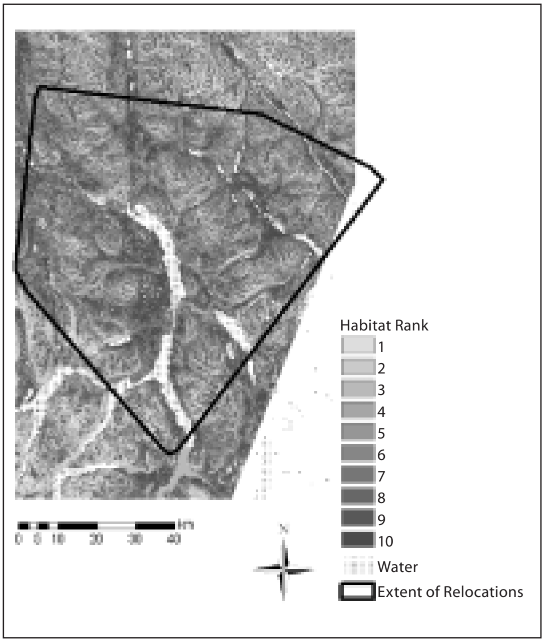

Fig. 4a. Current habitat ranking of caribou winter habitat in the Southern Lakes region of the Yukon Territory, Canada. The solid line is a 100% minimum convex polygon of all winter GPS relocations collected during the study.

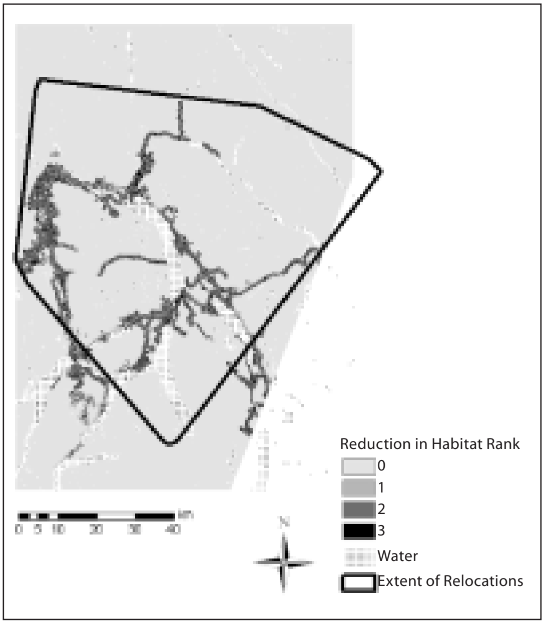

Fig. 4b. Reduction in winter caribou habitat ranking when the ZOI was included on the landscape in the Southern Lakes region of the Yukon Territory, Canada. The solid line is a 100% minimum convex polygon of all winter GPS relocations collected during the study

Within this same winter range, three First Nations have land interests through settlement of individual Land Claim Agreements. Collectively, First Nation controlled lands cover 24.4% of the Carcross caribou winter range. While collaboration in the Southern Lakes Caribou recovery plan can facilitate joint management of winter range under First Nation jurisdiction, it is important to recognize they are privately held lands. Consequently, private holdings, the ZOI around those holdings and First Nation held lands

Table 4. Proportional distribution of land cover classes remaining within the total Carcross caribou herd winter range (555 448 ha) but outside of the Zone Of Influence and of First Nation settlement land combined (64.6% of winter range).

	Outside of settlement land and outside of ZOI	
Land cover class	Area (%)	Proportion of total land cover class remaining (%)
CN	25.4	68.0
OXN	2.5	53.7
ONLi	2.4	34.3
OS	8.2	54.2
OP	8.5	51.1
CXND	2.3	82.5
OXND	6.5	69.4
WSh	1.5	68.7
WOt	1.5	62.6
CD	9.7	67.1
OD	0.8	53.7
OCTSh	2.6	77.9
CLSh	4.5	81.2
OLSh	3.8	80.5
OLShHb	1.5	72.9
OLShLi	2.5	68.6
DsOt	1.9	75.6
DsLi	1.1	71.0
DsHb	0.3	69.5
MYFb	0.1	77.5
Li	0.2	84.2
Wc	7.7	81.0
Rg	0.6	72.1
Sv	1.7	64.3
Other	2.3	
Total	100	64.6

currently account for 35.4% or just over a third of the winter range.

Cover types were not uniformly represented over the landscape. ONLi was substantially under represented as only 34% of this type is available within the unencumbered land base where proportional distribution would suggest values nearer 65% (Table 4). Other spruce and pine forest types, with the exception of CN are also somewhat lower than what would be proportional representation (51-54%). These patterns remained consistent when contrasted within the 85% kernel isopleth. Most vegetation types occurred in proportion to the entire winter range with the exception of ONLi and OP classes where these, similar to the ZOI assessment were over-represented suggesting concentration within a smaller proportion of the total winter range.

Habitat selection by GPS radio-collared caribou

Our assessment using Bonferonni confidence limits identified consistent selection for ONLi forest and DsOt shrub habitat types ($P<0.0001$, df =19) whereas use of CN forest cover types was significantly lower than would be predicted from availability ($P<0.0001$, df =19). Contrasts for other habitat types were not significant.

The final RSF model consisted of 25 317 points with 4220 used locations and 21 097 random locations. Five used locations from one individual and three random locations were censored from the dataset as they fell outside the coverage of our land cover classification. The most parsimonious model identified via the SWAIC procedure consisted of 14 coefficients (Table 5). The human infrastructure (HI) landcover category was dropped due to redundancy with the ZOI. The *k*-fold cross-validation procedure indicated the model was highly predictive (r_s = 0.96).

Table 5. Variables included in the most parsimonious model of adult female caribou winter habitat selection in the Southern Lakes region of the Yukon Territory, Canada.

Variable	Coefficient	Standard Error
TPI	0.02493	0.00675
Slope	-0.02213	0.00948
Hillshade	-0.00344	0.00228
Zone of influence	-0.43575	0.04807
Aspect – north	0.16895	0.13071
Aspect – east	0.05918	0.11410
Aspect - south	-0.05804	0.15910
Aspect - west	0.06037	0.13244
ONL	0.53678	0.14543
WNL	-1.00289	0.37499
CD	0.31652	0.07071
LSh	0.11203	0.12690
DSh	0.69814	0.22498
Non-vegetated	-1.11551	0.23307

An aggregate RSF (habitat) model generated by this analysis is presented in Fig. 4a. Probability of occurrence increased as the topographic position neared ridge or hilltops, and in open needleleaf, closed deciduous, low shrub, and dwarf shrub cover types. It decreased with increasing slope and hillshade, within the ZOI, and in woodland needleleaf and non-vegetated cover types. Relative to flat locations, occurrence was greater on north, east and west aspects, and lower on south aspects.

The reduction in habitat quality due to the ZOI (Fig. 4b) was estimated within a 100% MCP of all GPS relocations collected during the study. The MCP for this comparison is a close approximation of the Carcross caribou winter range in distribution and in overall area 53 4174 ha. Within this MCP, 9.2% of the area experienced a reduction in ranking when the ZOI was present. 1.3% was reduced by one rank, 6.1% reduced by two ranks, and 1.8% reduced by three ranks.

Discussion

Management of development activity on NMP caribou winter habitat embraces the concept of large undeveloped leave-areas (Smith *et al.*, 2000; Morgantini & Crosina, 2004) while increasing the intensity of activity in industrial zones. This could be an effective strategy for some Yukon herds, for example Wolf Lake (Farnell & McDonald, 1989) or Little Rancheria (Florkiewicz *et al.*, 2003), where caribou winter in relatively large and discrete areas. However, the Carcross range, bisected by large lake systems and mountain massifs, is arranged differently. Human activity through three Yukon highways, numerous private land dispositions and timber harvest areas are concentrated in forested valley bottoms also used by caribou. While the absolute area removed from the winter range through direct physical alienation appears relatively small, the projected influence characterized by the ZOI (Applied Ecosystem Management, 2004) demonstrates a much greater potential threat to caribou through avoidance of important wintering areas.

Salmo Consulting (2004) reviewed a substantial body of literature documenting both decline in southern caribou herds and avoidance of human development concurrent with increased human land use. Declines are often attributed to increased natural and human caused mortality (Seip, 1992; Harding & McCullum, 1994) and considered an example of cumulative effects of habitat loss, fragmentation and human development. Avoidance of human activity, considered an anti-predation strategy (Dyer, 1999; James and Stuart Smith, 2000) has also been documented for woodland caribou in west central Alberta (Oberg, 2001). Increasingly, the influence of human activity on caribou and other species are used to identify zones of reduced habitat value (Axys, 2001; Johnson & Boyce, 2001; Salmo Consulting, 2004; Johnson *et al.*, 2005) although the implications for caribou are difficult to demonstrate outside of theoretical models.

The disproportionate over-representation of two preferred habitat types (ONLi and OP) within our modelled ZOI and resultant under-representation in the remaining winter range is a concern. Similarly, significant avoidance of the ZOI by GPS radio-collared caribou suggests at least some influence on caribou from the existing footprint. Concentration of caribou into habitats outside of the ZOI would increase winter foraging pressure and potentially reduce lichen abundance in preferred habitat types. Increasing density of caribou on important winter feeding habitats may reduce the effectiveness of dispersion as an anti-predation strategy (Seip, 1992; James, 1999). Management of the remaining intact sections of winter range, particularly to avoid additional linear development and subsequent human activity is essential to maintaining Carcross caribou into the future.

Lichen producing habitats on the Carcross caribou winter range are dispersed, likely the result of the interaction between glacial deposition and post glacial hydrology in generating a complex assemblage of geologic land forms around the southern lakes. Classic glacio-fluvial origin pine stands (Cichowski, 1993; Florkiewicz *et al.*, 2003; Johnson *et al.*, 2004) are represented within the range although some areas have been modified by deposition and erosion events during periods of post glacial melt water release (Yukon Ecoregions Working Group, 2004). In conjunction with landform, low intensity ground fire is considered an important stand maintaining agent (Ahti & Hepburn, 1967; Applied Ecosystem Management, 1998; Goward, 2000) and possibly support long term persistence of postglacial caribou winter ranges on the landscape.

Lichen density within the Carcross range appears to be lower than in other ranges within the Yukon. Florkiewicz *et al.* (2003) identified mean lichen cover of 40% and ranging upwards to 95% on pine/lichen sites in some parts of the Little Rancheria caribou winter range. The depth and density of lichen mats also appeared greater than is generally noted for much of the Carcross winter range. Preferred lichen dominated habitats supported mean lichen cover ranging between 7% and 18% in Open Pine and 33.5% to 43% in Open Needleleaf Lichen types (Yukon Government, unpublished data). Overall, distribution of these habitats were widely dispersed over the landscape unlike the range of the Little Rancheria herd where much more entire and central to the wintering area (Florkiewicz *et al.,* 2003).

Core range use by caribou is often identified for caribou range (Schindler, 2004; Schmelzer *et al.*, 2004) and explicitly defined as the portion of a home range where use is high, exceeding an equal use pattern (Samuel *et al.,* 1985; Harris *et al.*, 1990; Kenward, 2001). Core areas may provide clearer measures of changing patterns of range use (Harris *et al.*, 1990). Based on the concept of exceeding equal use (Harris *et al.,* 1990) and discontinuity between successive kernel isopleths (Kenward, 2001), we suggest a core area at the 85% kernel for the Carcross caribou winter range. Although this represents only 27% of the winter range, the area supports 50% of the ONLi and 33% of the OP habitats preferred by GPS radio-collared caribou. Clearly, the concentration of both habitat and caribou into this area suggest it is critically important to the long term well being of this population.

Access to lichen may ultimately become a limiting factor for this herd. Parts of the lichen dominated historic range have largely excluded caribou (e.g., Cowley Creek and McClintock subdivisions) or are substantially altered as in the case of the Golden Horn subdivision and agricultural development to the east (UMA Engineering & Gartner Lee, 2004). It would be naive to consider that all activity within the area be halted. The demand for access to resources continues; a gas pipeline corridor has been proposed through the winter range since the 1970's along with the more immediate demand for domestic fuel wood, aggregate, and land for residential development (Nairn and Associates, 1993; UMA, 2004). Concurrently, off road vehicle (ORV) and snowmobile technology have greatly increased the human presence in all seasons (Hayes, 2000). Both humans and caribou have increased their use of the land over the recovery period for this herd. Settlement of three land claim agreements in the greater Whitehorse area have further complicated land management issues where part of the land base is excluded from consumptive public use that would otherwise meet some of the growth and development needs. Development is thereby concentrated onto the remaining land and managed by the Yukon Government. Co-operative management agreements on First Nation Settlement Land could, in future, satisfy some of the public demand for resources if caribou winter habitats are considered prior to development.

Regardless of the timescale, in resource development, the value of resource inventory and stewardship is to identify the most sensitive parameters and undertake management activities taking these into account. In most cases management is more likely to succeed if knowledge gained through assessments is used with full stakeholder participation, coordination in land management and planning and where government policy direction and leadership is strong (Morgantini & Schmiegelow, 2004).

Our study demonstrated that Carcross caribou select pine dominated vegetation types during winter and occupy relatively dispersed high density areas within a broad winter distribution. High value winter vegetation types are disproportionately over-represented within existing land use ZOI and private lands. This reflects the tendency for development in forested valley bottoms also home to wintering caribou. If development increases in high value vegetation types, either direct habitat loss or avoidance of areas associated with human influence will likely compress caribou into fewer remaining suitable sites. Concentration in this manner can increase their vulnerability to predation and increase the risks from fire or human caused (resource/residential/recreational) changes. Land planning and associated communication with land users will be essential to ensuring the successful recovery of the Carcross caribou on this suburban land base.

While the caribou concentration areas and important associated habitats were well represented through the 85% kernel home range polygon, areas of concentrated caribou winter vegetation and know concentration areas of caribou also occurred on the winter range outside of even the 95% kernel range limit. This can be remedied in future years as additional caribou are radio-collared. If the Carcross herd continues to grow, some used areas not represented through these data may become evident either through radio-collared animals or from periodic census survey work. This also highlights the need, in management, to apply more than one technique to assess wildlife habitat values.

Use of radio-collared females for this study suggests it is likely that the core range assessment through the kernel analysis will not adequately describe concentration areas for sexually segregated mature males. However, since population growth rates are most sensitive to female fitness (Gaillard *et al.*, 2000), and assuming that habitat occupancy does affect fitness, reductions in winter habitat quality for females is likely more important to the long-term conservation of the Carcross herd than human land use impacts on male winter habitat quality. Pooling males and females may in fact create more uncertainty in resource selection because of possible sexual segregation of males and females in winter.

Implications for management

Identification of important habitat types and core winter ranges are important components of the management program for the recovery of the Carcross caribou herd. However, it is also essential to maintain connectivity to ensure that caribou are able to move among important winter and other seasonal habitats. Refined habitat assessments and evaluation of detailed movement information from GPS collars should be completed as an essential component of the Carcross herd habitat assessment.

Core management areas should be designated within the caribou winter range where management is directed towards retaining high value lichen habitats for caribou. Although we anticipate an additional three years of information from existing radio-collars, we suggest the 85% kernel home range estimate to be the best representation of a core area for this herd. However, important lichen dominated stands outside of the kernel range must also be identified and incorporated into a final (connected) core winter range.

Over the entire winter range, development activity should be redirected from lichen dominated vegetation types (ONLi and OP) as an important part of any mitigation and cooperative management strategy. These habitats are most at risk as they are under-represented on the balance of the unencumbered public lands and over-represented within the private and ZOI portion of the land base. The potential for the additional influence of human activity (ZOI) must also be considered where development activities are contemplated adjacent to lichen dominated caribou habitat. The strategy of leaving large undisturbed tracts of important habitat for caribou (Racey & Armstrong, 2000; Smith *et al.*, 2000; Morgantini & Schmiegelow, 2004) is of limited value for this range due to its configuration and proximity to centres of human habitation. By identifying the remaining lichen dominated habitats where relatively little activity has occurred (i.e., outside of the current ZOI) as environmentally sensitive habitats, we can inform and collaborate with development interests to redirect activities to other appropriate locations.

Finally, it is essential that all levels of government (Territorial, Provincial, Municipal, and First Nation) work in conjunction with boards, councils and resource users towards an integrated land management strategy for resources in the greater Whitehorse area. Retaining caribou on this landscape into the future will require focused and directed management of habitats and land use on this winter range.

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Appendix. Zone of Influence identified for land use activities identified in the Carcross caribou winter range. Range of buffer widths are associated with estimated level of intensity for each activity. Only the lower buffer width was applied for ZOI calculation on the Carcross caribou winter range (after Applied Ecosystem Management Ltd. 2004).

Feature Class Code	Feature Type	Zone of Influence buffer width (m)			Original Source
		Lower	Middle	Upper	
AG	Agricultural Land	250	500	500	Professional Opinion
AG	Grazing Lease	0	250	500	Profession Opinion
IN	Cut Blocks	250	500	900	WCACSC*
IN	Electrical Utility Corridor	500	500	500	UNEP (2001)
IN	Excavation Sites	250	500	900	Professional Opinion
IN	Mine Site/Tailings (inactive)	250	250	250	Professional Opinion
IN	Survey Cut Line	0	250	500	WCACSC
RE	Backcountry Camp	900	900	900	Professional Opinion
RE	High Use Trail	500	500	500	WCACSC
RE	Low Use Trail	250	250	250	WCACSC
RE	Moderate Use Trail	500	500	500	WCACSC
RE	Winter Recreational Areas	Exclude polygon	Include polygon	Include polygon	Professional Opinion
TR	Airstrip	500	900	1000	UNEP (2001)
TR	Primary Road	500	900	1000	UNEP (2001)
TR	Railroad (disused)	500	500	500	Professional opinion
TR	Rough Road	500	500	500	WCACSC
TR	Rural Road	250	250	250	WCACSC
TR	Secondary Road	500	900	1000	UNEP (2001)
TR	Subdivision Road	250	500	500	WCACSC
UR	Commercial /Industrial	900	900	900	UNEP (2001)
UR	City of Whitehorse	0	0	0	Professional Opinion
UR	Public Recreation	500	500	500	Professional Opinion
UR	Public Service	900	900	900	UNEP (2001)
UR	Rural Residences	900	900	900	UNEP (2001)
UR	Urban Residences	900	900	900	UNEP (2001)

* WCACSC – West Central Alberta Caribou Steering Committee.

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Changes in vegetative cover on Western Arctic Herd winter range from 1981 to 2005: potential effects of grazing and climate change

Kyle Joly[1*], Randi R. Jandt[2], Cynthia R. Meyers[3] & Martha J. Cole[1]

[1] Bureau of Land Management, Fairbanks District Office, 1150 University Avenue, Fairbanks, AK, 99709, USA (*corresponding author: Kyle_Joly@blm.gov).
[2] Bureau of Land Management, Alaska Fire Service, P. O. Box 35005, Fort Wainwright, AK 99703, USA.
[3] Bureau of Land Management, Kotzebue Field Station, P. O. Box 1049, Kotzebue, AK 99752, USA.

Abstract: The population of the Western Arctic Herd, estimated at 490 000 caribou (*Rangifer tarandus granti*) in 2003, is at its highest level in 30 years. Twenty permanent range transects were established in the winter range of the Western Arctic Herd in 1981 to assess the impacts of grazing. These transects were revisited in 1995 and 1996 (1995/96). Only 18 of the transects were re-located, so an additional 7 transects were established in 1996. In 2005, all 25 remaining transects were revisited. Lichen coverage dropped by a relative 45.1% between 1981 and 1995/96 and by an additional relative 25.6% between 1995/96 and 2005. There was a significant decline in primary forage lichens between 1995/96 and 2005. Caribou use was greater in areas with high lichen abundance. Graminoid cover increased by a relative 118.4% from 1981 to 1995/96 and again by a relative 26.1% from 1995/96 to 2005. Shrub cover increased during the study whereas forb cover declined. The decline in lichen abundance on the winter range of the Western Arctic Herd over 24 years is an index of caribou habitat condition. The observed changes in vegetation cover can be attributed to caribou grazing, fire, and possibly global climate change. Continued declines in lichen cover could lead to population declines within the herd, range shifts, or both.

Key words: Alaska, assessment, habitat, lichens, monitoring, *Rangifer tarandus granti*, Western Arctic Herd, winter range.

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Introduction

The Western Arctic Herd (WAH), estimated at 490 000 individuals in 2003 by photocensus (Dau, 2005), is the largest caribou (*Rangifer tarandus granti*) herd in the region and is arguably the most important subsistence resource in northwestern Alaska. Approximately 15 000 animals are harvested annually from the herd (Dau, 2003), yielding some 500 000 kg of meat (Valkenburg, 1994). There are 40 villages that utilize the herd within the WAH's annual range, which covers about a ¼ of Alaska (Fig. 1). The status of the herd is not only of great importance to subsistence hunters and rural communities, but to sport hunters, recreationists, conservationists, biologists, land managers, and reindeer (*Rangifer t. tarandus*) herders as well.

Reindeer herding has occurred on the Seward Peninsula since 1891 (Stern *et al*., 1980; Swanson & Barker, 1992). The number of reindeer on the Seward Peninsula peaked in 1932 at around 127 000 and soon after there were signs of serious range deterioration (Stern *et al*., 1980; Swanson & Barker, 1992). The herding industry continues on the Seward Peninsula to this day. In 1981, permanent range transects were deployed in the Buckland Valley (Fig. 2), an area that potentially could have had both caribou and reindeer (Adams & Connery, 1981). These transects were deployed in an effort to monitor the effects of grazing, potentially by both caribou and reindeer, on winter range.

Between 1970 and 1976, the WAH experienced a dramatic crash in which the population plummeted from 242 000 to 75 000 individuals (Dau, 2003). From this low point, the herd rebounded quickly, growing at a rate of 13% annually until 1990 (Dau, 2003). The WAH has continued to grow, albeit at a

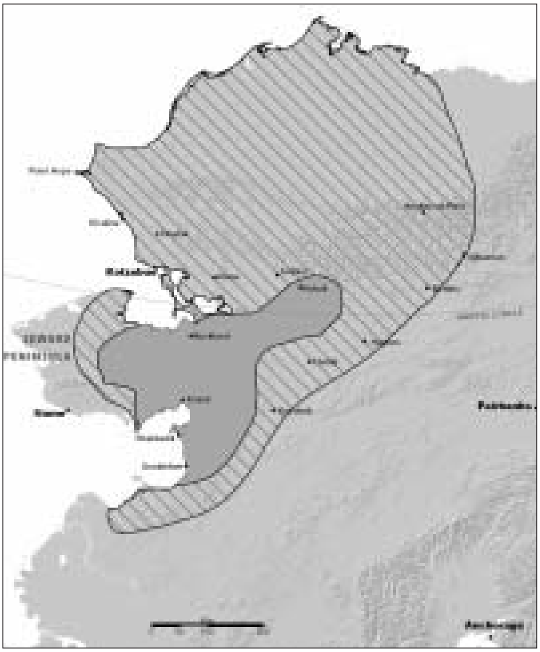

Fig. 1. Range of the Western Arctic Herd, 1981 – 2005, northwestern Alaska. Year-round distribution is hatched and core winter range is colored dark gray. Distribution is based on Alaska Department of Fish and Game data.

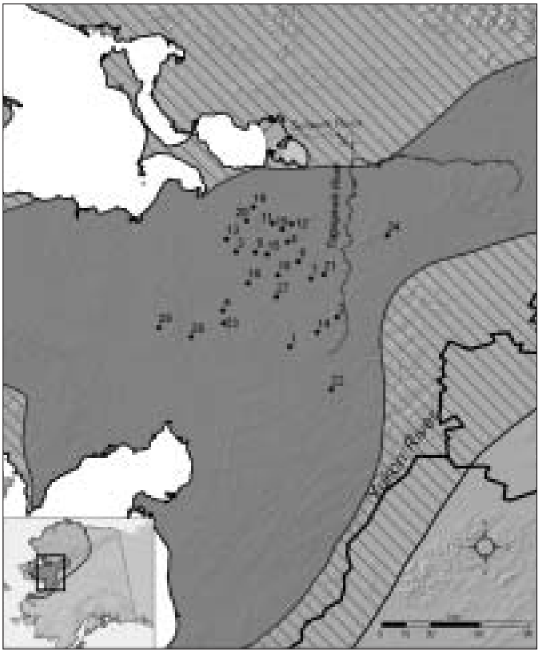

Fig. 2. Locations of the permanent range transects in the Buckland Valley, Seward Peninsula, Alaska. Transects 1 – 20 were deployed in 1981 and 21 – 27 in 1996. Transects #8 and #17 were not relocatable after 1981.

much more measured pace, until 2003 (Dau, 2005). As the WAH grew and expanded its range, the free-ranging reindeer would intermingle and depart their range with caribou as they migrated out in the spring, crippling the reindeer industry (Bader & Finstad, 2001). Since the range transects were deployed, only caribou have utilized the Buckland Valley, which they have done regularly over the years (Davis & Valkenburg, 1978; Davis *et al.*, 1982)

As the herd has grown, its winter range has concurrently expanded into new areas as well (Dau, 2005). The Buckland River valley, however, continues to be within the core winter range of the herd (Dau, 2003). The large size of the WAH has precipitated speculation about possible overgrazing of its range and when the inevitable decline of the herd will take place. The density (1.35/km^2) of caribou on the WAH's range in 2003 is 25% greater than the density (1.08/km^2) Messier (1988) thought to be excessive for the George River Herd in northern Quebec. These concerns have been magnified by recent reports of winter die-offs that have been linked to poor nutritional condition associated with severe winter weather (Dau, 2005) and the rapid decline of the Mulchatna Caribou Herd in southwestern Alaska from 1996 to 2004 (Hinkes *et al.*, 2005; Woolington, 2005). The contribution of range conditions to population dynamics has frequently been a subject of controversy, but actual studies of range conditions are very limited.

Our goals for the range monitoring study were 3-fold. First, we wanted to periodically assess range conditions and utilization. Second, we sought to identify changes in winter range over the 3 different decades for which we have quantitative range data. Finally, we hoped to assess changes in range condition in terms of overuse/community type (see van der Wal, 2006) and determine if these changes may have implications for the population status of the WAH.

Material and methods

Study area

Annually, the WAH ranged over 363 000 km^2 of northwestern Alaska (63° to 71°N and from 148° to 166°W; Fig. 1; Davis *et al.*, 1982; Dau, 2003). Although individual members of the WAH can be found across a broad swath of northwest Alaska, the Buckland River valley has been and continues to be in the core winter range (Davis & Valkenburg, 1978; Dau, 2003). The study area encompassed the entire Buckland River drainage, but also extended into surrounding uplands to the north, south, and southeast (Selawik Hills, Granite Mountain, and Nulato Hills, respectively).

The study area was dominated by treeless tussock tundra (primarily *Eriophorum vaginatum*), but contained rolling hills up to 900 m and large riparian corridors. Fruticose lichens (*Cladina* spp.), preferred caribou winter forage, mosses (primarily *Sphagnum* spp.) and shrubs (*Betula nana*, *Empetrum nigrum*, *Ledum palustre*, *Vaccinium uliginosum* and *V. vitis-idaea*) were important components of the tundra tussock community. Alpine communities were supported in the higher elevations. The riparian corridors were lined with willows (*Salix* spp.), alder (*Alnus crispa*) and white spruce (*Picea glauca*). Black spruce (*P. mariana*) stands were more common along the southern and eastern edges of the study area. Mean annual precipitation was about 30 – 40 cm. Snow cover, typically persisting from November through May, can be hard and crusted in wind scoured areas. Temperatures can drop to -45 °C during the winter months. However, mean temperatures have risen over the study period in this region, especially during the winter months (Stafford *et al.*, 2000).

Data collection and analysis

Twenty permanent vegetation transects were created in 1981 throughout the Buckland River valley. Canopy cover was ocularly estimated (Daubenmire, 1959) using a 20 cm x 50 cm quadrat placed every 2 m along a 50 m transect. Utilization (evidence of grazing such as signs of cratering and cropped or dropped lichens) was noted in each quadrat and reported as frequency for the transect. The transects were revisited and reread during 1995 and 1996 (henceforth 1995/96); however only 18 of the original 20 transects were located. A burn may have hidden 1 of these 2 transects from our survey team. Seven additional transects were created in 1996 (Fig. 2). These transects were selected because they fell within the core winter range and contained enough initial lichen cover so that changes could be detected. The methodology employed in 1981 was repeated during 1995/96, but all 25 transects were also reread using a more objective point intercept method (Floyd & Anderson, 1987). A 1.0 m x 0.5 m sampling frame was strung every 10 cm along both axes which created 50 intercepts. The frame was laid out every 4 m along the identical 50 m transect, for a total of 12 frames per transect (see Jandt *et al.*, 2003 for more details). The first species observed under the intercept was recorded. Non-vegetative observations (*e.g.*, rock, bare ground or water) were also recorded. In 2005, we only used the point intercept method. We employed transects as our sample unit for statistical analyses.

We assigned a category to each record; lichen, graminoid, shrub, forb, moss, or non-vegetated. *Andromeda polifolia* and *Oxycoccus microcarpus* were classified as forbs in 1981 (Adams & Connery, 1981). Though they are better categorized as shrubs (Viereck & Little, 1972), we adhered to the 1981 convention. Cover values for both of these species were extremely low (< 0.5%) and unlikely to influence analyses. *Rubus chamaemorus* was also classified as a forb. Other members of this genus are correctly categorized as shrubs but this species is not (Viereck & Little, 1972).

We further subdivided lichens into 3 categories, which were primary (most preferred forage species), secondary (other forage species), and non-forage lichens. *Cladina mitis*, *C. rangiferina*, *C. stellaris*, and *Cladonia uncialis* were assigned to the primary forage category based on published literature (Ahti, 1959; Scotter, 1967; Pegau, 1968; Holleman & Luick, 1977; Thomas & Hervieux, 1986; Thomas & Kiliaan, 1998) and our experience conducting range work in northwestern Alaska. We similarly assigned *Cetraria cucullata*, *C. ericetorum*, *C. islandica*, *C. nivalis*, *Cladonia amaurocraea*, and *C. gracilis* to the secondary forage lichen category. All other lichens were labeled as non-forage species. We tallied the number of different species to determine species richness (an index of diversity) for each transect for the 1995/96 and 2005 datasets. Utilization was calculated in the same manner as before.

We made 2 sets of comparisons. First, we compared ocular estimates from 1981 with ocular estimates from 1995/96 on the 18 relocated transects. Second, we compared point intercept estimates from 1995/96 with point intercept estimates from 2005 (n = 25). We employed paired t - tests to identify significant changes for both sets of comparisons. We utilized analysis of variance (ANOVA) to make other comparisons between the 1995/96 and 2005 point intercept data and between the original (1981) and newer transects (those added in 1996). We used linear regression techniques to test for association among elevation, utilization, species diversity, and change in lichen cover.

Results

The percent cover of the various categories (lichen, graminoid, shrub, forb, or moss) are displayed in Fig. 3. Based on the 1995/96 data, we found that both total lichen and primary forage lichen coverage were greater in the 7 transects added in 1996 than the original 18 transects deployed in 1981 ($F_{1, 24} = 8.53$, $P = 0.008$, $F_{1, 24} = 7.70$, $P = 0.011$, respectively). Average rate of utilization was not significantly ($F_{1, 49} = 0.25$, $P = 0.619$) different between 1995/96 (38.7%) and 2005 (35.0%). Utilization was able to loosely predict lichen coverage ($R^2 = 0.072$, F = 3.72, df = 49, $P = 0.060$; Fig. 4a). Caribou use of areas with < 5% lichen cover was negligible (Fig. 4a). Loss of lichen

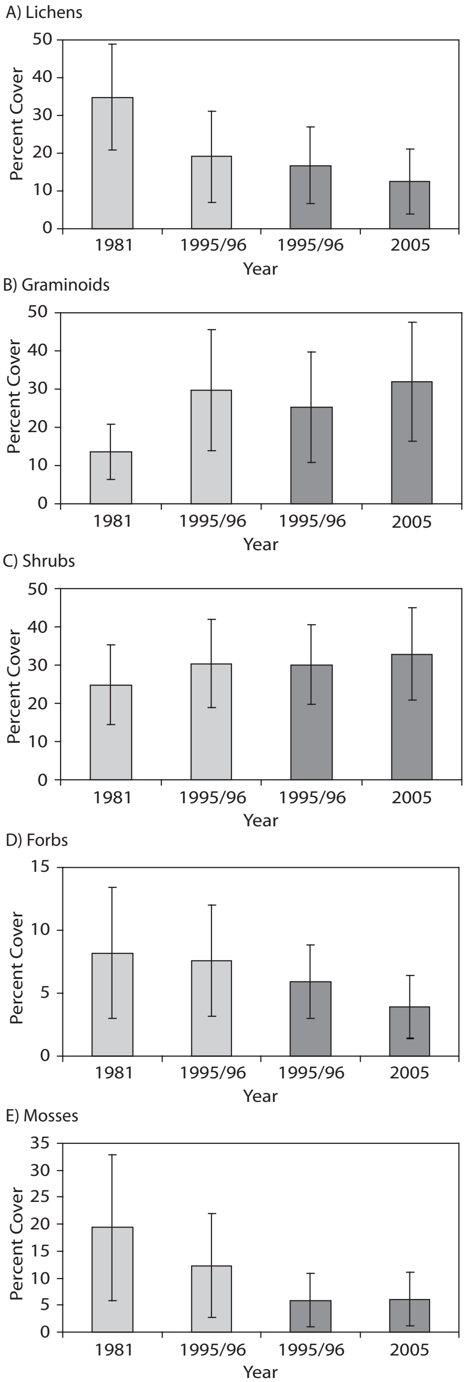

Fig. 3. Changes in the vegetative cover on winter range transects in the Buckland Valley, Seward Peninsula, Alaska from 1981 – 2005 for various categories. Ocular estimation techniques were employed during 1981 and 1995/96 (light gray bars), but a point intercept method was used in 1995/96 and 2005 (dark gray bars). Figure depicts mean ± SD.

cover from 1995/96 to 2005 was a good predictor of initial (1995/96) lichen cover (R^2 = 0.309, F = 10.27, df = 24, *P* = 0.004; Fig. 4b). Vegetative species richness was positively associated with elevation in 1995/96 (R^2 = 0.134, F = 3.55, df = 24, *P* = 0.072) and 2005 (R^2 = 0.174, F = 4.85, df = 24, *P* = 0.038). Percent lichen cover was not significantly associated with elevation in 1995/96 (R^2 = 0.009, F = 0.21, df = 24, *P* = 0.652) nor in 2005 (R^2 = 0.002, F = 0.05, df = 24, *P* = 0.825). Species richness was not significantly different between 1995/96 and 2005 ($F_{1,49}$ = 0.05, *P* = 0.816).

Lichen coverage declined significantly, from 34.8% to 19.1%, between 1981 and 1995/96 (*t* = 5.69, df = 17, *P* < 0.01). Both *Cladina rangiferina*, a primary forage lichen, and *Cetraria cucullata*, a secondary forage lichen, significantly declined in coverage between 1981 and 1995/96 (*t* = 2.92, df = 17, *P* < 0.01; *t* = 4.05, df = 17, *P* < 0.01, respectively). Moss also significantly decreased over this time period, from 19.4% to 12.3% (*t* = 3.74, df = 17, *P* < 0.01). Graminoid and shrub cover significantly increased from 13.6% to 29.7% (*t* = 5.63, df = 17, *P* < 0.01) and 24.8% to 30.4% (*t* = 3.87, df = 17, *P* < 0.01) between 1981 and 1995/96, respectively.

An analysis of the 1995/96 data revealed that differences in cover resulting from the differences between the ocular and point intercept methodologies were minor (see Fig. 3). Cover estimates were similar for most species, with an overall mean difference of just 0.7% (Jandt *et al.*, 2003). The two methods were in relatively close agreement even when comparing rare or inconspicuous species (Jandt *et al.*, 2003).

Our analysis of the point intercept data revealed that lichen cover declined significantly (*t* = 3.21, df = 24, *P* < 0.01) from 16.8% to 12.5% during the 1995/96 to 2005 time period. The decline in primary forage lichens, from 7.8% to 4.6%, was also significant (*t* = 3.62, df = 24, *P* < 0.01). *Cetraria cucullata*, a secondary forage lichen present on every transect, declined by a relative 17.1% from 1995/96 to 2005. However, changes in both secondary and non-forage lichens were not significant (*P* > 0.05) between 1995/96 and 2005. The decline in overall and primary forage lichen cover over the study period coincided with the rapid expansion of the number of individuals in the WAH (Fig. 5).

We found that the amount of lichen loss between 1995/96 and 2005 was a good predictor of percent cover of lichen in 1995/96 (R^2 = 0.309, F = 10.27, df = 24, *P* = 0.004). Only one transect (# 24) with high initial lichen cover (31.3%) did not show a decline in 2005. Lichen cover on this transect, which had no sign of utilization in 2005, increased to 37.3% by 2005. We were unable to detect an association between lichen loss and elevation (R^2 = 0.043, F = 1.02, df = 24, P = 0.323).

Our analysis revealed that graminoid cover significantly (t = 4.39, df = 24, P < 0.01) increased from 25.3% to 31.9% between 1995/96 and 2005. Increased cover in *Eriophorum* spp. (3.4%) and *Carex* spp. (1.5%) accounted for most of this change. The wetland species *Carex aquatilis* was the only member of the genus that did not demonstrate an increase (- 0.1% cover) during this period. Similarly, shrub cover significantly (t = 2.12, df = 24, P = 0.045) increased during this time period from 30.1% to 32.8%. The largest increase in cover was seen in *V. uliginosum* (1.5%), but *Dryas* spp., *V. vitis-idaea*, *Empetrum nigrum*, and *Arctostaphylos alpina* also increased. *Salix* spp. cover did not significantly change during this time period. *Ledum palustre* had the biggest decline in cover (1.0%) for a shrub species. We found that forb cover declined significantly (t = 3.86, df = 24, P < 0.01) between 1995/96 and 2005 from (5.9% to 3.9%), primarily due to a decline in *Rubus chamaemorus*. *A. polifolia* and *O. microcarpus* both slightly increased, which would only enhance (however slightly) the observed increase of shrubs and decline of forbs if categorized as shrubs rather than forbs. Moss cover was not significantly different between 1995/96 and 2005 (t = 0.43, df = 24, P = 0.673).

Discussion

The WAH has undergone a 30-year period of continuous growth, beginning in 1976. The pace of this growth has decelerated as the herd has reached 490 000 individuals (Dau, 2003; 2005). Portions of the herd have recently expanded into winter range outside the historic core range and there have been some indicators of poor nutrition associated with severe winter conditions (Dau, 2005). All of these factors have contributed to speculation as to when the herd will inevitably decline and if that decline will be precipitous. Our permanent range transects, deployed in 1981 and 1996, provide insight into 1 factor that plays into the complex calculus that shapes the herd's trajectory.

Terricolous lichens constitute the majority of diet for barren-ground caribou herds during winter (Thompson & McCourt, 1981; Boertje, 1984; Thomas, 1998) and the WAH is no exception (Saperstein, 1996; Jandt *et al.*, 2003). Evidence that lichens are not requisite for caribou come from low density, high Arctic, island populations (Thomas & Edmonds, 1983). Lichens appear to be a critical component of the diet of large migratory herds in North America (Klein, 1991). However, it has been argued that a transition from lichen-dominated tundra to sedge-dominated tundra due to *Rangifer* grazing is predictable and the new system could be highly productive (van der Wal, 2006). It appears that the WAH may be able to answer this question in the future.

We found that lichen cover declined significantly (by a relative 3.0% annually) from 1981 to 1995, during which time the WAH grew at a consistently very high rate. Lichen cover continued to decline

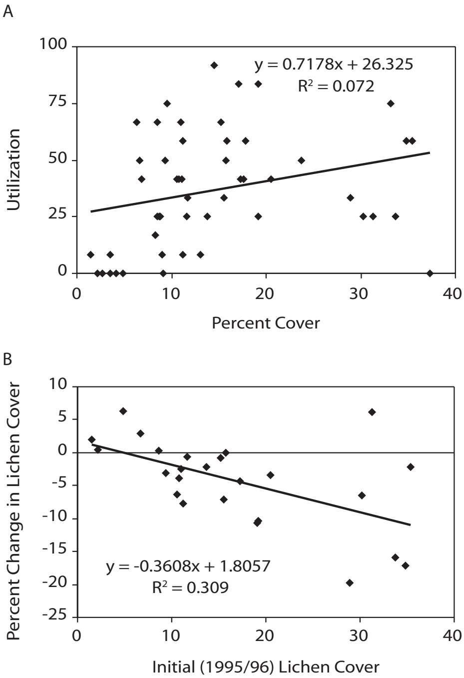

Fig. 4. Use of lichens by caribou in the Buckland Valley, Seward Peninsula, Alaska. A) Utilization versus amount of lichen cover (1995/96 and 2005 data) B) Percent change in lichen cover from 1995/96 to 2005 versus initial (1995/96) lichen cover.

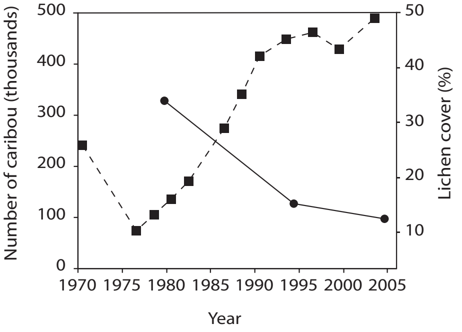

Fig. 5. The decline of lichen cover (solid line with circles) on the winter range of the WAH coincided with the rapid expansion of the number of individuals in the herd (dashed line with squares), northwest Alaska.

between 1996 and 2005. The rate of decline was slightly less (a relative 2.6 % annually) during this time period which was concurrent with the growth of the herd slowing and its expansion into new winter range (Dau, 2003). Importantly, primary forage lichens significantly declined during this time period. Utilization and the amount of decline in lichen cover were significantly associated with initial lichen cover, implying that caribou selected for areas with high lichen abundance. Although the decline in lichen cover cannot be directly correlated with the eruption of the WAH and increased grazing pressure, it does provide a compelling, simple, and logical inference (see also Moser *et al*., 1979; Arseneault *et al*., 1997; van der Wal, 2006). This is further supported by the fact that transect # 24 (the northeastern most transect, Fig. 2) was closest to the edge of the core winter range, contained no sign of utilization in 2005, and was the only transect with high lichen cover not to reveal a loss of lichen cover over the last decade (Fig. 4). Transects read in 1997 outside (at that time) the winter range of the herd on the southern Seward Peninsula had high lichen cover (BLM, unpubl. data). The effects of trampling may exacerbate the deterioration of lichen cover (Pegau, 1969; Manseau *et al*., 1996). Reindeer have been absent from the study area since its inception.

The consequences of global climate change (particularly warming and drying) have also been implicated as factors that may reduce lichen abundance in the tundra ecosystem (Chapin *et al*., 1995; Cornelissen *et al*., 2001; Epstein *et al*., 2004; Walker *et al*., 2006) and may have contributed to declining lichen cover that we observed. Lichen cover declined in recently burned (< 35 years old) areas with low initial cover (< 5%) that probably would not have been utilized by caribou (Arseneault *et al*., 1997; BLM, unpublished data).

Wildland fire, an environmental factor that can dramatically reduce lichen abundance (Viereck & Schandelmeier, 1980; Klein, 1982; Swanson & Barker, 1992; Thomas & Kiliaan, 1998; Rupp *et al*., 2006), is infrequent in the tundra ecosystem (Wein, 1976). Caribou foraging during winter avoid areas that have been burned by wildland fires (Schaefer & Pruitt, 1991; Thomas *et al*., 1998; Joly *et al*., 2003). The Seward Peninsula, including our study area, appears to have a relatively high fire frequency rate for tundra ecosystems (Racine *et al*., 1987) and it has been predicted that fire frequency and extent will continue to increase (Wein, 1976; Rupp *et al*., 2000; McCoy & Burn, 2005). Disturbance from fire was uncommon on our transects, though it did occur. One 1981 transect was presumably "lost" to a wildfire and a second transect burned between 1995 and 2005.

Our data did not reveal a reduction in species richness between 1995/96 and 2005, which is in contrast to the findings of other researchers investigating the consequences of global warming (Chapin *et al*., 1995; Walker *et al*., 2006). Species richness was positively associated with elevation, but even our highest transect was under 610 m. We found that graminoid cover doubled between 1981 and 1995/96 and increased again between 1995/96 and 2005 by a relative 26.0 %. These results are consistent with research suggesting that global warming, drier conditions, and mammalian grazing and trampling may lead to a conversion of the tundra ecosystem to a grassland steppe community (Zimov *et al*., 1995; Rupp *et al*., 2000, van der Wal, 2006).

Shrub cover also increased during this time period, though not as dramatically. A primary finding for research documenting the response of the tundra ecosystem to global warming is an increased abundance of shrubs (Chapin *et al*., 1995; Epstein *et al*., 2004; Tape *et al*., 2006; Walker *et al*., 2006). Increased shrub cover has been implicated as another factor negatively effecting lichen abundance (Pegau, 1970; Cornelissen *et al*., 2001). Shading and increased litter cover caused by these vascular plants may retard lichen growth, as well as alter snow melt patterns (Sturm *et al*., 2005). Vascular species also recover from grazing more quickly than lichens (Henry & Gunn, 1991).

We detected a significant decline in the cover of forbs during the last decade of the study; however this was not mirrored in Epstein *et al*.'s (2004) findings. *R. chamaemorus*, the species driving the decline in forbs, is typically found in wet, boggy areas (Viereck & Little, 1972). The significant decline of moss cover we found since the beginning of the study period is in accordance with previous findings on the effects of global warming (Chapin *et al*., 1995; Epstein *et al*., 2004; Walker *et al*., 2006), but possibly also grazing (van der Wal & Brooker, 2004; van der Wal, 2006). The reduction in moss cover could feed into a positive feedback loop and lead to increased drying of the tundra, a northward and westward shift of treeline and even more wild fires (Zimov *et al*., 1995; Rupp *et al*., 2000; Rupp *et al*., 2002).

Caribou populations naturally fluctuate and these cycles are dependant on the complex relationships among climate, the caribou, their range and predation (Messier, 1991; Gunn, 2003). Grazing is an important ecosystem driver (Hobbs, 1996; Augustine & McNaughton, 1998; Mysterud, 2006; Wisdom *et al*., 2006). Our results are in agreement with the assertion that grazing by caribou can be an important factor in the depletion of lichen of large areas of continental ranges (Moser *et al*., 1979; Messier *et al*., 1988, Arseneault *et al*., 1997) and the rapid transition from lichen-dominated to graminoid-dominated tundra communities (van der Wal, 2006). All indications show that the Arctic is already warming (Hansen *et al.*, 1999; Barber *et al.*, 2000; Oechel *et al.*, 2000; Serreze *et al.*, 2000; Goetz *et al.*, 2005). The response to this warming will likely include changes in vegetative communities (Chapin *et al.*, 1995; Epstein *et al.*, 2004; Tape *et al.*, 2006; Walker *et al.*, 2006; this study) and increased wildland fire (Rupp *et al.*, 2000; Goetz *et al.*, 2005; McCoy & Burn, 2005). Changes in the vegetative communities may accelerate the rise in fire frequency (Starfield & Chapin, 1996; Rupp *et al.*, 2000). Our study was not designed to tease apart the relative contributions of grazing and global warming to the rapid and radical changes in the tundra ecosystem that we documented, though both appear to be important ecosystem drivers.

The WAH is currently at a known population high, has shown signs of poor nutrition associated with severe winter weather and has expanded its range (Dau, 2003; 2005). These signs were also present prior to the recent crash of the Mulchatna Caribou Herd (Hinkes *et al.*, 2005). The decline of this herd may displace additional sport hunting pressure on to the WAH. We have gone further, in the case of the WAH, by showing that lichen cover has decreased over the last 24 years and that the decline in primary caribou forage lichens was significant. Conditions on the WAH's core winter range, in terms of lichen cover, are deteriorating. All of these factors are interrelated and may or may not increase the rate of change. Although no one can accurately predict how the complex interaction of these factors will affect the WAH, the status of the indices we do have indicate that conditions are suitable for a decline in the herd.

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Determining effects of an all weather logging road on winter woodland caribou habitat use in south-eastern Manitoba

Doug W. Schindler[1,*], **David Walker**[2], **Tim Davis**[1] **& Richard Westwood**[1]

[1] University of Winnipeg, Centre for Forest Interdisciplinary Research, Winnipeg Canada R3B 2E9 (*corresponding author: d.schindler@uwinnipeg.ca).
[2] University of Manitoba, Winnipeg Canada R3T 2N2.

Abstract: The Owl Lake boreal woodland caribou population is the most southerly population in Manitoba. It is provincially ranked as a High Conservation Concern Population. Forestry operations exist in the area and there are plans for further forest harvest and renewal. The Happy Lake logging road is the only main access through the Owl Lake winter range. This logging road is currently closed to the public and access is limited to forestry operations during specific times of the year. An integrated forestry/caribou management strategy for the area provides for the maintenance of minimum areas of functional habitat. Habitat quality along the road was compared to habitat quality in the winter core use areas, within the winter range and outside the winter range. To evaluate the extent of functional habitat near the road, we conducted animal location and movement analysis using GPS data collected from January 2002 to March 2006. Habitat quality in the winter range, core use areas and along the road were assessed and found to be similar. Analysis of caribou locations and movement illustrate less use of high quality habitat adjacent to the Happy Lake Road. Loss of functional habitat is suggested to occur within 1 kilometre of the road. This potential loss of functional habitat should be incorporated into integrated forestry and caribou conservation strategies. Road management is recommended to minimize the potential sensory disturbance and associated impacts of all weather access on boreal woodland caribou.

Key words: access, functional habitat, movement.

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Introduction

Manitoba's woodland Caribou (*Rangifer tarandus caribou*) are designated as a threatened species under the Manitoba Endangered Species Act (1990). In response to the federal Species at Risk Act (SARA), Manitoba Conservation released a Conservation and Recovery Strategy for Boreal Woodland Caribou in Manitoba (Manitoba Conservation, 2006). This strategy identifies ten boreal woodland caribou ranges in the province, of which three are identified as "High Conservation Concern", including the Owl Lake herd. An integrated forestry/woodland caribou management strategy was developed to provide a framework for forest harvest and renewal based on quantifiable habitat objectives for the conservation of the Owl Lake Range (EMWCAC, 2005).

The Owl Lake herd has been studied using standard very high frequency (VHF) and global positioning system (GPS) telemetry monitoring since 1986. The Owl Lake range is contained almost entirely in south-eastern Manitoba within a portion of the Lac Seul Boreal Upland (Ecological Stratification Working Group, 1995) or Eco-Region 90 (Fig. 1). Based on historical and current data, the home range has remained relatively constant and is currently estimated at 927 km^2 (Schindler, 2005). The Owl Lake herd is considered to be a sedentary population estimated at approximately 75 animals (EMWCAC, 2005). This population has remained stable since the early 1980s based on historical reports and unpublished government records (Carbyn, 1968; Larche, 1972; Crichton, 1987; TAEM, 1999). There are currently 6 VHF and 7 GPS collared animals in this range representing a sample intensity of 17%.

Owl Lake animals are known to utilize different portions of their range during different seasons and may travel up to 30 kilometres between summer range in the east and winter range in the west (Schindler, 2005). Much of the summer range is located in provincial park zones that do not allow commercial resource development. The core winter range is not protected and commercial resource development is allowed. Approximately 10% of the entire winter range has been subjected to forest harvesting during the 1970s and early 1980s. A large experimental forest harvest is currently being conducted along the easterly portion of the winter range, mainly outside of core use areas, and represents less than 10% of the current winter range (EMWCAC, 2005).

The Happy Lake logging road was constructed in 1992 and is the only all-weather access in the winter range. Other linear development is limited with one snowmobile trail and a small section of electric transmission located at the eastern periphery of the winter range. The logging road is gated and public access is not permitted with the exception of vehicle use pertaining to forestry operations and commercial trapping (EMWCAC, 2005). The Owl Lake boreal woodland caribou are protected by a hunting closure that includes the prohibition of First Nations subsistence hunting (EMWCAC, 2005).

Although the Owl Lake caribou population is stable, there is concern that expanded resource development may affect its long-term viability. Factors of concern include direct and indirect negative effects associated with access and habitat alteration, changes to alternate prey and predator dynamics, illegal hunting and disturbance associated with access (EMWCAC, 2005).

Specifically, there is a need to understand the effects of all weather access in integrated forestry and caribou management planning and to provide quantitative evidence of caribou habitat utilization near all weather access. James and Stuart Smith (2000) assessed caribou and wolf activity relative to roads, trails and seismic lines and found that caribou locations were significantly further from linear features compared to wolf locations that were significantly closer to linear features. They also found that caribou predation by wolves and humans was closer to roads than live locations suggesting that industrial development and the associated access could result in an increased risk of mortality on caribou. Habitat selection and use by caribou also acts as a function of predator avoidance. James *et al.* (2004) found that caribou select habitat that is less suitable for moose, resulting in a spatial separation away from wolves. This suggests that access into caribou habitat reduces the refuge value of these habitats and can potentially increase predation rates on caribou (James *et al.*, 2004). Rettie & Messier (2000) also found that caribou in central Saskatchewan largely illustrate a preference for peatlands and black spruce forest and avoid disturbed and early successional forest. Furthermore, habitat selection is driven by predation at a coarse landscape scale.

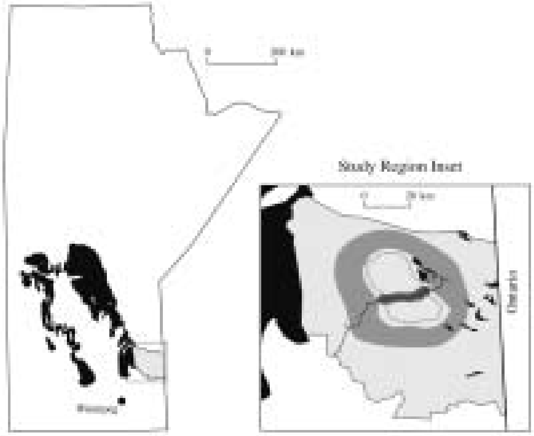

Fig. 1. Manitoba map showing location of the Owl Lake study area within the province (dotted box) relative to Winnipeg and the major lakes (black). Within the study region (inset map) the Happy lake road is shown (black bold line), as is the 'core area' that contains all core kernels in the winter range that are discussed in this paper (dotted line). Also identified is the area immediately surrounding the winter range (medium grey 'halo') and the habitat in the core area along the road (dark grey).

One key objective of the Owl Lake integrated forestry/woodland caribou strategy is the maintenance of two-thirds of a winter management zone in large blocks of un-fragmented high quality habitat with low predator densities. Similar to forest harvest, the sensory effects of logging access may cause reduced use of functional habitat which in turn may influence management decisions regarding integrated forestry/caribou planning. Development of mitigation and management tools are necessary in a multi resource use environment to minimize the negative cumulative effects of resource development on boreal woodland caribou including access (Armstrong, 1996).

To better understand the potential effects of the logging road on caribou, we first assessed the habitat conditions within the winter range. We used GPS collar data gathered from 2002 to 2006 to determine current core use areas and compared these to historical core use areas using standard telemetry data collected prior to road construction for the period 1986 to 1992. We evaluated habitat quality in the winter range and compared differences in habitat suitability along the road to core use areas, within the winter range, and outside the winter range to determine if habitat suitability is significantly higher away from the road. We then assessed animal movements and densities of animal locations relative to the road during the winters of 2004-05 and 2005-06. We used winter GPS location data for 2005 and 2006 to assess specific animal movements and location densities during the time the road was actively used for forestry operations and hauling. Our main research question was to determine if animals used high quality habitat adjacent to the road less than other areas and if there is loss of high quality functional habitat adjacent to the logging road.

Methods

Areas where wildlife utilize habitat at significantly higher rates within home ranges can be described as core areas (Semlitsch & Jensen, 2001). Delineating areas of high use within a home range better captures changing patterns of resource utilization and more precisely identifies important habitat components than statistics derived from total range area (Harris *et al.*, 1990). However, determination of core areas within a range requires the construction of density functions with sufficient location information to provide robust estimates of use. The use of GPS in automated telemetry has been thoroughly studied to determine the appropriateness of conducting animal movement research (Rodgers & Anson, 1994; Moen *et al.*, 1996; Rodgers *et al.*, 1996; Moen *et al.*, 1997; Dussault *et al.*, 2001). GPS collars are capable of collecting multiple daily fixes over an extended time and provide an unbiased and precise estimate of animal locations. The spatial and temporal resolution of GPS data allows researchers to study interactions of animals and their habitat at an unprecedented level of detail (Rempel *et al.*, 1995; Rempel & Rodgers, 1997).

GPS data from 7 female Owl Lake caribou were collected from January 2002 to March of 2006. These data represent approximately 10% of the population and consist of 12 637 data records. To assess winter habitat use relative to the logging road, we identified and mapped core habitat by applying an objective criterion to an adaptive kernel analysis (Schindler, 2005). Individual animal data included one, three and four hour fix frequency intervals. All individual animal data were normalized to a 4-hour fix rate to reduce effects of autocorrelation. All normalized GPS data were pooled and stratified into separate monthly winter data sets for all individual animals.

Adaptive kernel analysis for each animal by winter month and all animals by winter month were conducted using the Home Range Extension (HRE) in Arcview (Rogers & Carr, 1998). The adaptive kernel estimate of monthly home range for all animals by month was used to generate core use areas containing all winter ranges used by each individual animal. The monthly winter kernel polygons were amalgamated and mapped. This resulted in overall winter utilization distribution (UD) isopleths generated at 10% volume intervals. Historical core use areas were also estimated using VHF data collected from 1986 to 1992. A total of 271 winter locations were used in an adaptive kernel analysis to provide an estimation of historical core use areas.

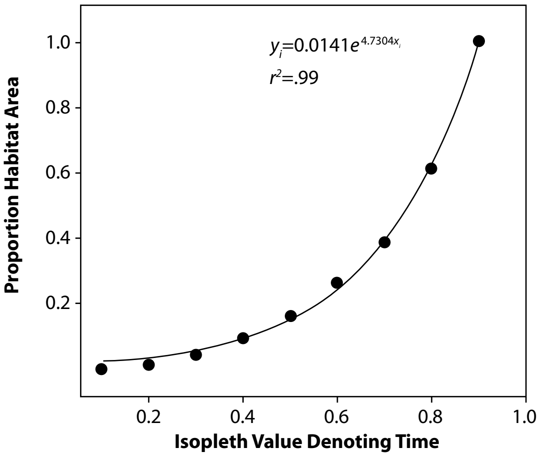

Fig. 2. Example of an exponential fit model for December GPS data and the unique solution for Eq. 1 for this month. The first derivative of this solution achieves a value of one at a volume of 0.572.

To identify the UD isopleth that best describes current core use areas, we first conducted an exponential regression fit model to determine the relationship between UD isopleths denoting time and area used (home range), both expressed as proportions. The following general equation was solved:

$$y_i = b_1 e^{b_2 x_i} \quad \text{(Eq 1.)}$$

where b_1 and b_2 are coefficients found by a least-squares fit to the observed data. The UD isopleth contour representing the area where animals spent the greatest amount of time in the least amount of area was determined as the isopleth value at which the first derivative of the exponential model (Eq. 1) equalled one (Van der Wal, 2004). Exponential regressions were conducted separately for each winter month using proportion of area used (y-axis) in each 10% isopleth denoting time (x-axis). Fig. 2 illustrates an example exponential fit model for December GPS collar data. We used the mean of these as representing the isopleth value that optimally and objectively identifies core use areas following Van der Wal (2004).

To evaluate habitat differences within the winter range, along the road, and in the region surrounding the winter range (Fig. 1, inset), we utilized a re-sampling

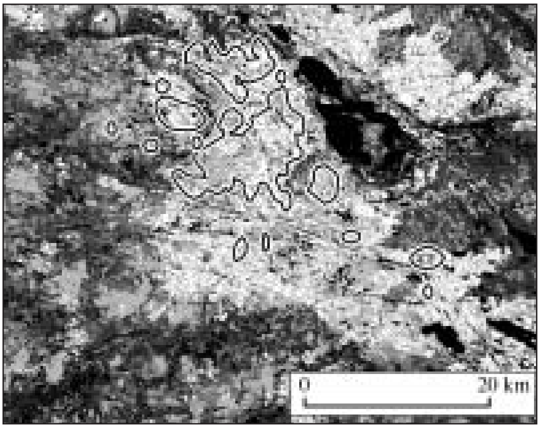

Fig. 3. Map of HSI values where increasingly brighter grey shade indicates higher habitat suitability (ie. black=lowest to white=highest HSI). For reference, eleven core kernel areas are also shown (black on white lines).

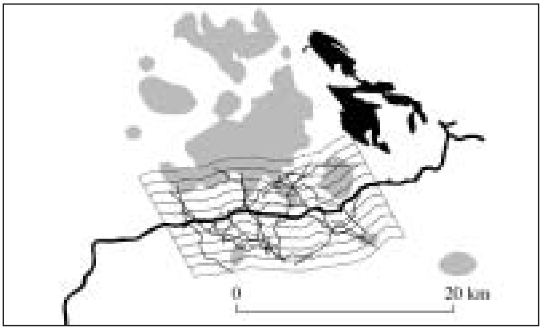

Fig. 4. Illustration of the study design used to examine the influence of the Happy Lake Road (bold black line) on caribou movement patterns. Also pictured are the Manigotagan lakes (black polygons) and core kernel areas (light grey) for reference. The buffer zones used are indicated as symmetrical bands on either side of the road. Overlaid on these zones are examples of the random roads used in the road crossing analysis. Note this example uses a small subset of the random roads used in the analysis, results presented in this paper include roads that were placed throughout the MCP.

random windows technique (Potvin *et al.*, 2001). Habitat comparisons were based on mean habitat values calculated using the current Manitoba Habitat Suitability Index (HSI) model for woodland caribou in eastern Manitoba (Schindler & Lidgett, 2006). This third version HSI is based on forest structure and composition attributes contained in the digital Forest Resource Inventory (FRI) for Manitoba and was developed using a delphi technique for HSI models (Crance, 1987). The caribou HSI is a habitat analysis tool designed to assess habitat quality over large areas and assumes a relationship between forest composition and various life stage requirement such as winter food (lichen), cover (refuge) and reproductive habitat (USFW, 1980). It is expressed as an index between zero and one (USFW, 1980). High quality habitat for management purposes is defined using a minimum threshold value (EMWCAC, 2005). Fig. 3 provides an illustration of HSI habitat mapping in the Owl Lake Range.

Differences in habitat use were tested following Potvin *et al.* (2001) by randomized sampling of habitat. Random sampling windows or discs were generated based on the average monthly winter core area size. These sample discs were randomly located within the entire winter kernel area using a random point generator with a sample disc placed at the centroid of each random point. Based on Potvin *et al.* (2001), we allocated 50 random sample discs in the winter range, 50 random discs along the portion of the road that intersected the kernel range estimate, 80 in the area surrounding the winter range (Fig. 1, inset). The numbers of disks used reflects the area available and the need to reduce overlap as much as possible while providing a sample size approaching that used by other authors (e.g. Potvin *et al.*, 2001). Fourteen disks situated over the core winter range kernel polygons were sampled to provide baseline habitat values for core use areas.

The area-weighted HSI value for each of the forest stands within the sample disks were summed to give an overall value for habitat suitability within the disks. Forest stands were sampled with some replacement. Overlapping sample discs were included in the analysis; however, sample disks containing a high proportion of water were removed to avoid biased estimates in lake rich areas on the periphery of the winter range. The randomization utilized a bootstrapping technique by randomly selecting 14 sample disks from the set of random sample disks for each sampling areas (Potvin *et al.*, 2001; Manly, 1991). The 14 randomly selected disks simulated the selection of 14 core kernel areas chosen at random on the landscape. The average of the 14 disks was calculated and this was repeated 10 000 times for each sampling area. We compared the area-weighted HSI values for the observed fourteen high use winter kernel areas with those from the bootstrapped random distribution. The proportion of random sample discs in each sampling area with HSI values exceeding those observed for the Happy Lake caribou are reported. The HSI model was developed by analysis of habitat characteristics in known areas and detects differences in habitat suitability on the landscape. Thus, the purpose of this comparative approach was not to detect HSI significance, but to detect the relative and potentially substantial differences in the spatial pattern of suitable habitat within the region in relation to the areas in use by caribou.

To evaluate the potential loss of functional habitat along the road, we utilized winter 2005 to 2006 data that corresponded with the period when the road had active traffic related to logging and hauling. Traffic volume was not specifically measured; however, based on hauling rates estimated by weight scale summaries, between 10 to 60 one-way trips per day occurred throughout the winter. Traffic was sporadic and there were extended periods where no hauling occurred; however, it is likely that other traffic related to forestry operations continued. No estimates of other traffic were available.

We established a sampling area encompassing approximately 5 kilometres on each side of the road within the winter kernel range and established 5 successive one-kilometre buffers north and south of the road (Fig. 4). The main wintering areas are located north of the road and were not included in the assessment of road use due to the distance and lack of road effect in remote areas. For each of these buffer zones, we counted the number of GPS telemetry points within the zone and expressed these values as point densities as a function of distance from the road. To determine if movement distances vary as a function of the road, data from five individual animals were evaluated and used in this analysis. Path trajectories for each animal using the four hour normalized data were generated using the Animal Movement Extension in ArcView GIS (Hooge & Eichenlaub, 1997). Four-hour travel path segment lengths in each buffer zone were calculated and enumerated using Hawth's Tools v3.24 extension for ArcGIS (Beyer, 2006). The normalized 4-hour movement distances for each animal were pooled and the median distance values were compared in each 1 kilometre buffer zone.

The frequency and speed of animals crossing the road can also provide insight into sensory effects and illustrate habitat use patterns adjacent linear features. Dyer *et al.* (2002) compared rates of caribou crossings on roads and seismic lines to simulated linear features using GIS. They found that roads were semi-permeable barriers and may cause a loss of functional habitat due to animal avoidance. Ungulate movement patterns consist of periods of travel and periods of resting and feeding (Saher & Schmiegelow, 2004). Disruption of these patters could result in increased energy expenditures and loss of body mass. Bradshaw *et al.* (1998) modelled the cumulative influence of disturbance from petroleum exploration and found that there is a potential effect on individual energy and mass loss on caribou in north-eastern Alberta.

To assess animal movement and use along the road we conducted a separate analysis that compared the number of animal crossings of the actual road to crossings on 1000 randomly located sample roads. We used the 10.8 kilometre segment of the Happy Lake Road within the winter kernel range as a random projection segment to emulate simulated roads in the minimum convex polygon (MCP) for each animal that crossed the road during winters of 2004 to 2006. We used the Alternate Animal Movement Routes Extension (Jenness, 2005) to generate and randomly place 1000 duplicate road segments. The simulated roads were randomly placed both in location and orientation throughout the MCP. The actual number and length of each crossing of the actual road were compared to number and length of crossings on the 1000 random roads generated for each animal. Examples of random roads that coincide with the buffer zones are overlaid on Fig. 4 as a reference. Significance between actual road crossings and mean crossings on random roads was carried out using a chi square test. This was carried out for seven individual case studies.

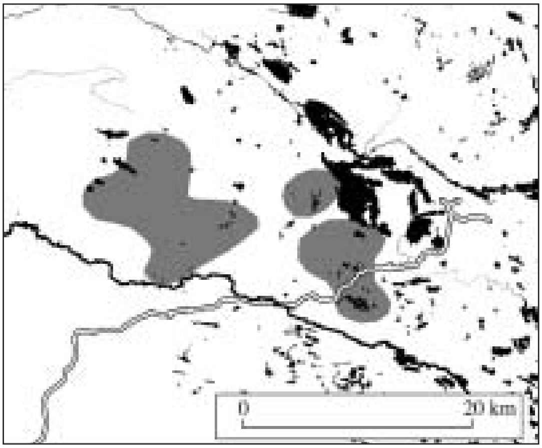

Fig. 5. Historical range of the Owl Lake caribou (grey) prior to road construction (for reference the road is included, white-on-black line). Water and river features are indicated in black. The dominant linear feature prior to road construction was Black River (bold black line), which arcs south-east across the bottom third of the region shown here.

Results

The adaptive kernel analysis using the historical telemetry data from 1986 to 1991 illustrates core use of habitat where the road now exists (Fig. 5). For current data, the mean winter monthly UD value calculated using Eq. 1 was the 58% isopleth, which represents the minimum area where animals spent the maximum amount of time. We rounded this value to 60% due to the constraints of the GIS software. The winter core area analysis resulted in the identification of 14 high use areas within the winter range (Fig. 3). The mean weighted HSI value observed in the winter core area was 0.72 and this value was then used to compare against the random disk analysis. In that analysis, we found a mean value for randomly selected disks in the winter kernel area of 0.68 and a mean HSI for disks along the road of 0.71 (Table 1). Habitat values observed outside the winter kernel were much lower with a mean HSI value of 0.48. When comparing the HSI in the random samples against the observed core winter area mean, we found that 6% of the random discs in the winter kernel area and 15% of sample discs along the road had a value of 0.72 or greater. No set of random disks sampled in the area surrounding the core winter range had a mean HSI value equal to or greater than the core winter habitat.

We found that density of telemetry positions and movement path lengths differed as a function of distance from the road. Density of location data within the 1 kilometre buffer was 0.01 observations per square kilometre compared to 0.05 in the 3 kilometre buffer (Fig. 6). Distances traveled by caribou were greater within 1 kilometre of the road compared to travel path segments in other buffer zones. Path segments in the 1 kilometre buffer are much longer by often two to three times the lengths of those found in the buffers further from the road (Table 2). For example,

Table 1. Summary of the random kernel analysis for disks located within the core winter range, along the Happy Lake road and in the region surrounding but outside the winter range. The proportion of random disks exceeding the mean HSI for the observed caribou kernels is also given.

Location	Number of Disks	Average HSI	Standard Deviation	Proportion Exceeding Observed
Winter Core Area Randomization	50	0.68	0.02	0.06
Road Area Randomization	50	0.71	0.01	0.15
Area Surrounding Core Randomization	80	0.48	0.05	< 0.0001
Observed Caribou Winter Kernel	14	0.72	0.09	Observed

Table 2. Median and quartiles calculated for path segment lengths intercepting the buffer zones adjacent to the Happy Lake Road.

	1000	2000	3000	4000	5000	Combined
1st Quartile	336.5	178.8	161	177.5	197	179
Median	1261	481.5	478	669	720	601
3rd Quartile	2620.5	1117.2	1184	1709	2446	1620

Table 3. Actual and randomly distributed road crossing in the Happy Lake core winter range. Analysis was restricted to animals that crossed the road between 2004 and 2006 (identified by animal ID). Results for the Chi-square test are also presented.

	Crossing counts			Average Crossing Length (m)	
Animal ID	Actual	Random Average	(O-E)^2/E	Actual	Random
owl18w06	6	16.5	6.7	2650.9	1822.3
owl17w06	5	12.1	4.1	2181.4	1399.8
owl11w06	1	15.6	13.7	4272.6	1230.9
owl11w05	8	35.6	21.4	4234.4	1925.2
owl10w06	11	18.6	3.1	1861.0	1136.1
owl10w05	8	19.9	7.1	1892.9	1231.0
owl07w06	2	8.3	4.8	2267.2	895.1
average	5.9	18.1		2765.8	1377.2
Significance=0.05		X^2 Observed:	61.0		
Degrees of freedom=6		X^2 Critical:	12.6	*P*-value:	< .0001

the median distance travelled by all animals adjacent to the road was 1261 meters compared to 481 meters in the 2 kilometre buffer.

The simulated road crossing analysis illustrates that caribou are crossing random roads at a much higher rate than the actual road. The chi-square value of 60.96 indicates that the actual number of crossings (18.1) and expected number of crossing (5.9) are significantly differ from one another (Table 3). The average distance between fixes for actual crossings is 2765 meters compared to 1377 meters for the 1000 controls, illustrating that caribou movement in distance and time is greater compared to other movements away from the Happy Lake Road.

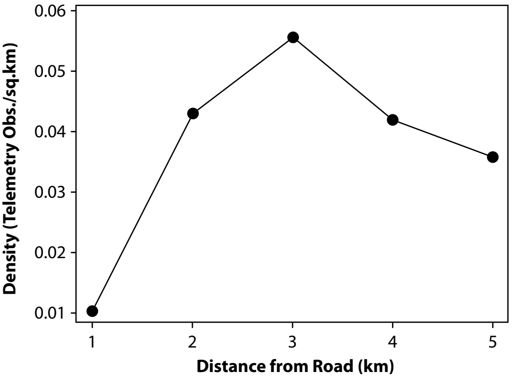

Fig. 6. Density of animal locations per sq km as a function of distance from the Happy Lake Road.

Discussion

The analysis illustrates that habitat quality is consistent between core use areas, within the winter kernel area, and along the Happy Lake Road. This suggests that most habitat within the core kernel area is suitable, including areas by the Happy Lake Road that are generally under utilized, whereas areas adjacent to, but outside the core, tend to have lower suitability. Although not significant, mean habitat values for core areas was the highest followed by the road corridor then the winter kernel area. The habitat outside the winter range is significantly different and of lower quality. This result is expected as the Owl Lake winter range is contained within a large contiguous complex of near mature to mature coniferous forest. We suggest that the road location is not dependent upon any special habitat characteristic and habitat quality and quantity are similar throughout the winter range. Although not significant, caribou did concentrate their activities in the highest quality habitat within their range north of the road.

This study suggests that there is less use of high quality habitat along the logging road compared to other areas in the winter range. Specific causes for reduced use of habitat near the road cannot be determined by this study; however, they could include sensory disturbance and predator avoidance as there is considerable anecdotal information of wolf and moose activity along the road. Moose are attracted to roadside habitat and disturbed habitat associated with access and forestry, in turn attracting wolves (Cumming & Beange, 1993). Wolves occupy habitat near linear features resulting in higher mortality to woodland caribou than what would be expected in linear feature free environments (James & Stuart-Smith 2000). Caribou are also known to separate themselves from moose and wolves by migrating into more rugged terrain (Seip, 1992). These may be factors explaining the reduced use of high quality habitat by caribou along the Happy Lake Road.

The extent to which woodland caribou avoid human development is also dependent on the level of human activity (Dyer *et al.*, 2001; 2002). Higher energetics associated with industrial disturbance may also cause reduction in caribou mass depending on the cumulative influence of that activity (Bradshaw *et al.*, 1998). Reduction of use of high quality forage can also be a factor in decreasing tolerance of human activity through caribou displacement into poorer habitat resulting in lower fecundity (Nellemann & Cameron, 1998). Loss of functional habitat may also occur as a result of energetic consequences of disturbance from human development (Dyer *et al.*, 2001; Oberg, 2001). The location densities and travel path distances relative to the 1 kilometre buffers suggest some loss of functional habitat along the road. We were able to illustrate that caribou previously used areas along the road but were unable to statistically determine the extent of functional habitat loss or the distance at which habitat use is significant. We do suggest that there is a noticeable reduction of habitat use and increased movement within the 1 kilometre buffer zone. The random road analysis also illustrates that caribou movement rates across the logging road are significantly higher than other movements within the winter range.

Industrial development has the potential to change predator-prey dynamics through the alteration of spatial distribution of caribou, wolves, and moose with minor increases in predation pressure that could have negative consequences to local boreal woodland caribou populations (James *et al., 2004*; Rettie & Messier, 1998; Cumming & Beange, 1993). Increased incidental predation as a result from wolves taking advantage of packed road surfaces has the potential to cause negative cumulative effects on the Owl Lake population. In the Happy Lake Road analysis, the fact that Owl Lake animals tend to avoid the road, may be a significant advantage to this population. By avoiding the road, risk of mortality from predator and humans may be reduced. Habitat is likely not a limiting factor for the Owl Lake caribou, but rather mortality. The Owl Lake caribou habitat selection and movement patterns are consistent with predator avoidance strategies and reduce risk of mortality from humans and predators.

The Happy Lake Road is unique in that it is a managed resource road and access is restricted to permitted traffic associated primarily with forestry activity (EMWCAC, 2005). Sensory disturbance resulting from traffic may be minimized due to these road restrictions. The analysis suggests that the Happy Road affects some loss of functional habitat. The potential negative effects of the Happy Lake Road need to be considered in long-term road management. These potential effects should continue to be considered in the ongoing conservation of the Owl Lake boreal woodland caribou population through continued road access management.

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West Greenland caribou explosion: What happened? What about the future?

Christine Cuyler

Greenland Institute of Natural Resources, P.O. Box 570, DK-3900 Nuuk, Greenland (chcu@natur.gl).

Abstract: In West Greenland, the 1993 caribou (*Rangifer tarandus groenlandicus*) population size estimate was 7000 to 9000 animals. Eight years later in 2001, the estimate was ca. 140 000. Relatively rapid rise and fall cycles of abundance in West Greenland caribou have been noted since the 1700s. Caribou have no natural predators in West Greenland. Combined with their high fertility and recruitment, this suggests that overabundance might be their greatest threat to stability. The 2005 population surveys indicate poor recruitment in two major populations and decreasing abundance in one. Given stocking densities are three to six-times the value considered sustainable, we expect strong competition between individuals for available food resources. Although the management goal is sustainable harvest of natural resources, if populations continue at their current size or increase further, there is a clear risk of range overgrazing and trampling. Unsustainable range use may result in density-dependent forage limitation with subsequent relatively rapid population decline over a series of years, e.g. a decade. As in the past, populations are expected to recover, and if true to the past, recovery will take the better part of a century. Furthermore, the role of catastrophic weather events may be of major importance. Abrupt collapse could be precipitated by a disastrous single year event, e.g. thaw-freeze icing or deep snow, because possibilities for dispersal to new ranges are limited. Regardless of management initiatives taken now, population declines or crashes may be inevitable for some West Greenland herds in the foreseeable future, but accurate predictions about herd trends are impossible. To understand the potential impact of future developments, Greenland caribou and their range must be studied within the wider context of climate change.

Key words: Aerial survey, catastrophic weather, climate change, estimates, population collapse, population cycles, *Rangifer*, reproduction.

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Introduction

West Greenland caribou abundance was high in the early 1970s and speculated at approximately 100 000 caribou (Clausen *et al.*, 1980; Thing & Clausen, 1980; Grønnow *et al.*, 1983; Roby & Thing, 1985; Vibe, 1990; Thing & Falk, 1990). This was followed by surveys in the 1980s and 1990s suggesting low abundance. Then, in less than 10 years, caribou in West Greenland swung from being considered by the managers as few in number to more than ever before estimated. Since range is a finite quantity in West Greenland, the recent high abundance created caribou densities that could defeat the sustainable harvest goal of the Greenland Home Rule managers because the range may be compromised by overgrazing and trampling. Current estimates indicate decreasing abundance or poor recruitment in two of the major populations. With no natural predators and a documented potential for high fertility and recruitment (Cuyler & Østergaard, 2005), forage induced population cycles might be inevitable. This paper reviews recent and past population trends and discusses the possible future for caribou in West Greenland.

Background

As recently as 1993-1996, caribou in West Greenland were managed as one herd, although several discrete populations existed (Fig. 1). Further, policy makers believed that caribou were few based on fixed-wing aerial surveys of abundance (Fig. 2). However, these population estimates must be viewed cautiously. In the past, West Greenland aerial surveys estimating caribou abundance were invalidated by harvest data. For example, in 1980 the estimated population size was 7000 to 9000 caribou, which increased to 15 000 by 1982. At the same time, the reported harvest in 1980 was 6000 animals and over 9000 animals in both 1982 and 1983 (Fig. 3). If the 1980s estimates

Fig. 1. Three West Greenland (North, Central, South) regions and the four caribou herds studied.

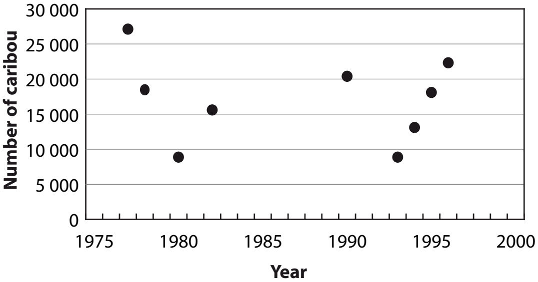

Fig. 2. Caribou population estimates resulting from aerial surveys, 1977 to 1996 (Clausen *et al.*, 1980; Thing, 1980; Strandgaard *et al.*, 1983; Holthe & Lassen, unpubl. in: Thing, 1984; Roby & Thing, 1985; Thing & Falk 1990; Rasmussen, 1995; Ydemann & Pedersen, 1999). All estimates lack confidence intervals, and prior to 1993 systematic method was absent.

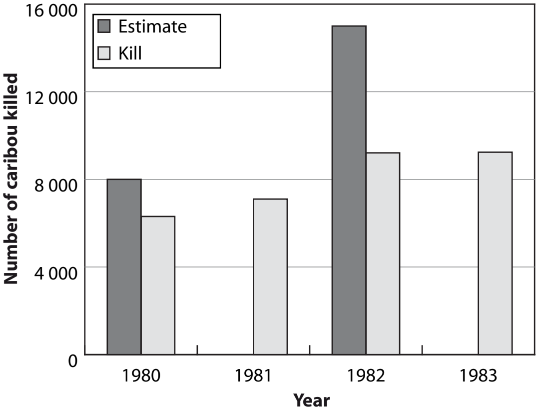

Fig. 3. Comparison of aerial survey estimates of caribou number and reported caribou harvest from1980 to 1983.

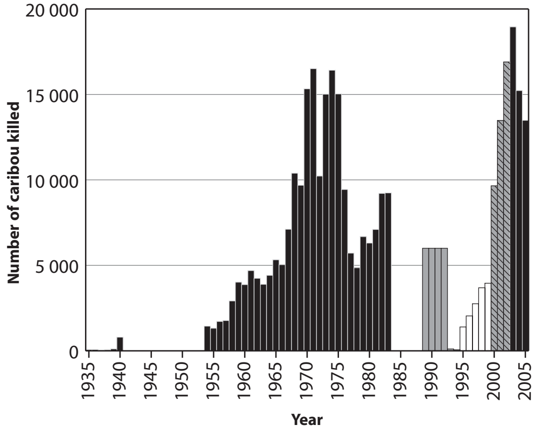

Fig. 4. Caribou harvest records 1935-2005 (Anon: Grønlands fangstlister, Piniarneq). No records were kept from 1983 to 1995. Dark columns, 1935-1983 and 2003-2005, are open harvest. Light grey columns, 1989-1992, are assumed harvest level (Peter Nielsen, pers. comm.). Open columns, 1995-1999, are harvests attained when legal quotas were low. Grey columns with diagonal lines, 2000-2002, are reported harvests attained when legal quotas were dramatically increased.

were accurate then extirpation of the caribou population would have been expected, even if one assumes a generous annual 1.3 increase in population. At the time no restrictive management initiatives were taken and this discrepancy between estimates and harvests went unnoticed.

The late winter pre-calving surveys conducted in 1993 - 1996 were the first well-designed, systematic surveys conducted to date and employed distance sampling. Nonetheless, like their predecessors, they were of questionable accuracy because they were not tailored to Greenland's rugged mountain landscape, a shortcoming that likely promoted missing many animals present on surveyed transects. Methods included using a fixed-wing aircraft at high speed (167 km/h), high and variable altitude (≥ 152 m) and wide strip width (1.4 km). Caribou detectability was further compromised by observer fatigue, as long transects (80 to 100 km) were not unusual and the north south transect orientation meant that half the

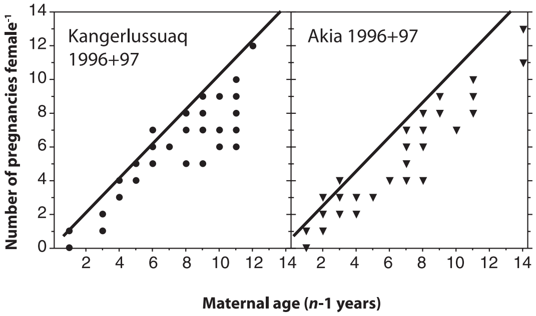

Fig. 5. Fertility of Kangerlussuaq-Sisimiut and Akia-Maniitsoq females (Cuyler & Østergaard, 2005). The line indicates the maximum lifetime reproductive potential, i.e. one calf produced for each year of age. Age is given as reproductive lifespan age (*n*-1 year). One Kangerlussuaq and two Akia females exceeded this maximum.

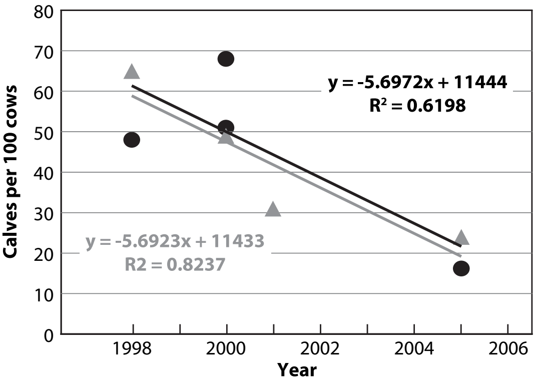

Fig. 6. Changes in late winter recruitment (calves per 100 cows) in two West Greenland herds, Kangerlussuaq-Sisimiut stock (●,— , P = 0.21), and Akia-Maniitsoq stock (▲, — , P = 0.092); linear regression lines with R^2 values.

observation time was spent squinting against solar glare. Regardless of estimate accuracy, the results from the 1993-1996 surveys should be comparable, since methods, observers and analysis were consistent. There appears to have been a trend of steady population growth from 1993 to 1996.

The 1993 aerial survey indicated 7000 to 9000 caribou in West Greenland (Ydemann & Pedersen, 1999). Harvest data, which could have assisted assessment of this estimate, were not available because Greenland had ceased to collect harvest data 10 years earlier. Prior to 1983, however, reported annual harvests indicated a steady increase from almost nothing in the 1930s to over 16 000 in the 1970s, while harvests in the early 1980s ranged from 7000 to 9000 animals per year (Fig. 4). Further, policy makers assumed the annual harvest was from 4000 to 6000 caribou (Peter Nielsen, pers. comm.) for the four years prior to the 1993 survey. With the 1993 maximum of 9000 caribou and an assumed 50% population reduction since 1990, a crisis was declared and restrictive management initiatives were implemented. All hunting was prohibited for two years until the summer of 1995.

After the 1995 and 1996 estimates of 18 000 and 22 000 caribou respectively (Ydemann & Pedersen, 1999), policy makers permitted quotas of 2000 to 4000 animals from 1995 to 1999. The two-year prohibition and subsequent low quotas resulted in heavy debate and scepticism from hunters, who were unanimous that caribou were plentiful (Cuyler *et al*., 2003). My own anecdotal observations on the Ameralik caribou population supported the local knowledge. On 28 October 1998, in six hours sailing along 33 km of the Davis Strait coast, I counted 951 caribou and these were only the animals visible within the first 300 metres from the shore.

Fertility and late winter recruitment

In 1996/97, based on Cuyler & Østergaard's (2005) retrospective ovarian analysis, two West Greenland caribou populations, the Kangerlussuaq-Sisimiut and the Akia-Maniitsoq, had a high percentage of pregnant subadults (females under 3-years old) and 25% of all females attained their maximum reproductive potential, while 2-4% of collected animals exceeded that maximum (Fig. 5). Observations of conception in a female caribou's second autumn and twinning suggest that West Greenland caribou ranges were excellent prior to 1996 (Cuyler & Østergaard, 2005).

Meanwhile from 1998 to 2000, calf recruitment in March was between 48 and 68 calves per 100 cows (Fig. 6). Four to five years later, March calf recruitment dropped to 16-24 calves per 100 cows. In fact, late winter calf recruitment appears to have declined steadily since 1998. Regression R^2 values are close to 1 and indicate the strength of the relationship observed; however, the P-values were not significant. Aside from suspected increased intra-specific competition, no apparent causes (e.g. severe winter weather events) have occurred that could account for the decrease in recruitment (Cuyler *et al.,* 2005).

2000 and after

Given the scepticism surrounding earlier caribou estimates, aerial surveys techniques in West Greenland were further improved (Cuyler *et al.,* 2002; 2003; 2005). Helicopters replaced fixed-wing aircraft, because when flying transects, helicopters can maintain a slow speed and constant altitude over mountainous terrain. Reliable estimates of abundance require detection of most, if not all the animals actually present within the surveyed transects. In Greenland, methods required to achieve this standard include low flight speed (45-65 km/h), low constant altitude (15 m) and narrow strip width (0.6 km). The 0.6 km strip width (300 m x 2) was based on observer capability to detect caribou given small group size and behaviour (remaining lying down or stationary) in combination with the difficult terrain and snow cover typical of West Greenland (Cuyler *et al.,* 2002; 2004). Although West Greenland is treeless alpine, tundra, exposed rock or ice, survey observers sighted most caribou between 0 and 300 m from the helicopter. Few were sighted beyond 300 m, although animals were just as likely to be present in that strip area (Cuyler *et al.,* 2002; 2004). Caribou detectability was aided by reducing observer fatigue with: 1) short transects (7.5 km), which limited the time spent in full concentration by observers; and 2) flight path in a direction not looking directly into the sun when on a transect. Direction of flight was also important because solar glare reflecting off the snow surface reduces caribou sightability (Cuyler *et al*., 2005). Transects of random location and heading were possible because in late winter (March-April) caribou group size averages less than 6 animals and variability is low (Roby & Thing, 1985; Thing, 1982; Thing & Falk, 1990; Ydemann & Pedersen, 1999; Cuyler *et al.,* 2002; 2003; 2005), which reduces sampling error and aids precision. The mean group size, ca. three, remained constant even when herds were large and the caribou were widely scattered over all elevations throughout a region (Cuyler *et al.,* 2002; 2003; 2005). A correction for missed caribou was also incorporated into the resulting population estimates, following Cuyler *et al.* (2003). The 2001-2005 surveys might still have underestimated herd sizes, because the low flight altitude (15 m) often created "dead-ground", i.e. terrain features could hide some of the strip width.

New survey results available by spring 2001 supported local hunter knowledge and estimated a total of about 135 000 caribou for only four West Greenland populations (Table 1). Just five years earlier, the total for all six or seven populations in West Greenland was about 22 000. With estimates over six times that number, caribou management changed overnight. Rather than few, they were now considered abundant. Given the finite range available in

Table 1. Recent pre-calving estimates of caribou abundance in four West Greenland herds.

Region	Population	1993[1]	1996[1]	2000[3]	2001[2]	2005[3]
North	Kangerlussuaq-Sisimiut	3800	10 900	51 600 (42 664 – 61 495)		90 464 (70 276 – 113 614)
Central	Akia-Maniitsoq	3500	6800		46 200 (37 115 – 55 808)	35 807 (27 474 – 44 720)
South	Ameralik	1200	4500		31 900 (24 721 – 39 305)	-
South	Qeqertarsuatsiaat	181	-		5400 (2864 – 8244)	-

[1] Ydemann & Pedersen (1999).
[2] non-parametric (bootstrap) 80% CI's (Cuyler *et al.,* 2003).
[3] non-parametric (bootstrap) 90% CI's (Cuyler *et al.,* 2002; 2005).

Table 2. Recent estimates of caribou density in four West Greenland herds.

		High density stratum[1]	
Region	Population	2000 – 2001	2005
North	Kangerlussuaq-Sisimiut	2.8 / km^2	6.2 / km^2
Central	Akia-Maniitsoq	4.0 / km^2	3.0 / km^2
South	Ameralik	3.8 / km^2	-
South	Qeqertarsuatsiaat	1.1 / km^2	-

[1] Cuyler *et al.* (2002; 2003; 2005).

West Greenland, caribou densities up to 4 per km^2 in 2001 (Table 2), and overgrazing a possibility, policy makers now sought to reduce abundance to protect the future of caribou herds and their ranges. An imprecise conservative target density of 1.2 per km^2 was recommended to the policy makers.

The target is based on studies of carrying capacity elsewhere. At densities of 1.03 to 1.41 reindeer per km^2, females become sexually mature and conceive for the first time when just over 1-year old, which suggests this density is compatible with optimal range (Reimers *et al.,* 1983). In contrast, a density of 4 reindeer per km^2 is too high to sustain lichen heath at optimal condition in Finland (Helle *et al.,* 1990). Observations from Svalbard (Norway) support this. Fifteen reindeer introduced on the Brøggerhalvøya peninsula (Svalbard) at an initial density of 0.25 per km^2 increased over 15 years to 400, or 6.7 per km^2, and the once lush preferred macro-lichens *Cetraria nivalis* and *Cladonia mitis* had disappeared (Staaland *et al.,* 1993). In a winter icing event, the population crashed to 100 (Jacobsen & Wegener, 1995), but animals had already begun to leave the peninsula (Staaland, pers. comm.). Skogland (1985) observed that recruitment fell sharply at densities over 2.5 per km^2 owing to a decline in calf productivity of the sub-adult females, but that calf productivity of females 3-years old and older also fell slightly even at densities of 2 per km^2. When caribou reach densities exceeding 2 per km^2, movement increases and distribution can be unpredictable (Skoog, 1968; Baskin, 1990). Although possibilities are limited, dispersal or movement have been observed in West Greenland populations (Cuyler *et al.,* 2003). Population dispersal or movement shifts to new range could delay the effects of food shortage in limiting numbers and Messier *et al.* (1988) suggested that caribou populations could overshoot range capacity because of these delays. Although the target density of 1.2 per km^2 is not now based on studies of carrying capacity on West Greenland ranges, it may favour the preservation of range quality and availability, which will benefit caribou populations and the sustainability of future harvests. A halt to population increase, or a reduction in numbers, would give time for more precise target densities to be derived from appropriate studies.

If reducing abundance was to be achieved, increasing the portion of females in the harvest was important, since caribou harvests (mid-August to mid-September) until then were otherwise about 90% male-biased (Loison *et al.,* 2000). To reduce abundance, season length was increased from one month to five and a half months, which included the rut, and was broken into an autumn and winter hunt. More animals were shot, specifically more females, as rutting males are considered unpalatable. Beginning in 2000, harvest quotas rose by about 10 000 animals each year until 2003, when open harvests were implemented. Reported harvests rose to and exceeded levels observed in the 1970s.

A 2005 aerial transect survey for the two largest caribou herds in West Greenland revealed a dramatic decline in recruitment (Fig. 6), while densities remained well above the recommended target (Cuyler *et al.,* 2005). The Akia-Maniitsoq herd had decreased in abundance by 22% over four years. In contrast the estimate for the Kangerlussuaq-Sisimiut herd was almost double the 2000 estimate but an interpretation of population trend is difficult since methods differed. The Kangerlussuaq-Sisimiut survey of 2000 was the first employing the new survey methods and highlighted the need to further reduce altitude, speed and strip width to detect most or all caribou on transect. In contrast to all subsequent surveys, in 2000, the altitude, speed and strip width were 100 m, 100 km/h, and 1 km respectively (Cuyler *et al.,* 2002). The presence of more experienced observers in 2005 probably also affected numbers detected, making the 2005 estimate more accurate.

Discussion

The 2000-2001 helicopter surveys, which used improved methods to reduce the negative bias of missed caribou, resulted in a pre-calving estimate of caribou numbers six times greater than estimated in 1996. How was this possible? Although caribou numbers can increase rapidly given ideal conditions (Heard & Ouellet 1994; Staaland *et al.,* 1993), was fertility alone responsible for the large jump in herd sizes from 1996 to 2000-2001? While small, the

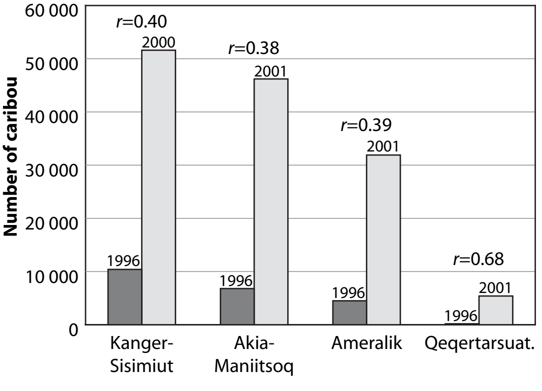

Fig. 7. Caribou abundance and calculated actual rates of increase "*r*" for four herds in West Greenland from 1996 to 2000-2001.

harvest quotas in place from 1995 to 1999 were 10-18% of the 1996 estimated abundance and could have been sufficient to prevent population growth. West Greenland caribou, however, were surprisingly fertile and had high recruitment rates (Cuyler & Østergaard, 2005). Both provided the potential for rapid population growth in West Greenland in the 1990s, but do not account for the disparity between population estimates from 1996 to 2000-2001. The actual rate of increase between estimates can be calculated (Krebs, 1972):

$$r = \frac{\mathit{ln}\text{ herd size } t_2 - \mathit{ln}\text{ herd size } t_1}{\text{Time period in years}}$$

Resulting r values are unrealistic, i.e. 0.40, 0.38, 0.39 and 0.68 in four West Greenland populations (Fig. 7), since the maximum or intrinsic rate of increase, r_m, for caribou in a predator and harvest free environment is 0.30 (Bergerud, 1980). The rate of increase for the growth trend observed from 1993 to 1996 was also improbably high, being 0.32 with a finite rate of $\lambda = 1.377$ per individual per year ($\lambda = e^{rm}$ (Krebs, 1972)). In contrast, caribou on Southampton Island in the Canadian Arctic had a rate of increase of 0.233 ($\lambda = 1.262$) (Heard & Ouellet, 1994), although like West Greenland there were no predators, the range was good, and the caribou showed no decrease in population growth even as density increased. The unrealistic estimated rates of growth, in combination with the 1993-1996 survey methods and consistent local knowledge to the contrary, make it probable that the 1993-1996 surveys underestimated herd sizes. Also possibility the 1993-1996 surveys were not as consistent as previously assumed, e.g. otherwise experienced observers became more proficient at sighting caribou with each survey, thus increasing each subsequent estimate. Alternately, recent surveys may have been optimistic if observers consistently made caribou observations over a larger area than stated. However, this is unlikely given the methods used by Cuyler *et al.*, (2002; 2003; 2005). The inaccurate 1990s surveys resulted in conservative management decisions (two-year hunting prohibition 1993-94, followed by five years of restrictive quotas), which contributed to herd growth and the high densities observed on West Greenland ranges by 2000. Male-biased hunting, the lack of large predators, and excellent range conditions in the 1980s and 1990s (Aastrup, 1984a, 1984b; Thing & Falk, 1990) were also factors. An area examined in the South region revealed average lichen cover was 45-55% (Aastrup, 1986), which provided the ideal conditions for fertility and recruitment.

Annual harvest data for the past 40 years suggest that caribou abundance has been relatively high since the late 1960s. Given local knowledge and the 2000-2005 abundance estimates, it is possible that caribou density has been high for about a decade. If too many caribou have been present for too many years on the finite amount of range available between the Ice Cap and sea, it could result in overuse of available vegetation and therefore compromise the abundance of these herds, owing to density-dependent forage limitation. Three cycles of caribou abundance in West Greenland have been noted since the 1700s (Fig. 8), suggesting that high abundance might be the greatest threat to population stability and lead to a new population decline. As in past cycles, populations are expected to recover slowly over the better part of a century.

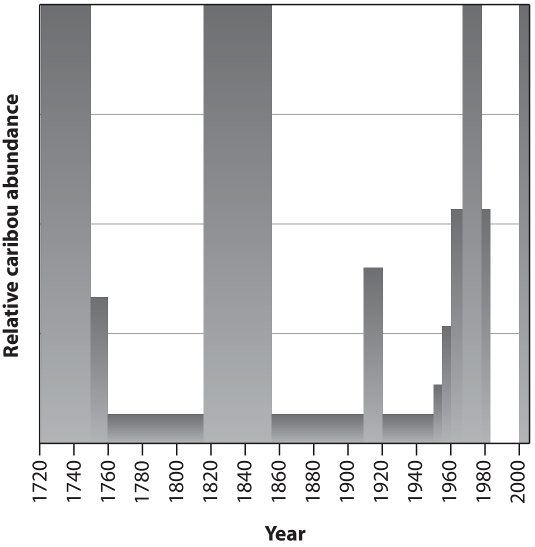

Fig. 8. Historical rise and fall cycles of relative caribou abundance in West Greenland based on Vibe (1967), Meldgaard (1986) and the 2001 abundance estimate. Only general trends are illustrated, since the caribou populations in West Greenland do not cycle in absolute synchrony (Meldgaard, 1986), and estimates were unavailable except for in 2001. During periods of low abundance, records suggest the caribou had disappeared almost entirely. No harvest records were available from 1983 to 1995.

Have there been too many caribou? Late winter calf recruitment is in decline in the two largest herds. Are density-dependant factors at work? Since densities are 3 to 6x the recommended target there is reason to suspect intra-specific competition for food resources. Although no quantitative studies exist, overgrazing and trampling of lichens has been observed on the Akia-Maniitsoq and Ameralik winter ranges (Cuyler *et al.,* 2003; pers. observation), and general trampling of vegetation has been noted on the Kangerlussuaq-Sisimiut range (Cuyler *et al.,* 2005; pers. observation).

How long can this situation continue before substantial protracted declines in caribou population size occur?

West Greenland caribou are fortunate to live in a simple predator-free low arctic environment, which is topographically isolated. They have few competing herbivores, i.e. muskox *Ovibos moschatus*, arctic hare *Lepus arcticus*, geese *Anser* and *Branta* spp., rock ptarmigan *Lagopus mutus,* and human development is minimal or limited to the seacoast. However, the various caribou populations currently inhabit most available range. Under present conditions, dispersal possibilities are limited or non-existent. This makes the future of West Greenland caribou uncertain. In addition to protracted decline brought on by density-dependent forage limitation, disastrous weather events may be of major importance and able to cause abrupt collapse in several or all herds (Vibe, 1967; Meldgaard, 1986). Temperatures and precipitation are expected to increase in Northeast Greenland (Rysgaard *et al*., 2003). Temperature trends, however, are often opposite between east and west Greenland (Box, 2002). Will climate change bring better or worse conditions? For example will there be changes in winter length, snow depths, severity or frequency of winter thaw-freeze icing events, summer precipitation, or other? Extreme icing or snow depth restrict access to forage and may cause near total mortality across age classes (Miller, 1990; Jacobsen & Wegener, 1995). Although in West Greenland spring and summer temperatures over the past century cooled and several of the coldest winters coincided with major volcanic eruptions (Box, 2002; Hassol, 2004), a general warming and greater precipitation is expected, but it will not be as pronounced as in Northeast Greenland (Rysgaard *et al.,* 2003). Equally important is how climate change will affect the vegetation, because in West Greenland caribou abundance and distribution is controlled from the "bottom-up", i.e. through the quantity, quality and availability of vegetation. Regardless of management initiatives taken now, population declines may be inevitable for some West Greenland herds within the foreseeable future, but accurate predictions about herd trends are impossible. To understand the potential impact of future developments, caribou and their range must be studied within the wider context of climate change.

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Populations of wild and feral reindeer in Siberia and Far East of Russia

Leonid M. Baskin[1] **& Frank L. Miller**[2]

[1] Institute of Ecology and Evolution, Russian Academy of Sciences, 33 Leninsky Pr., Moscow, 119071 Russia (baskin@orc.ru).
[2] Canadian Wildlife Service, Environment Canada, Prairie & Northern Region, Room 200, 4999 – 98th Avenue, Edmonton, Alberta T6B 2X3, Canada.

Abstract: Identification and cataloging of discrete reindeer (*Rangifer tarandus*) populations in Siberia and the Far East of Russia has not been carried out. This prohibits accurate measures of population structure and dynamics that would allow more intensive management of this important renewable resource. To rectify the lack of information, an inventory was made that identifies 84 wild populations and 3 feral populations originating from domestic reindeer. This inventory summarizes the information available on the location, approximate population size, approximate range size, and occurrence by ecoregions and habitat types of each of those 87 reindeer populations. The 87 reindeer populations used a collective landmass of about 3 000 000 km^2. The range size for each population was calculated to be between 446 km^2 and 392 267 km^2, with a mean ± SE of 34 033 ± 5734 km^2. The 86 populations for which population size could be approximated totaled 790 655 reindeer, with an approximate mean ± SE of 9194 ± 2517, a minimum size of 50, and maximum size of 145 000. The location of the calving grounds could be determined for only 26 (30%) of the 87 reindeer populations.

Key words: Far East of Russia, population identification and cataloging, *Rangifer tarandus*, Siberia.

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Introduction

Prior to this inventory, identification and cataloging of discrete reindeer (*Rangifer tarandus*) populations in Siberia and the Far East of Russia had not been carried out and no detailed assessment at the level of the population for the status of reindeer in those vast regions could be made. This lack of information prohibited measures of population structure and dynamics that would allow more intensive management of this important renewable resource. The inventory was made without the aid of data from animal-marking, radio-tracking, or satellite telemetry studies.

Encouragement to complete this effort came from the listing of statistics for many populations of North American caribou and Norwegian reindeer that had been identified, their sizes estimated, and their ranges delineated before radio-collaring and satellite telemetry studies were widespread and had been conducted (e.g., Skoog, 1968; Hemming, 1971; Klein & White, 1978; Williams & Heard, 1986; Skogland, 1989; Ferguson & Gauthier, 1992). For example, as data accumulated, it became apparent that the earlier concept of a "center of habitation" with only one caribou population throughout Alaska (Skoog, 1968), should be replaced with a management scheme based on many discrete populations (e.g., Valkenburg, 1998, 2001). Also, as time passed, a greater number of populations were identified in Canada (e.g., Williams & Heard, 1986; Ferguson & Gauthier, 1992). The following reports the compilation of information that could be obtained for identifying and describing reindeer populations in Siberia and the Far East of Russia (Maps in Figs. 1-26).

Methods

We collected data on reindeer distribution in Siberia and the Far East of Russia and put them into GIS maps. For each population, we then mapped range limits based on known perimeter points collected over the years from various sources and joined them together in GIS to create a range map from which an approximate range size was calculated (Figs. 2-26). This facilitated the incorporation of observations made over time. As a result, however, the apparent accuracy of each reported numerical value does not necessarily reflect the accuracy of the approximated range size (e.g., the maximum range size of 392 267 km^2 would most likely be just as accurate if reported as 390 000 km^2).

Although the accepted standard for naming *Rangifer* populations (herds) in North America is usually after the location of their calving grounds (e.g., Thomas, 1967; Klein & White, 1978; Valkenburg, 1998; Russell *et al.*, 2002), this could not be done for most reindeer populations in this inventory because that information is not often available in Russia. Only a few studies of reindeer distribution during the calving season have been made: primarily in the Taymyr by Kuksov (1981) and subsequently in Yakutia by Safronov *et al.* (1999). We obtained a little information on calving grounds from Shtilmark & Azarov (1975), Malygina (2000), Zhukov (2000), Shirshov (2003), Chernyavsky (1984), and Kupriyanov (2003), and also from V. I. Mosolov (pers. comm.) and V. I. Fil (unpubl. data).

Because of the limited information, there is even uncertainty about populations whose calving grounds are known. For example, in the Western Taymyr, tundra calving grounds are known in the basins of Pura and Agapa Rivers (Fig. 7, Kuksov, 1981; Kolpashchikov, 2000). Tens of thousands of reindeer arrive for calving in this area from different directions – SE from Eastern Evenkiya and Yakutia, SSE from Evenkiya, through Putorany Mountains, and SW from the left bank of Enisey River. It is most likely that these reindeer represent two different populations (No. 13 and 17, in Table 1). However, Syroechkovsky (1986), Pavlov *et al.* (1996), and Kolpashchikov (2000) believe that there is a single numerous Taymyr population, including populations No. 13, 14, 17 and 21 in Table 1.

Another controversial locality is Western Yakutia, where numerous reindeer inhabit the northern parts of the basins of Lena and Olenek rivers (Fig. 2, populations No. 36, 37, 38, 45). One of the calving areas is on the delta of the Lena River (Fig. 15). In 1960s, the population that calved there was very large (tens of thousands) and its range overlapped ranges of neighboring populations (Egorov, 1965). Now, because of human persecution, this population has been diminished to a few hundred (Population No. 45 in Table 1).

We used data on reindeer distributions in all seasons in order to make the information in this inventory more complete. The approximations of the sizes of different populations were obtained from a wide spectrum of sources that yielded data of markedly different quality and thus their relative accuracies varied. Ecoregions are presented according to Bailey (1998) and the main habitat types occupied by each population are noted. One asterisk (*) was used in Table 1 to identify a population that probably includes some individuals from any other population or possibly even more than one other population. Two asterisks (**) were used in Table 1 to identify a population whose information is out-of-date and needs to be updated.

Each of the 36 populations in the inventory with rough approximations of population size was adjusted to a single value. That is, all populations identified as being "A few 100" animals were arbitrarily set at 300 reindeer, any > or < qualification was ignored (eg. > 1000 or < 1000 was treated as 1000), and each population reported as a spread of values (e.g., 1500–2000) was assigned its mid-point value (e.g., 1500–2000 = 1750). This procedure allowed an assessment of 86 (99%) of the populations rather than of just the 50 (58%) possibly with more accurate approximations of population size. All 87 populations were used in calculating the overall statistics for range size.

Wild and Feral Populations

To rectify the lack of information on populations of reindeer in Siberia and the Far East of Russia, an inventory was made that identifies 84 wild populations and 3 feral populations originating from domestic reindeer (Tables 1, 2, 3). This inventory summarizes the information available on the location, approximate population size, approximate size, and occurrence by ecoregions and habitat types of those 87 reindeer populations.

The location of the calving grounds could be determined for only 26 (30%) of the 87 reindeer populations (Table 2). Another 27 (31%) of the populations exist on ranges separated from each other and therefore, because of their isolation, they seemingly can be identified with confidence. These are island populations or populations inhabiting ranges surrounded by vacant areas where reindeer have been exterminated. For example, on the Kamchatka Peninsula, three populations are isolated from each other (Voropanov *et al.*, 2003). The remaining 34 (39%) of the 87 populations inhabit taiga and mountain taiga, based on data obtained mostly during winter. However, much of the evidence for these 34 populations comes only from indirect but frequent observations of reindeer tracks. Obviously, it is hard to determine if these animals live separately from all other reindeer in neighboring localities. Future investigations using radio-collaring will help determine how many populations exist in these areas.

These 87 reindeer populations used a collective landmass of about 3 000 000 km^2. The range size for each population was calculated to be between 446 km^2 and 392 267 km^2, with a mean ± SE range size of 34 033 ± 5734 km^2. Only 25 (29%) of the 87 reindeer populations occupied ranges larger than the mean range size but collectively 81% of the approximated number of reindeer occurred on those ranges. The 86 populations for which some measure of population size could be approximated totaled 790 655 reindeer. Those 86 populations occupied 99% of the collective range of the 87 reindeer populations. The 12 largest reindeer populations collectively occupied only 43% of the entire reindeer range of the 86 populations, but contributed 85% of the approximated number of reindeer. No approximation of population size could be made for one of the 87 populations (Table 1, No. 38).

Enough information exists to allow further examination of the basic statistics for 86 of the 87 reindeer populations by comparing the 50 populations with a more accurate approximation of population size to the 36 populations with a less accurate approximation of population size (Table 3). The ranges occupied by those 50 and 36 reindeer populations represented 82% and 17% respectively, of the total range occupied by the 87 populations. As there did not appear to be any consistent relationship between the sizes of the populations and the amounts of range that they occupied, it follows that there is also no relationship between the overall mean density of a population and the size of the range that it used (Tables 1, 3).

Although this inventory is far from complete, it is a necessary first step. This compilation will form the basis for building a more complete inventory of data for reindeer populations in Siberia and the Far East of Russia.

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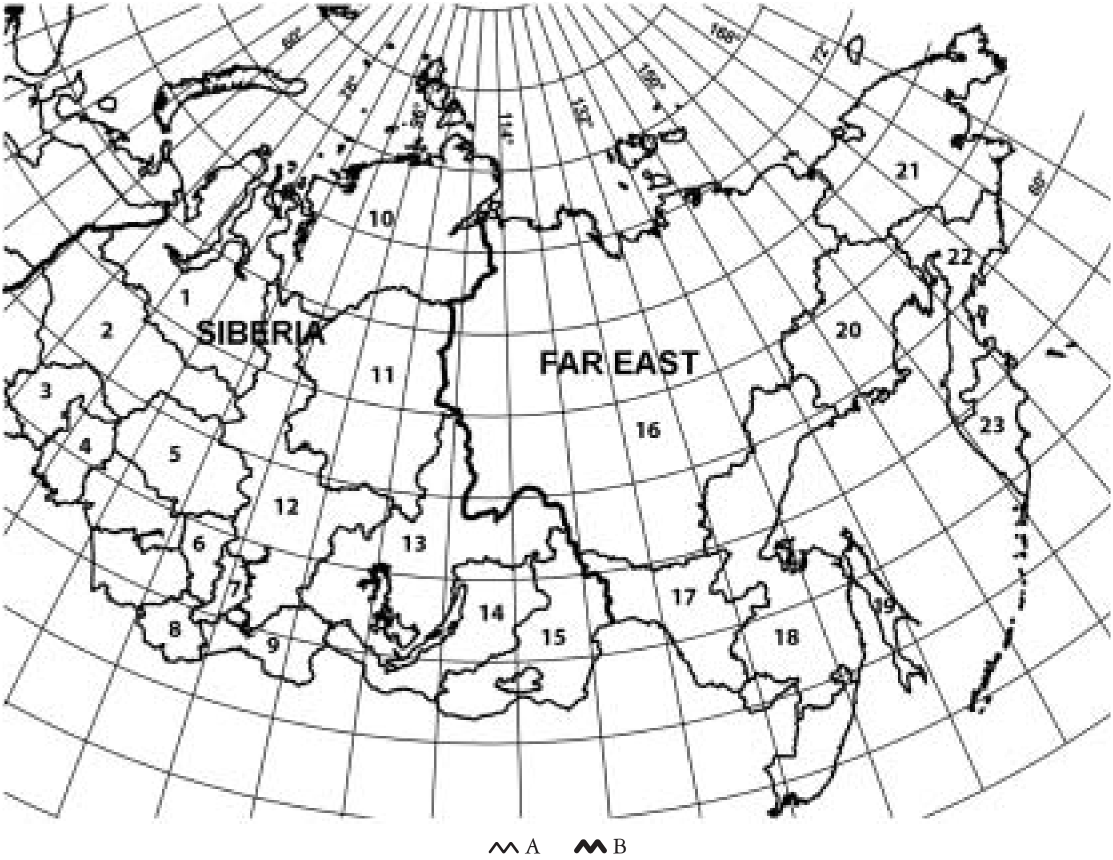

Fig. 1. Map of Russia, showing the geographical locations of Siberia and the Far East of Russia. A: borders of administrative regions; B: Siberian and Far East border. Administrative regions with wild and feral reindeer are 1 Yamalo-Nenetsky AO; 2 Khanty-Mansiysky AO; 3 Tumenskaya oblast; 4 Omskaya oblast; 5 Tomskaya oblast; 6 Kemerovskaya oblast; 7 The Republic of Khakasia; 8 The Republic of Altay; 9 The Republic of Tyva; 10 Taimyrsky AO; 11 Evenksky AO; 12 Krasnoyarsky krai; 13 Irkutskaya oblast; 14 The Republic of Buryatia; 15 Chitinskaya oblast; 16 The Republic of Sakha (Yakutia); 17 Amurskaya oblast; 18 Khabarovsky krai; 19 Sakhalinskaya oblast: 20 Magadanskaya oblast; 21 Chukotsky AO; 22 Koryaksky AO; 23 Kamchatskaya oblast.

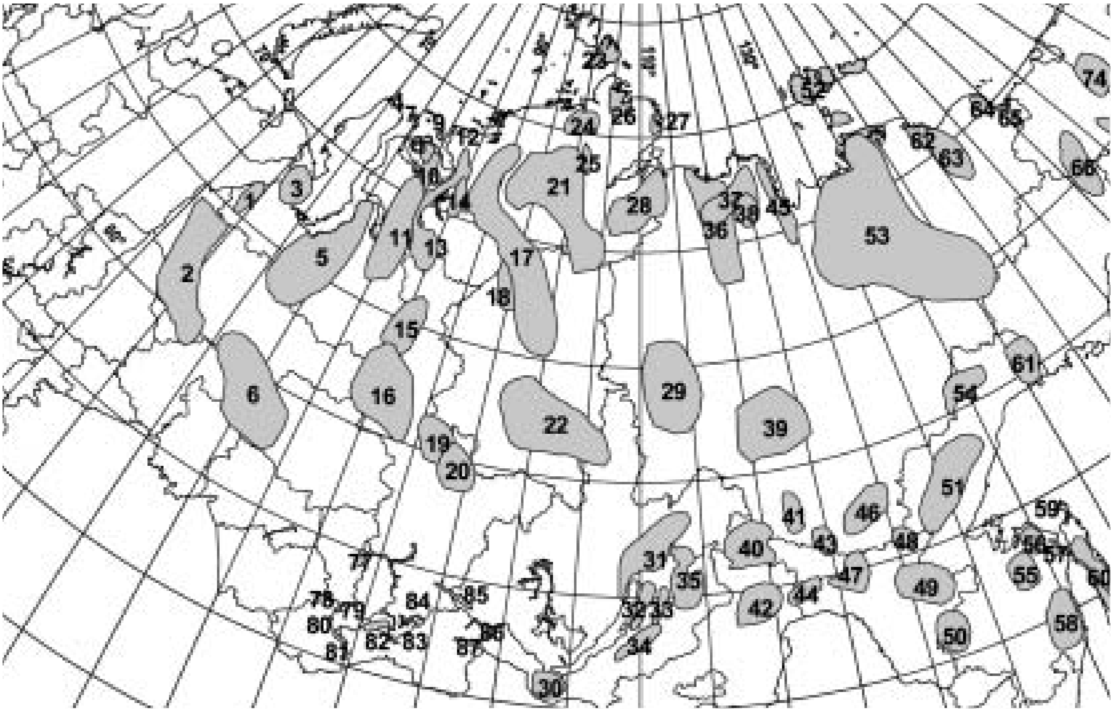

Fig. 2. Reindeer populations (Nos. 1-35 and 77-87) in Siberia (I.D. No. in figure correspond to the I.D. No. for populations listed in Tables 1 and 2).

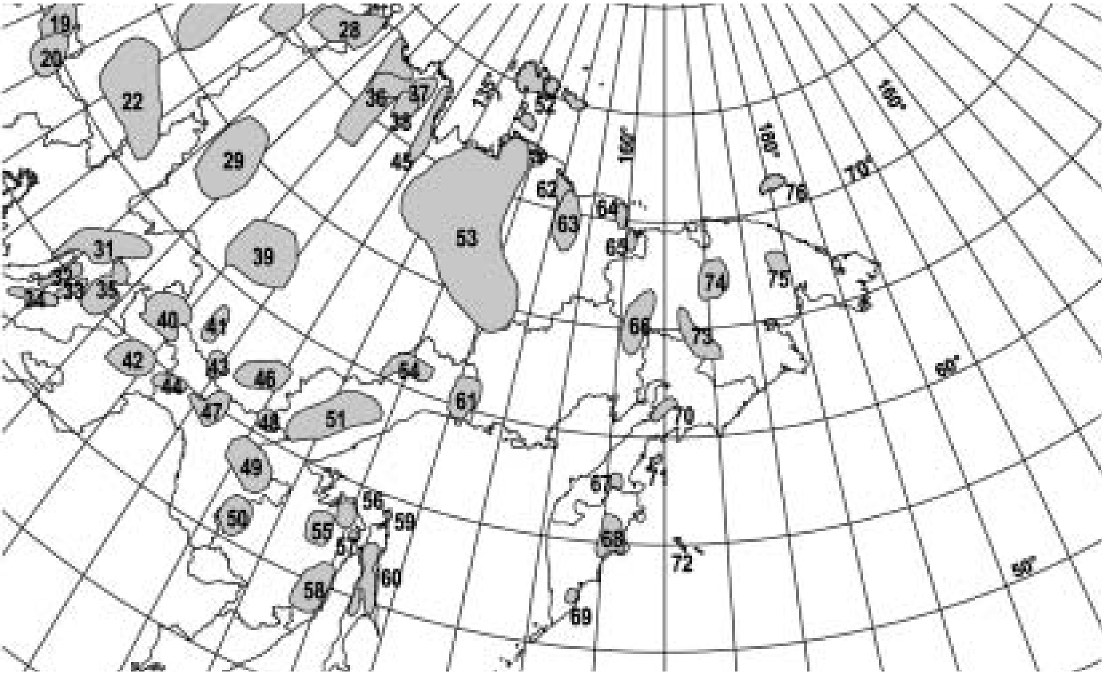

Fig. 3. Reindeer populations (Nos. 36-76) in Far East of Russia (I.D. No. in figure correspond to the I.D. No. for populations listed in Tables 1 and 2).

Table 1. Inventory of 87 wild and feral reindeer populations identified in Siberia and the Far East of Russia, 2006[a].

I.D. No.	Location[b]	Approximate population size	Approx. Range size (km^2)	Eco-regions[c]	Habitat types[d]	Authority
1	Shuryshkarskoe L. (Fig. 2)	200	10 644	TRM	MTu	Shirshov, 2003
2	Konda and Sosva R. (Fig. 2, 4)	5500	114 992	TD	B, PTa	Novikov *et al.*, 2003
3	Shchuchinskoe L. (Fig. 2)	> 100	22 774	TRM	MTu, LS	Shirshov, 2003
4	Belyi Is. (Fig. 2)	2000**	1858	TD	PTu, SS	Kupriyanov *et al.*, 1985
5	Nadym and Pur R. (Fig. 2, 5)	30 000	117 677	TD, SD	HTu, B, PTa	Kupriyanov, 2003
6	Yugan R. (Fig. 2)	600	124 276	SD	B, PTa	Azarov & Afanasev, 2003
7	Yavay P. and Shokalskogo Is. (Fig. 2)	A few 100**	1751	TD	PTu, SS	Shirshov, 2003
8	Mamonta P. (Fig. 2)	A few 100**	5454	TD	PTu, SS	Shirshov, 2003
9	Sibiryakova Is. (Fig. 2)	300	838	TD	PTu, SS	Kupriyanov *et al.*, 1985; Novikov, 1983
10	Gydan P. (Fig. 2)	1500	12 920	TD	PTu	Shirshov, 2003
11	Pur and Taz R. (Fig. 2, 6)	1500–2000	72 811	TD, SD	HTu, B, PTa	Kupriyanov, 2003
12	Chichagov Shore (Fig. 2)	A few 100**	1572	TD	PTu, SS	Uchitkin, 1990
13	Western Taymyr (Fig. 2, 7)	70 000**	42 850	TD, SD	HTu, PTu, B	Kolpashchikov, 2000
14	Agapa R (Fig. 2, 7)	A few 100**	9874	TD	HTu	Kolpashchikov, 2000
15	Turukhan R. (Fig. 2, 8)	800–2000	38 178	TD, SD	HTu, PTa, B	Zhukov, 2000
16	Upper Taz R. (Fig. 2, 9)	1000	98 169	TD, SD	HTu, PTa, B	Zhukov, 2000
17	Pura R. (Fig. 2, 7)	145 000	168 141	TD, SD	HTu, MTa	Tikhonov *et al.*, 2003
18	Putorany Mt. (Fig. 2)	A few 100**	22 836	SRM	MTu	Michurin & Mironenko, 1966.
19	Enisey R. (Fig. 2, 10)	11 800	31 796	SRM	MTa	Lutsky & Zyryanov, 2003
20	Angara R. (Fig. 2)	5000	31 695	SRM	MTa	Lutsky & Zyryanov, 2003
21	Dudypta R. (Fig. 2, 11)	110 000	139 795	TD, SD	PTu, HTu, MTa	Tikhonov *et al.*, 2003
22	Middle Siberian* (Fig. 2)	55 000	135 079	SD	PTa	Paponov, 2000; Lutsky & Zyryanov, 2003
23	Severnaya Zemlya Archipelago (Fig. 2)	A few 100**	11 260	TD	HTu	Kupriyanov *et al.*, 1985; Novikov, 1983
24	Nizhnya Taymyra R. (Fig. 2)	A few 100**	15 826	TD	HTu, MTu	Uchitkin, 1990
25	Taymyr L. (Fig. 2, 12)	5000	4675	TD	Tu, LS	Malygina, 2000
26	Faddey B. (Fig. 2)	A few 100**	11 544	TD	HTu, SS	Uchitkin, 1990
27	Mariya Pronchishcheva B. (Fig. 2, 13)	A few 100**	3896	TD	HTu, SS	Uchitkin, 1990
28	Popigay R. (Fig. 2, 14)	31 000	53 793	TD, SD	PTu, HTu, MTa	Popov, 2003

29	Western Yakutia (Fig. 2)	3300	101 601	SRM	MTa	Revin, 1989
30	Khamar-Daban Range (Fig. 2)	200	17 260	SRM	MTu	Noskov & Shchepin, 2003
31	Northern Baikal * (Fig. 2)	4000	57 639	SRM	MTu	Noskov & Shchepin, 2003
32	Barguzinsky Range (Fig. 2)	500	11 878	SRM	MTu	Noskov & Shchepin, 2003
33	Ikatsky Range (Fig. 2)	650	7253	SRM	MTu	Noskov & Shchepin, 2003
34	Ulan-Burgassy Range (Fig. 2)	150	15 931	SRM	MTu	Noskov & Shchepin, 2003
35	Muysky Range (Fig. 2)	2100	34 769	SRM	MTu	Noskov & Shchepin, 2003
36	Lena and Olenek R. (Fig. 3, 15)	33 000	80 488	TD, SD, SRM	HTu, MTu, MTa	Popov, 2003
37	Bulun R. (Fig. 3)	57 000	39 607	TD, SD, SRM	HTu, MTu, MTa, SS	Safronov, 2002; Popov, 2003
38	Kystyk Uplands (Fig. 3, 16)	?	14 653	SRM	MTu	Safronov *et al.*, 1999
39	Lena and Viluy R. (Fig. 3)	2000	94 547	SRM	MTa	Noskov & Shchepin, 2003
40	Chara R. (Fig. 3)	A few 100**	43 184	SRM	MTu, MTa	Revin, 1989; Bolotov, 2003
41	Amga R. (Fig. 3)	A few 100**	15 123	SRM	MTu, MTa	Revin, 1989
42	Tungir and Olekma R. (Fig. 3)	700	34 747	SRM	MTu, MTa	Bolotov, 2003
43	Timpton R. (Fig. 3)	A few 100**	10 880	SRM	MTu, MTa	Revin, 1989
44	Oldoy R. (Fig. 3)	> 1000	12 055	SRM	MTu, MTa	Telkov, 2003
45	Lena Delta R. (Fig. 3, 15)	A few 100**	22 438	TD	PTu	Safronov *et al.*, 1989
46	Gonam R. (Fig. 3)	A few 100**	33 971	SRM	MTu, MTa	Popov, 2003
47	Giluy R. (Fig. 3)	> 1000	23 821	SRM	MTu, MTa	Telkov, 2003
48	Bolshoe Tokko L. (Fig. 3)	A few 100**	9563	SRM	MTu, MTa	Revin, 1989
49	Selemzha R. (Fig. 3)	2000	46 162	SRM	MTu, MTa	Telkov, 2003
50	Bureya R. (Fig. 3)	2000	26 389	SRM	MTu, MTa	Telkov, 2003
51	Maya R. (Fig. 3)	2000	77 854	SRM	MTu, MTa	Telkov, 2003
52	Novosibirskie Is. (Fig. 3, 17)	17 000	52 884	TD	PT, SS	Labutin & Kurilyuk, 1981
53	Yana and Indigirka R. (Fig. 3, 18)	40 000	392 267	TD, SRM	HTu, MTu, MTa	Safronov, 2002; Popov, 2003
54	Yudoma R. (Fig. 3)	> 2000	23 240	SRM	MTu, MTa	Dunishenko *et al.*, 2003
55	Amgun R. (Fig. 3)	1000	20 583	SRM	MTu, MTa	Dunishenko *et al.*, 2003
56	Dzhap R. (Fig. 3)	A few 100**	11 443	SD	PTa, B	Dunishenko *et al.*, 2003
57	Tym R. (Fig. 3)	A few 100**	2128	SD	PTa, B	Dunishenko *et al.*, 2003
58	Tumnin R. (Fig. 3)	150	37 687	SD	PTa, B	Dunishenko *et al.*, 2003
59	Shmidt P. (Fig. 3)	A few 100**	1806	SRM	MTa, PTu, SS	Eremin, 2003
60	Nogliki R. (Fig. 3, 19)	3500	29 521	SRM	PTu, MTa, SS	Eremin, 2003

61	Kava R. (Fig. 3)	1000	26 858	SRM	PTu, MTa, SS	Bobykin, 2003
62	Indigirka R. (Fig. 3)	A few 100**	11 096	TD	PTu	Popov, 2003
63	Sudrunskaya (Fig. 3, 20)	30 000	31 868	TD, SDM	PTu, MTu, MTa	Popov, 2003
64	Galgavam R. (Fig. 3)	2000	5988	TD	PTu, SS	Safronov, 2002
65	Kolyma R. (Fig. 3)	A few 100**	4117	TD	PTu, SS	Popov, 2003
66	Omolon R. (Fig. 3)	20 000–30 000	34 447	SRM	MTu, MTa	Zhelesnov & Panovik, 2003
67	Elovka-Uka R. (Fig. 3, 21)	300–500	4225	SRM	MTu	Polkanov, 2003; V. I. Fil (unpubl. data)
68	Kronotsko-Zhupanovskaya (Fig. 3, 22)	2700	22 451	SRM	MTu, SS	Voropanov *et al*., 2003
69	Southern Kamchatka (Fig. 3, 23)	50	3612	SRM	MTu	Voropanov *et al*., 2003; V. I. Fil (unpubl. data)
70	Parapolsky Lowlands (Fig. 3)	300–400	8189	TD	PTu	Polkanov, 2003
71	Karaginsky Is. (Fig. 3)	300	1968	SRM	MTu	L. M. Baskin (unpubl. data)
72	Bering Is. (Fig. 3)	900	1189	TD	PTu	Voropanov *et al*. 2003
73	Mine R. (Fig. 3, 24)	50 000	27 383	SRM	MTu	Polkanov, 2003
74	Elgygytkyn L. (Fig. 3, 25)	8500	26 154	SRM	MTu	Zheleznov-Chukotsky & Panovik, 2003
75	Amguema R. (Fig. 3)	A few 1000**	10 631	TD, SRM	HTu, MTu	Zheleznov-Chukotsky & Panovik, 2003
76	Vrangel Is. (Fig. 3, 26)	3000	7711	TD, TRM	PTu, MTu	Baskin & Skogland, 1997
77	Kuznetsky Alatau Range (Fig. 2)	180	2865	SRM	MTu	Vasilchenko, 2003
78	Biyskaya Griva Range (Fig. 2)	200**	694	SRM	MTu	Sobansky, 1992
79	Abakan Range (Fig. 2)	100**	599	SRM	MTu	Sobansky, 1992
80	Korbu Range (Fig. 2)	< 100**	446	SRM	MTu	Sobansky, 1992
81	Shapshal R. (Fig. 2)	< 100**	1608	SRM	MTu	Sobansky, 1992
82	Kantegir* (Fig. 2)	200-250**	4308	SRM	MTu	Sokolov, 1983
83	Kazyr-Suk R.* (Fig. 2)	600–650**	1220	SRM	MTu	Sokolov, 1983
84	Us R. (Fig. 2)	200–250**	1994	SRM	MTu	Sokolov, 1983
85	Sayany Mnt.* (Fig. 2)	A few 100**	4040	SRM	MTu	Sokolov, 1983
86	Khamsyra R.* (Fig. 2)	2000	2358	SRM	MTu	Batkar, 2003
87	Azas R.* (Fig. 2)	1000	2531	SRM	MTu	Batkar, 2003

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[a] Ninety-seven per cent (*n* = 84; I.D. No.: 1–70, 73–75, 77–87) of the 87 reindeer populations have wild origins and the remaining 3 (3%: I.D. No.: 71, 72, 76) are feral, having originated from domestic animals.

[b] One asterisk (*) identifies a population that probably includes some individuals from any other populations; and two asterisks (**) identifies a population whose information is out-of-date and needs to be updated.

[c] Ecoregions types equal (TD) Tundra Division), (TRM) Tundra Regime Mts., (SD) Subarctic Division, (SRM) Subarctic Regime Mnt. (Bailey 1998).

[d] Habitat types equal (PTu) Plain Tundra, (HTu) Hilly Tundra, (MTu) Mountain Tundra, (B) Bogs, (PTa) Plain Taiga, (HTa) Hilly Taiga, (MTa) Mountain Taiga, (SS) Sea Shore, (LS) Lake Shore.

Table 2. Known location of calving grounds for 26 reindeer populations in Siberia and the Far East of Russia.

I.D. No.[a]	Location of calving grounds
2	Srednesosvinskie and Verkhnevolinskie Uvaly Upland (Fig. 4)
5	Tazovsky Peninsula (Fig. 5)
11	Gydanskaya Gryada Upland (Fig. 6)
13	Basins of Agapa and Mokhovaya Rivers (Fig. 7)
14	Hills along Upper Agapa River (Fig. 7)
15	Hills of Nizhneeniseyskaya Upland (Fig. 8)
16	Verkhnetazovskaya Upland (Fig. 9)
17	Between Pura and Agapa Rivers (Fig. 7)
19	Western Slope of Enisey Kryazh Range (Fig. 10)
21	Kamen-Kherbey Uplands (Fig. 11)
25	Kalamisamo Peninsula (Taymyr Lake) (Fig. 12)
27	SE Spurs of Byrranga Range at Mariya Pronchishcheva Bay (Fig. 13)
28	Suryakh-Dzhangy Kryazh Mountains (Fig. 14)
36	Pronchishcheva Kryazh Mountains (Fig. 15)
38	Kystyk Plateau (Fig. 16)
45	Lena Delta (Fig. 15)
52	Novosibirskie Archipelago (Fig. 17)
53	Churpuniya, Zimovie, Muksunikha-Tas, Khaar-Stan and Uryung-Khastakh Hills (Fig. 18)
60	Basin of Nogliki River (Fig. 19)
63	Southern Slope of Ulakhan-Tas Range (Fig. 20)
67	Upper Elovka River (Fig. 21)
68	Sea Shore Tundra near Kronotskaya River (Fig. 22)
69	Sea Shore Tundra between Khodutka and Asacha Rivers (Fig. 23)
73	Right Side of Anadyr River Basin (Yablon, Peledon and Mechkereva Rivers) (Fig. 24)
74	Elgygytkyn Lake Area, Upper Yurumkuuveem and Enmyvaam Rivers (Fig. 25)
76	Basins of Mamontovaya and Tundrovaya Rivers (Fig. 26)

[a] I.D. No. corresponds to the population location on Figs. 2 and 3.

Table 3. Various statistics for 86 reindeer populations in Siberia and the Far East of Russia.

Statistic	Approximation of population size	Approximation of range size (km^2)	Approximation of mean density (reindeer • 100 km^{-2})
50 populations with a single approximation for each population size			
Summation	747 080	2 439 363	–
Median	2000	28 452	13.6
Mean	14 942	48 787	34.7
±SE	4129	9308	6.3
Min-Max	50–145 000	599–392 267	0.4–182.6
36 populations with only a rough approximation[a] *for each population size*			
Summation	43 575	506 880	–
Median	300	10 253	5.4
Mean	1210	14 080	10.1
±SE	687	2540	2.4
Min-Max	100–25 000	466–72 811	0.4–72.6
All 86 populations combined from above			
Summation	790 655	2 946 243	–
Median	800	15 879	7.6
Mean	9194	34 259	24.4
±SE	2517	5796	4.0
Min-Max	50–145 000	466–392 267	0.4–182.6

[a] Populations identified as being "A few 100" animals were arbitrarily set at 300 reindeer, any > or < qualification was ignored (e.g., > 1000 or < 1000 was treated as 1000), and each population with its size reported as a spread of values (e.g., 1500–2000) was assigned its mid-point value (e.g., 1500–2000 = 1750).

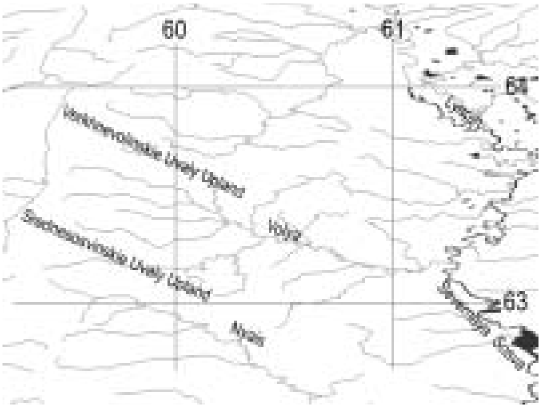

Fig. 4. Map of Srednesosvinskie and Verkhnevolinskie Uvaly Upland calving grounds.

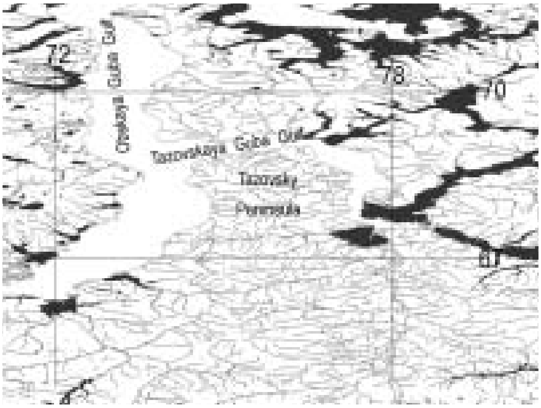

Fig. 5. Map of Tazovsky Peninsula calving grounds.

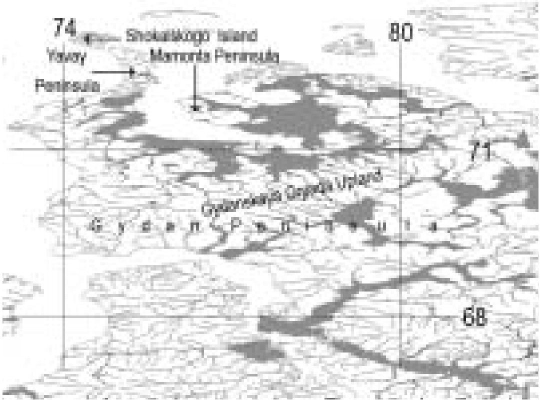

Fig. 6. Map of Gydanskaya Gryada Upland calving grounds.

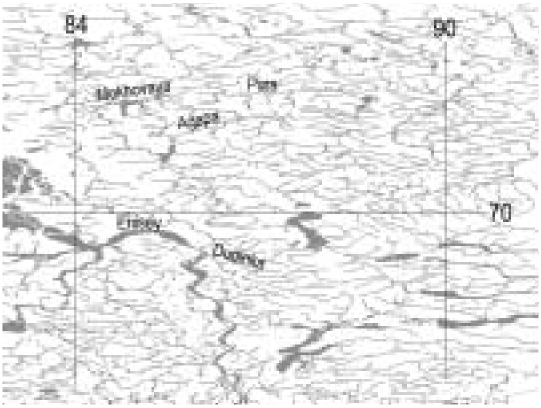

Fig. 7. Map of Basins of Agapa and Mokhovaya Rivers, Hills along Upper Agapa River, and Between Pura and Agapa Rivers calving grounds.

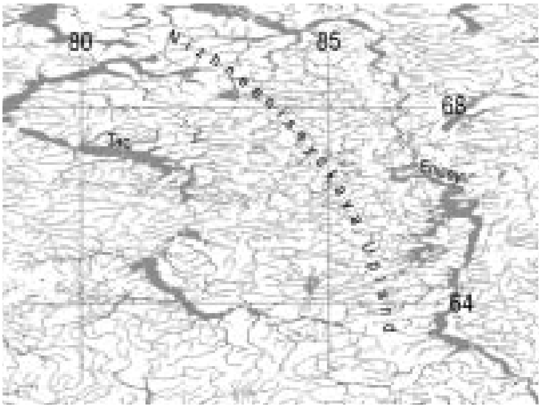

Fig. 8. Map of Hills of Nizhneeniseyskaya Upland calving grounds.

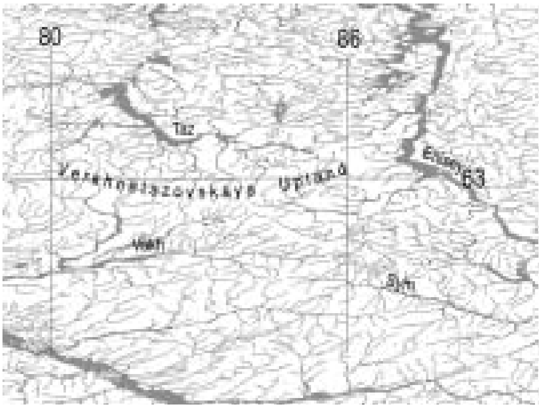

Fig. 9. Map of Verkhnetazovskaya Upland calving grounds.

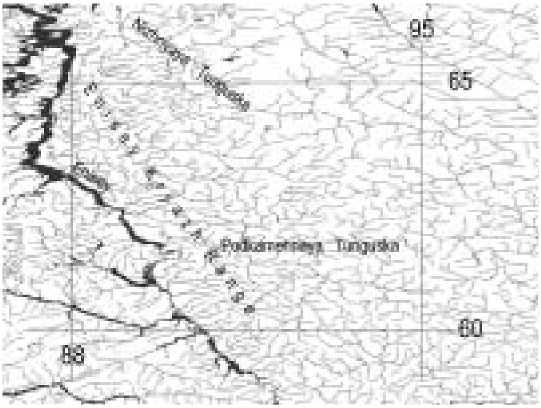

Fig. 10. Map of Western Slope of Enisey Kryazh Range calving grounds.

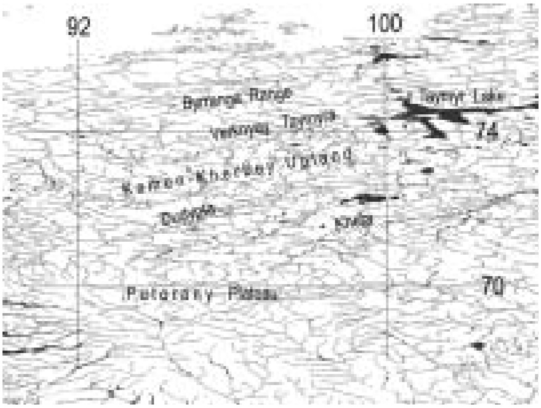

Fig. 11. Map of Kamen-Kherbey Uplands calving grounds.

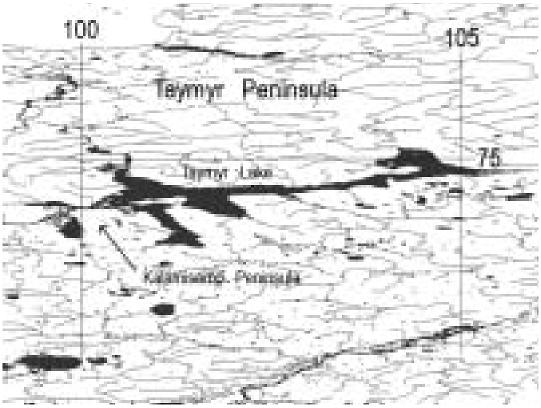

Fig. 12. Map of Kalamisamo Peninsula (Taymyr Lake) calving grounds.

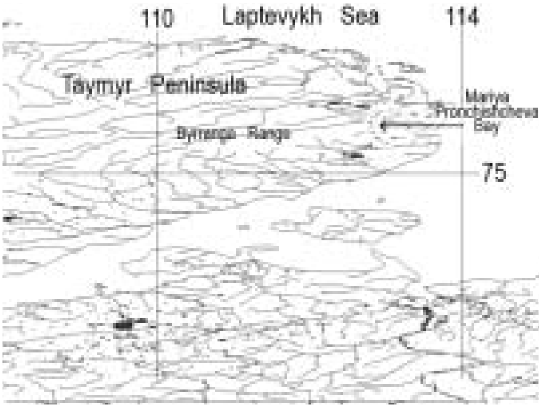

Fig. 13. Map of SE Spurs of Byrranga Range at Mariya Pronchishcheva Bay calving grounds.

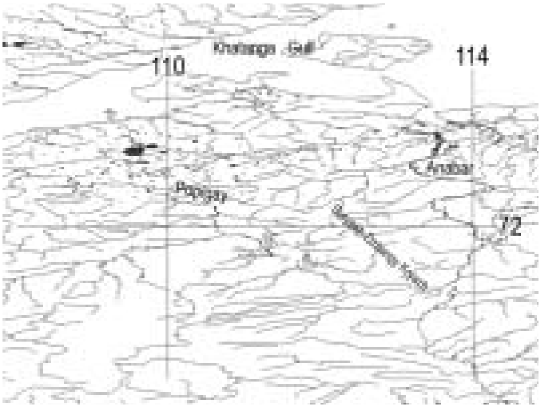

Fig. 14. Map of Suryakh-Dzhangy Kryazh Mountains calving grounds.

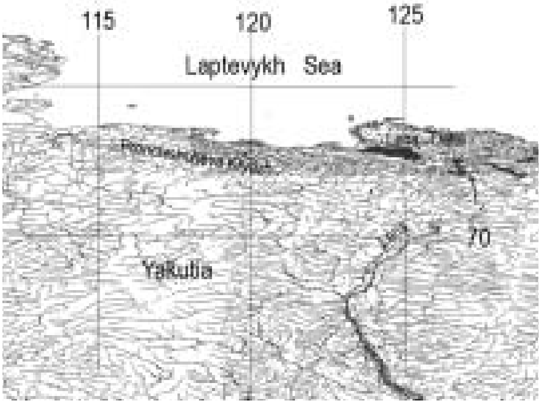

Fig. 15. Map of Pronchishcheva Kryazh Mountains and Lena Delta calving grounds.

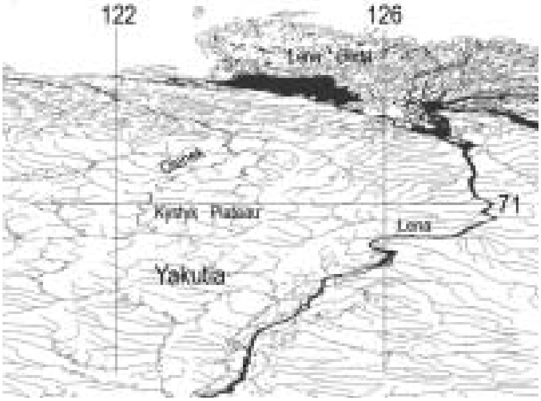

Fig. 16. Map of Kystyk Plateau calving grounds.

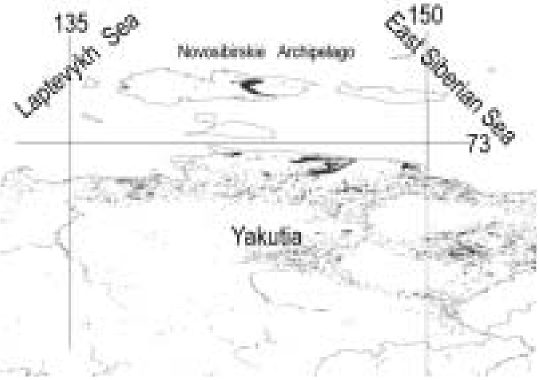

Fig. 17. Map of Novosibirskie Archipelago calving grounds.

Fig. 18. Map of Churpuniya, Zimovie, Muksunikha-Tas, Khaar-Stan and Uryung-Khastakh Hills calving grounds.

Fig. 19. Map of Basin of Nogliki River calving grounds.

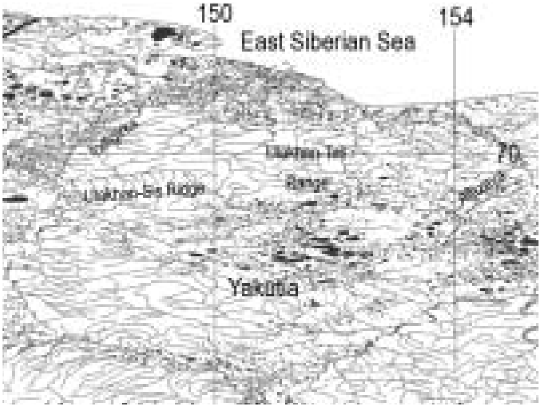

Fig. 20. Map of Southern Slope of Ulakhan-Tas Range calving grounds.

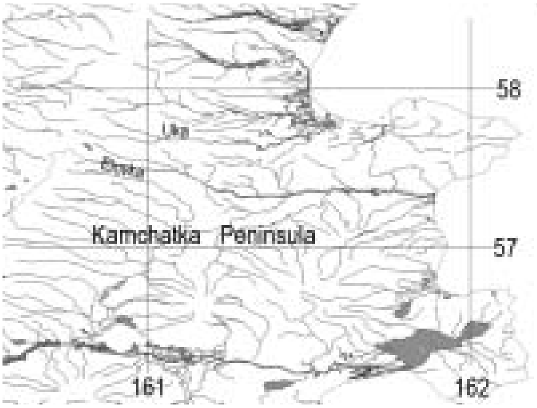

Fig. 21. Map of Upper Elovka River calving grounds.

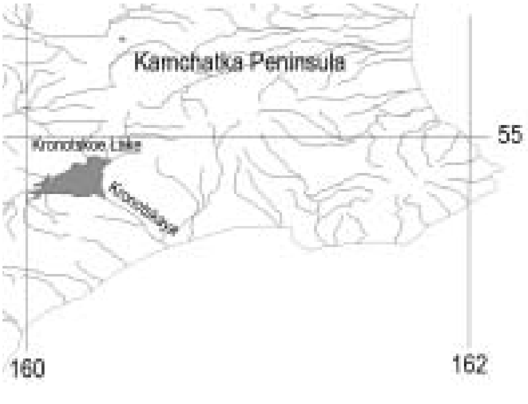

Fig. 22. Map of Sea Shore Tundra near Kronotskaya River calving grounds.

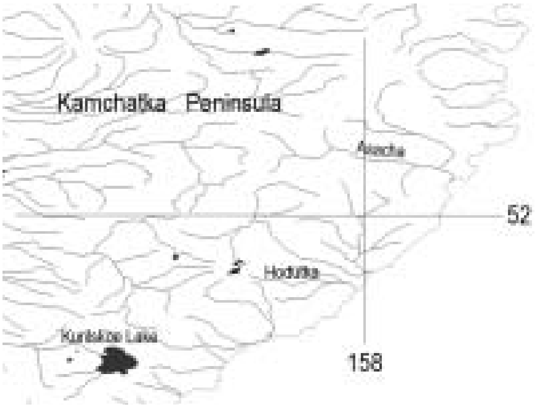

Fig. 23. Map of Sea Shore Tundra between Khodutka and Asacha Rivers calving grounds.

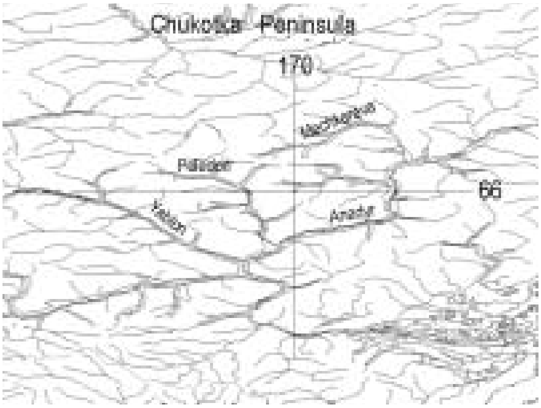

Fig. 24. Map of Right side of Anadyr River Basin (Yablon, Peledon and Mechkereva Rivers) calving grounds.

Fig. 25. Map of Elgygytkyn Lake Area, Upper Yurumkuuveem and Enmyvaam Rivers calving grounds.

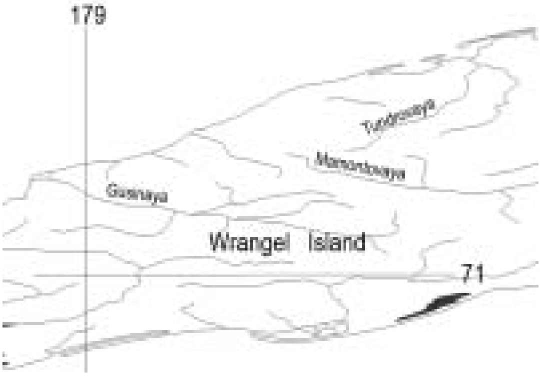

Fig. 26. Map of Basins of Mamontovaya and Tundrovaya Rivers calving grounds.

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Expanded abstract

The role of seasonal migration in the near-total loss of caribou on south-central Canadian Arctic Islands

Frank L. Miller, Samuel J. Barry & Wendy A. Calvert

Canadian Wildlife Service, Environment Canada, Prairie & Northern Region, Room 200, 4999 – 98th Avenue, Edmonton, Alberta T6B 2X3, Canada (frank.miller@ec.gc.ca).

In 1980 the caribou (*Rangifer tarandus*) on Prince of Wales, Russell, and Somerset islands represented a healthy geographic population of an Arctic-island caribou ecotype on the southern tier of Canadian Arctic Islands. Those caribou exhibited complex patterns of seasonal range occupancy, involving annual seasonal migrations between and among the three islands and Boothia Peninsula (Miller *et al*., 1982, 2005; Miller, 1990). A large segment of the population migrated annually from the islands to Boothia Peninsula in early winter, wintered there, and then returned to the islands in the following late winter and spring. There is no evidence for large-scale emigration of caribou anywhere in the study area (Gunn *et al*., 2006).

Caribou on Boothia Peninsula occur as two distinct ecotypes that are genetically different from the Arctic-island ecotype that occurred on Prince of Wales, Russell, and Somerset islands (e.g., Zittlau, 2004). Both the Boothia Peninsula ecotype and the Mainland ecotype calve mostly on northern Boothia Peninsula, northwest and northeast sections respectively (Gunn *et al*., 2000). After summering on the peninsula, most individuals of both ecotypes migrate south of the Boothia Isthmus onto adjacent mainland areas (Gunn *et al*., 2000). As a result, there were about the same number of caribou wintering on Boothia Peninsula when migrant caribou from Prince of Wales, Russell, and Somerset islands wintered there, as in summer when the migrant Arctic-island caribou had returned to Prince of Wales, Russell, and Somerset islands and the migrant Boothia Peninsula and Mainland caribou ecotypes had returned from their winter ranges farther south on the mainland to their calving areas and summer ranges on Boothia Peninsula. We treat both caribou ecotypes on Boothia Peninsula as just one geographic population for our assessment.

The Arctic-island caribou ecotype on Prince of Wales, Russell, and Somerset islands declined about 98% from the estimated 5097 1+ yr-old caribou in 1980 to fewer than 100 1+ yr-old caribou in 1995 (Gunn & Decker, 1984; Miller, 1997; Gunn & Dragon, 1998; Gunn *et al*., 2006). This loss of caribou on those islands amounts to a near-total loss of a genetically distinctive group of Arctic-island caribou (e.g., Zittlau, 2004). In contrast, the estimated number of caribou in the geographic population on Boothia Peninsula appeared to increase by 1.4-fold from 4831 to 6658 1+ yr-old caribou between 1985 and 1995, although annual harvesting pressure was heavy. It was biologically impossible for the Boothia Peninsula geographic population at its 1985 estimated size to have persisted until 1995, let alone to have increased, under the estimated average annual harvest regime of 1100 1+ yr-old caribou • yr^{-1}. There is no evidence that the Boothia Peninsula population was underestimated in 1985. It would have required a population in 1985 at least twice as great as the calculated estimate to sustain the estimated annual harvest between 1985 and 1995. An underestimate of such magnitude is too great to be probable.

In our examination of the survey results, we could find no reason to question that the calculated population estimates were not reasonable approximations. The fixed-wing aerial surveys in 1980 (Gunn & Decker, 1984), 1985 (Gunn & Ashevak, 1990), and 1995 (Gunn & Dragon, 1998) were highly comparable, well designed and executed, using standard procedures for a fixed-width, strip-transect, systematic aerial survey of caribou. One of the two observers was the same experienced survey biologist in all 3 years, the second observer in 1980 was an experienced survey biologist and in 1985 and 1995 was an experienced Inuit hunter familiar with the area, and the pilot was the same on all surveys and had flown many systematic surveys of caribou on the Canadian Arctic Archipelago and mainland Canada.

Helicopter searches of known caribou ranges on Prince of Wales, Russell, and Somerset islands that were carried out in late winter 1996 under ideal viewing conditions yielded only two caribou on Somerset Island and none on Prince of Wales Island or Russell Island (Miller, 1997). In 2004, a combination aerial and ground survey of caribou by the Nunavut Wildlife Service, using a helicopter and snowmobile-mounted Inuit observers, failed to find even one caribou or any recent sign of caribou on Prince of Wales and Somerset islands (Gunn *et al*., 2006).

Gunn *et al*. (2006) found no evidence that an absolute shortage of forage, relative unavailability of forage due to extreme snow and ice conditions, intraspecific competition with muskoxen (*Ovibos moschatus*), large-scale emigration,

widespread disease, or heavy parasite burdens played a major role in the near-total loss of caribou on Prince of Wales, Russell, and Somerset islands. They did, however, conclude that both wolf (*Canis lupus*) predation and hunting on Prince of Wales, Russell, and Somerset islands most likely contributed to and deepened the final stage of the decline. The role of annual seasonal migration between the islands and Boothia Peninsula was not considered by Gunn *et al*. (2006). Therefore, we investigated how annual seasonal migration of the Arctic-island caribou ecotype from Prince of Wales, Russell, and Somerset islands to Boothia Peninsula could have played the major role by providing a yearly ongoing supply of caribou "recruits" on Boothia Peninsula to buffer the heavy annual harvest of caribou there.

We carried out a series of multiple analyses of required population structure, required proportion of females producing calves, required proportion of calves surviving to yearlings, allowable annual harvest, and resultant annual harvest shortfall (the number of caribou lost annually at the estimated level of annual harvest or the number of additional caribou required annually from beyond Boothia Peninsula to sustain the annual harvest) in relation to the required size of the 1985 caribou population on Boothia Peninsula. We derived the annual harvest estimates from data presented in Gunn *et al*. (1986) and Jingfors (1986), which yielded a per capita mean annual harvest of 3.1 caribou • person^{-1} • yr^{-1} throughout the Kitikmeot region and at Taloyoak. We believe the extrapolated annual harvest estimates are conservative, as we did not inflate them to account for the 1.6-fold increase in the human population at Taloyoak between 1980 and 1995 and the Inuit hunters did not report any lack of caribou or hardships in obtaining them during that time.

Inuit hunters prefer the meat of Arctic-island caribou to that of either the Boothia Peninsula ecotype or the Mainland ecotype. Thus, individuals of the Arctic-island caribou ecotype were shot each winter while they wintered on Boothia Peninsula in preference to both the Boothia Peninsula and the Mainland caribou ecotypes. Although caribou are killed year-round and there is no restriction on how many can be killed, most caribou hunting takes place during winter, when hunters can travel longer distances and haul carcasses back to the settlements more easily by snow machines.

Our analyses and assessment of the changes over time in the sizes of the two caribou populations under consideration led us to three primary conclusions. 1) It was biologically impossible for the 4831 1+ yr-old caribou estimated on Boothia Peninsula in 1985 to have sustained the estimated average annual harvest of 1100 1+ yr-old animals for 10 years: the caribou population on the Boothia Peninsula would have been in a steady state of decline and, with the population performing at expected levels, would have been reduced to a remnant or even extirpated as early as 1992. 2) Although the estimated harvest level was unsustainable by the Boothia Peninsula population, the decline was masked by an annual winter infusion of the migrant Arctic-island caribou ecotype from Prince of Wales, Somerset and Russell islands onto Boothia Peninsula during the peak annual hunting period: without the infusion of caribou from the islands, the Inuit of Taloyoak could only have realized, on average, about two-fifths of the estimated annual harvests between 1985 and 1995 without the Boothia Peninsula population entering into a steady state of decline. 3) Migrant Arctic-island caribou from Prince of Wales, Russell, and Somerset islands wintered each year on Boothia Peninsula and this resulted in the persistence of caribou on the Boothia Peninsula, but led to the simultaneous near-demise of the caribou in the Prince of Wales, Russell, and Somerset islands geographic population.

The caribou resource within the entire Prince of Wales-Russell-Somerset islands-Boothia Peninsula complex must be managed as a single unit. Effective management is not possible without ongoing assessment of the annual harvest combined with periodic monitoring of population size being carried out on all of those three islands and on Boothia Peninsula at the same times. To date this has not happened.

A serious effort should be made to obtain annual harvest statistics yearly and population estimates every 3 years. The interval between population surveys could be stretched to 5 years if the budget demands it, but 6-10 years or more between surveys should be viewed as totally unacceptable. All population surveys should be carried out in July, to obtain population estimate and sex and age composition of the population at the same time during each year and long enough after June calving to get a good measure of the early survival of calves. If any evidence is obtained for large-scale ingress or egress, the population should be surveyed the following July and the magnitude and direction of population change determined and evaluated in relation to current annual harvest estimates. The population should be surveyed the following July after every exceptionally severe winter when a major die-off is probable due to extremely unfavorable snow and ice conditions.

All responsible parties (renewable resource agencies and Inuit users) must have the will to act on the findings obtained from the monitoring efforts. Most importantly, they must take the necessary actions in a timely manner, if the findings indicate that the Boothia Peninsula caribou population is in a state of decline. Setting hunting regulations and enforcing harvest limits that are not agreed to by the Inuit users is not practical; therefore, only self-restraint by Inuit hunters will safeguard this valuable renewable caribou resource. The conservation of this hunted caribou population is complicated because preserving only a relatively few caribou is not a satisfactory goal. There must be enough caribou in the population to sustain the desired level of annual harvest or the annual harvest must be quickly adjusted downward to the sustainable level. Otherwise, with a steadily growing human population at Taloyoak, the future of the geographic population of caribou on Boothia Peninsula is not promising and most likely its continual use as a valuable renewable resource is in jeopardy. For further details on this subject see Miller *et al.* (2007).

Key words: Canadian Arctic, caribou harvest, population decline, *Rangifer*, seasonal migrations.

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Abstract

Movements of boreal caribou in the James Bay lowlands

Taylor, M.E.* & M. Ruthven

AMEC Earth & Environmental.160 Traders Blvd East, Mississauga, Ontario L4Z 3K7. **Present address*: AMEC Earth and Environmental, 2227 Douglas Road, Burnaby, B.C. V5C 5A9, Canada.

Little is known about the movements and home range of boreal woodland caribou (*Rangifer tarandus*) in the James Bay lowlands. As part of ongoing studies to measure the potential effects of the De Beers Victor Project on the local and regional environment, a study of woodland caribou was initiated. This study involves the use of GPS collars with Argos satellite system uplink to monitor movements of caribou. Additional aerial surveys of a study area (22 000 km^2) in the early and late winter are used to provide an overall indication of the usage of the area around Victor by caribou and other wildlife. Animals were collared in December 2004 at varying distances from the Victor site (max. 60 km). Preliminary data for 2005 has been analysed. During 2005, some animals moved large distances >480 km from Victor, while others were relatively sedentary. One animal (from the total of ten) was harvested by a hunter in March. The only obvious trend in movement patterns occurred in the middle of November when all the collared animals began to move north-west. The daily distances moved in November were much greater (10-20 km/d) than earlier in the year (0.5-10 km/d) and by mid December they were all north and west of their locations when first collared, in some cases more than 480 km to the northwest of their initial capture sites. The minimum annual distances covered for the nine remaining animals ranged between 900 and 1500 km. The home ranges of the caribou ranged from 8000 km^2 to 56 380 km^2 with a mean home range of 23 434 km^2, which is much greater than boreal woodland caribou in other parts of Ontario.

Key words: Home range, Victor Project, woodland caribou.

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Using ultrasound measurements of rump fat to assess nutritional condition of woodland caribou in northern British Columbia, Canada

David D. Gustine[1], **Katherine L. Parker**[2] **& Douglas C. Heard**[3]

[1] Institute of Arctic Biology, Department of Biology and Wildlife, University of Alaska Fairbanks, Fairbanks, AK, 99775-7000, U.S.A (corresponding author: ftddg@uaf.edu).
[2] Natural Resources and Environmental Studies, University of Northern British Columbia, Prince George, BC, V2N 4Z9, Canada.
[3] British Columbia Ministry of Environment, 4051 18th Avenue, Prince George, BC, V2N 1B3, Canada.

Absttact: Body reserves (fat and protein) of cervids are important to the reproductive success of individuals, and therefore may limit productivity of populations. We used a portable ultrasound machine to measure thickness of rump fat for 39 woodland caribou (*Rangifer tarandus caribou*) captured in the winters (January–February) of 2003 and 2004. We compared thickness of rump fat between pregnant and non-pregnant individuals in the Besa-Prophet drainage of northern British Columbia, Canada. Thirty-eight of the 39 females captured in British Columbia were adults and 34 of the adult caribou were pregnant (89.5 ± 5.1%, $\bar{x}$ ± binomial SE). Pregnant individuals had more rump fat (0.60 ± 0.067 cm) than non-pregnant animals (0.20 ± 0.029 cm). Recognizing that deposition and mobilization of fat vary with age and possibly across the winter season, ultrasonography can be used as a non-invasive technique in the field to assist in estimating body fat of caribou.

Key words: body condition, body fat, index, nutrition, pregnancy rate, *Rangifer*, ultrasonography.

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Introduction

Assessing the nutritional condition of cervids is an important tool in identifying limitations in the productivity of cervid populations (Anderson *et al.*, 1972; Dauphiné, 1976; Gerhart *et al.*, 1996*a*; Heard *et al.*, 1997). Nutritional condition is the state of body components for an individual that may influence current and/or future fitness (Harder & Kirkpatrick, 1994). Therefore, it affects the reproductive capacity of a population (Adams & Dale, 1998*a,b*; Albon *et al.*, 1986; Cameron *et al.*, 1993; Cameron & Ver Hoef, 1994; Heard *et al.*, 1997; Ouellet *et al.*, 1997) and may provide insights into the quality of habitats that animals occupy (Stephenson *et al.*, 2002). Body condition may also affect appetite (Boertje, 1990) which could alter the levels of predation risk within foraging strategies (Stephens & Krebs, 1986).

Quantifying body fat and protein is an important component of defining the nutritional condition of individuals within populations (Gerhart *et al.*, 1996*a*), and has typically involved harvesting individuals (e.g., Anderson *et al.*, 1972; Heard *et al.*, 1997; Ouellet *et al.*, 1997; Chan-McLeod *et al.*, 1999). Harvesting animals may be appropriate for highly reproductive and/or large populations of cervids [e.g., barren-ground caribou (*R. t. groenlandicus*)], but is not applicable for cervid populations that occur at low densities, are endangered, and/or have low rates of recruitment [e.g., woodland caribou (*R. t. caribou*)]. 'Destructive' sampling also precludes multi-year assessments of changes in an individual's body condition over time. Stephenson *et al.* (1998, 2002) showed that ultrasonography is a valid technique for estimating the maximum thickness of rump fat, which correlates well with the total body fat (%) in live moose (*Alces alces*) and mule deer (*Odocoileus hemionus*). Cook *et al.* (2002) reported that maximum thickness of rump fat

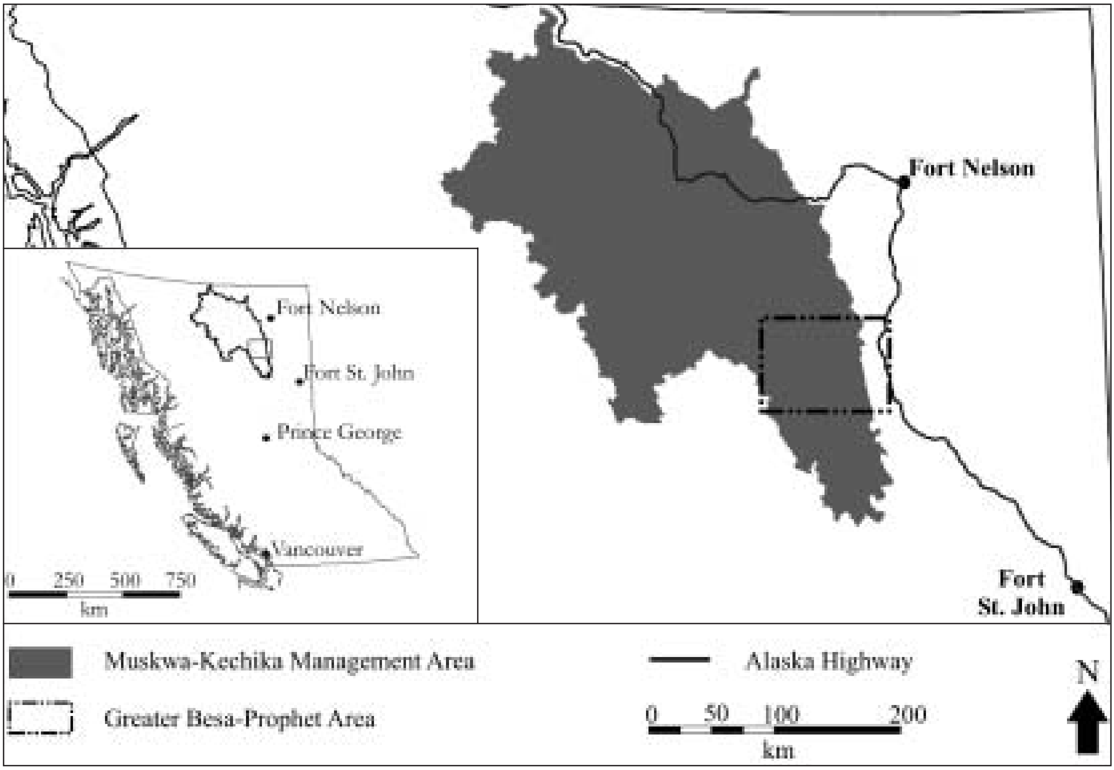

Fig. 1. The Greater Besa-Prophet Area of the Muskwa-Kechika Management Area in northern British Columbia, Canada.

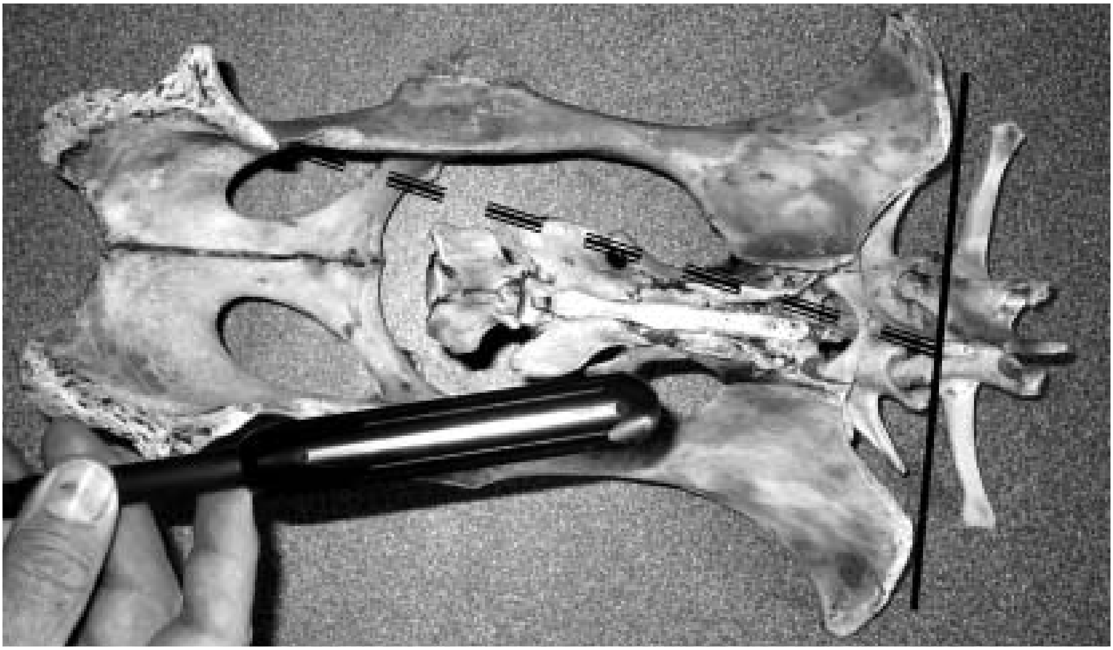

Fig. 2. Ultrasound probe for measuring thickness of rump fat in relation to the caribou pelvic girdle. The dashed line represents the line along which the ultrasound transducer probe should be positioned. The dashed line extends from the pin bone (cranial process of the tuber ischium) to a point along the spine between the hip bones (tuber coxae), as shown by the black line. Rump fat should be recorded at the point of maximum fat depth immediately adjacent to the pin bone.

in combination with a body condition score (Gerhart *et al.*, 1996*a*) was also the best in vivo predictor of percent body fat for elk (*Cervus elaphus*).

Reproductive status during winter may be indicative of body condition in autumn (Cameron *et al.*, 1993). Animals with very low body fat commonly do not come into estrus (Dauphiné, 1976; Thomas & Kiliaan, 1998) or, more rarely, do not carry fetuses to term (Dauphiné, 1976; Russell *et al.*, 1998). Non-pregnant caribou also may have lower body mass than pregnant individuals (Cameron & Ver Hoef, 1994). A valuable index of body condition for caribou in winter should, therefore, be non-destructive, distinguish between reproductive classes, and provide a repeatable measure of relative condition for an individual over time.

We used ultrasound measurements of the thickness of rump fat to determine relative body condition of pregnant and non-pregnant woodland caribou (northern ecotype; Heard & Vagt, 1998) in north-central British Columbia, Canada. We submit that with some limitations and further research, ultrasonography, as reported for other cervids, is a valuable field technique to measure rump fat and enables biologists to estimate percent body fat and trends in nutritional condition of woodland caribou.

Material and methods

Thirty-nine female woodland caribou were captured in February of 2003 ($n = 20$) and January 2004 ($n = 19$) in the Greater Besa-Prophet Area (57°11' and 57°15'N, and 121°51' and 124°31'W) of the Muskwa-Kechika Management Area in northern British Columbia, Canada (Fig. 1). Descriptions for this study area are available in Gustine *et al.* (2006). Caribou were not immobilized for capture, rather we captured individuals with a net-gun (Rongstad & McCabe, 1984) from a helicopter (Bell Jet Ranger II-206B) and 'hobbled' them with leather restraints. Blood samples (approx 10 ml) were taken to determine reproductive condition of caribou via serum progesterone concentrations (Prairie Diagnostics Services, Saskatoon, SK, Canada; Russell *et al.,* 1998). We estimated thickness (cm) of rump fat using a portable ultrasound machine (Medison Sonovet 600 with variable 4–6 MHz linear probe, Universal Medical Systems Ltd, Bedford Hills, NY, USA) as outlined in Stephenson *et al.* (1998) with the location for measurements provided by T. Stephenson (unpublished data) (Fig. 2). We used an unpublished linear equation to estimate body fat (%) for caribou from the measurements of rump fat: body fat (%) = 5.76 + [2.27*(thickness of rump fat (cm)] (T. Stephenson, unpubl. data). We used analysis of variance to examine the effect of capture date on thickness of rump fat (Zar, 1999). We did not examine the effect of year because dates of collection were specific to capture date in each year (i.e., all animals were captured in either February 2003 or January 2004; therefore capture date was synonymous with year). We tested the hypothesis that non-pregnant woodland caribou females would have less rump fat, and therefore lower estimates of body fat, than pregnant females (Dauphiné, 1976; Gerhart *et al.*, 1996*a*; Heard *et al.*, 1997; Thomas & Kiliaan, 1998). If there was no effect of capture date on thickness of rump fat, we pooled data across years and examined thickness of rump fat for adults (>3 years) by reproductive status using a one-tailed t-test (Zar, 1999). Because of violations in the assumption of normality, we log-transformed rump-fat measurements for all tests. We used Stata 9.0 (Stata Corporation, College Station, TX, USA) for analyses and assumed significance for all tests at $\alpha = 0.05$.

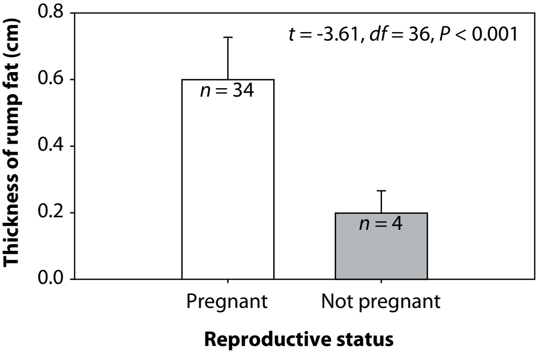

Fig. 3. Ultrasound estimates of thickness of rump fat (cm, $\bar{x}$ ± 95% CI) by reproductive status for woodland caribou in the Greater Besa-Prophet Area, northern British Columbia, Canada, 2003–2004.

Results

Thirty-eight of the 39 woodland caribou females captured were adults (Table 1) and 34 of the adult caribou were pregnant (89.5 ± 5.1%, $\bar{x}$ ± binomial SE). The individual <1.5 years of age had one of the lowest estimates of body fat and was not pregnant (Table 1), and, subsequently, was not included in comparisons. There was no effect of capture date ($F_{(1, 36)} = 1.030$, $P = 0.316$) on estimates of body fat, so we pooled all data to examine differences in thickness of rump fat for pregnant and non-pregnant animals. Pregnant caribou had more rump fat (Fig. 3) and, therefore, higher estimates of percent body fat (7.1 ± 0.15%, $\bar{x}$ ± SE) than non-pregnant caribou (6.1 ± 0.06%). Estimates of body fat ranged from 6.0–9.6% in pregnant caribou and 6.0–6.2% in non-pregnant animals, but we only had estimates for four non-pregnant adults (Table 1).

Table 1. Reproductive status and ultrasound estimates of rump fat for female woodland caribou in the Greater Besa-Prophet Area in northern British Columbia, 2003–2004. Reproductive status for 38A was confirmed via necropsy and 33A was <1.5 years old.

Animal	Date of capture	Progesterone (ng/ml)[1]	Reproductive status	Thickness of rump fat (cm)	Body fat (%)[2]
26A	10-Feb-03	4.7	Pregnant	0.3	6.4
27A	10-Feb-03	4.3	Pregnant	0.1	6.0
21B	11-Feb-03	3.7	Pregnant	0.5	6.9
25B	11-Feb-03	3.9	Pregnant	0.7	7.3
28A	11-Feb-03	7.3	Pregnant	0.4	6.7
29A	11-Feb-03	4.8	Pregnant	0.2	6.2
30A	11-Feb-03	2.7	Pregnant	0.9	7.8
31A	11-Feb-03	3.8	Pregnant	0.5	6.9
32A	12-Feb-03	5.0	Pregnant	1.3	8.7
33A	12-Feb-03	<0.2	Not pregnant	0.1	6.0
34A	12-Feb-03	5.8	Pregnant	0.5	6.9
35A	12-Feb-03	3.1	Pregnant	1.6	9.4
36A	12-Feb-03	<0.2	Not pregnant	0.1	6.0
37A	12-Feb-03	<0.2	Not pregnant	0.1	6.0
38A	13-Feb-03	n/a	Pregnant	0.4	6.7
39A	13-Feb-03	4.7	Pregnant	0.3	6.4
40A	13-Feb-03	10.9	Pregnant	0.7	7.3
41A	14-Feb-03	4.3	Pregnant	0.9	7.8
42A	14-Feb-03	6.2	Pregnant	0.2	6.2
43A	14-Feb-03	4.8	Pregnant	1.7	9.6
44A	20-Jan-04	7.2	Pregnant	0.4	6.7
45A	20-Jan-04	<0.2	Not pregnant	0.2	6.2
46A	20-Jan-04	3.8	Pregnant	0.5	6.9
47A	20-Jan-04	4.4	Pregnant	0.3	6.4
48A	20-Jan-04	7.8	Pregnant	0.9	7.8
49A	20-Jan-04	<0.2	Not pregnant	0.2	6.2
50A	20-Jan-04	5.7	Pregnant	0.4	6.7
51A	20-Jan-04	4.5	Pregnant	0.2	6.2
52A	20-Jan-04	5.6	Pregnant	0.6	7.1
53A	21-Jan-04	5.0	Pregnant	0.3	6.4
54A	21-Jan-04	4.8	Pregnant	0.5	6.9
55A	21-Jan-04	3.9	Pregnant	0.6	7.1
56A	21-Jan-04	5.4	Pregnant	0.2	6.2
57A	21-Jan-04	6.1	Pregnant	0.3	6.4
58A	21-Jan-04	12.4	Pregnant	0.3	6.4
59A	21-Jan-04	3.4	Pregnant	0.4	6.7
60A	21-Jan-04	4.8	Pregnant	0.9	7.8
61A	21-Jan-04	5.3	Pregnant	1.1	8.3
62A	21-Jan-04	5.6	Pregnant	0.4	6.7

[1] Determined from serum progesterone assays (Prairie Diagnostics Services, Saskatoon, SK, Canada; Russell *et al.,* 1998).

[2] Estimated using the equation $y = 5.76 + 2.27x$, where y = estimate of body fat (%), and x = ultrasound measurement of rump fat (cm); $r^2 = 0.77$ (T. R. Stephenson, unpublished data for caribou).

Discussion

Ultrasonography was effective in differentiating the variation in rump fat between pregnant and non-pregnant female woodland caribou in the Greater Besa-Prophet Area. With sufficient training and access to an ultrasound machine, biologists can incorporate this technique into annual capture and collaring operations (Stephenson *et al.*, 1998). Data on snow conditions during winter, changes in energetic reserves by individuals within and among years, and estimates of calf productivity will become increasingly useful for predicting population trajectories as climatic factors and vegetative parameters become more variable (Lenart *et al.*, 2002; Adams, 2005).

Maternal body mass affects the probability of pregnancy in autumn (Reimers, 1983; Cameron *et al.*, 1993; Cameron & Ver Hoef, 1994) as well as calf survival through summer (Eloranta & Nieminen, 1986; Gustafson *et al.*, 1998). Specific components (i.e., fat and protein) of body mass, however, are better predictors of pregnancy (Gerhart *et al.*, 1996*a*; Ouellet *et al.*, 1997). The role that fat and/or protein set points, or thresholds, have in determining the probability of pregnancy, viability of the fetus, and/or calf growth and survival in caribou is undetermined. Relative to energetic reserves, Crête *et al.* (1993) suggested that body fat must be 7.8% or approximately 7.0 kg of the ingesta-free body mass in autumn–early winter for pregnancy to occur in caribou. Ouellet *et al.* (1997) recommended that the threshold is probably lower (approx 6.0%). Five of the 10 animals that we measured with ≤6.2% body fat were pregnant and of the 4 animals with 6.0% body fat, only one was pregnant (Table 1). Recognizing that loss of fat through winter is expected and that the rates of this loss are largely undetermined, the observed similarities in rump fat for non-pregnant woodland caribou suggest that animals with body-fat levels of 6.0–7.0% in mid-winter may have approached the limit needed for pregnancy in fall. Some of the pregnant woodland caribou in the Greater Besa-Prophet Area may be at or near this limit (Table 1). Neonatal calf weights for woodland caribou in our study area [males, 8.09 ± 0.52 kg, $\overline{x}$ ± SE, n = 19; females, 7.78 ± 0.28 kg, n = 31 (Gustine *et al.*, 2006)], however, were similar to the 10-year average of calf weights (males, 8.04 ± 0.07 kg; n = 244; females, 7.50 ± 0.07 kg, n = 267) from barren-ground caribou in generally excellent condition (Denali herd; Adams, 2005). Low body fat, therefore, may not necessarily result in lower calf weights for those caribou that do reproduce, although it is not currently known if winter body-fat levels of 6–7% are low enough to evoke a 'threshold' effect in fetal development.

A means of monitoring body protein in late winter would be a valuable complement to ultrasonography, given that fetal tissue is comprised primarily of maternal protein (P. Barboza & K. Parker, unpublished data). Nutritional restrictions in late winter associated with decreased forage availability (e.g., increased snow depth or hardness) may increase both energetic costs (e.g., movement) and catabolism of energetic and protein reserves to maintain body processes (Parker *et al.*, 2005). Fetal development and subsequently, fetal and neonatal viability [e.g., white-tailed deer (*O. virginianus;* Sams *et al.*, 1995)] may be compromised when maternal protein is progressively depleted to meet energetic demands. Pregnant females are likely most sensitive to these types of restrictions during the third trimester when physiological demands of fetal growth are the highest. Monitoring changes in body protein, however, is challenging because of the relatively small changes that occur throughout the year (approx 9.5–11.2% of body mass for breeding female caribou, Chan McLeod *et al.*, 1999). Recent use of nitrogen isotopes in snow urine to assess nitrogen balance in late winter (Parker *et al.*, 2005; Barboza & Parker, 2006) is promising, but this technique requires validation in wild populations of caribou.

Certainly there are limitations to the ultrasound technique as well as challenges in interpreting the observed differences in the thickness of rump fat between reproductive classes of woodland caribou. First, ultrasound estimates of rump fat are not useful for animals with no rump fat (Stephenson *et al.*, 1998; 2000; Cook *et al.*, 2002) because lack of measurable rump fat does not indicate 0% body fat (e.g., caribou with no rump fat could have up to 5.76% body fat based on the linear equation used to estimate body fat from rump fat). At very low levels of rump fat, it also can be difficult to determine the difference between muscle fascia and fat on ultrasound images depending on field conditions (e.g., sun may limit the visibility of the screen), observer experience, and resolution of the ultrasound screen. It may be more correct to interpret low values of rump fat as a range in condition (e.g., caribou with 0.10 cm of rump fat have <6.1% body fat), but investigators would have difficulty comparing samples with descriptive statistics. With few exceptions (see set point discussion above), reclassifying individuals in our sample this way would not effect our general conclusions: pregnant females had thicker rump fat than non-pregnant females and ultrasonography appears to be a valuable tool for assessing relative condition of woodland caribou. Chan-McLeod *et al.* (1995) documented large variation in percent body fat for animals with no rump fat (approx 3–14%, min–max), using measurements made manually on carcasses and not with ultrasonography. It is possible, therefore, that we also could have underestimated percent body fat for animals with little or no rump fat. As recommended by Cook *et al.* (2002), an estimation of body fat probably should combine ultrasound measurements of rump fat with body condition scores (Gerhart *et al.*, 1996*b*) to increase utility of the technique across the full range of body conditions (approx 0–25% body fat). Second, fat deposition and pregnancy rates vary with age. Because young animals must meet the demands of growth, younger animals deposit less fat and generally have lower pregnancy rates than adults (Dauphiné, 1976; Heard *et al.*, 1997; Thomas & Kiliaan, 1998). Researchers should attempt to either age animals within their samples or incorporate this as a source of bias in their estimates of condition.

The positive relationship between probability of pregnancy and body fat in *Rangifer* spp. is well documented (Dauphiné, 1976; Cameron *et al.*, 1991; Gerhart *et al.*, 1996*a*; Heard *et al.*, 1997; Thomas & Kiliaan, 1998) and has been useful for evaluating nutritional condition of individual animals and populations. The importance of body condition in *Rangifer* spp. though has been discussed almost exclusively relative to fluctuations in populations of Arctic barren-ground caribou. In contrast, research on populations of woodland caribou has focused typically on habitat fragmentation and predation risk, and indices of body condition have received little attention. Consequently, there are few data reported that index the condition of woodland caribou and we recommend that more studies quantify nutritional condition as an integrator of the food-predation-environment trade-off. The relationship between body reserves and the probability of pregnancy may be similar among woodland and barren-ground subspecies and/or ecotypes, but variation in biotic (e.g., vegetation, snow conditions, seasonal distribution of predators and other ungulates) and abiotic factors (e.g., topography) as well as associated annual and seasonal energetic costs, suggest that there may be differences in nutrient partitioning strategies (e.g., magnitude of fat deposition). We were unable to make direct comparisons of our measurements of rump fat with those of Arctic populations because back fat of barren-ground animals mostly was measured manually and at different locations on animal carcasses. Ultrasonography with standardized protocols is now being used to determine thickness of rump fat in both live barren-ground and woodland caribou for captive (Parker *et al.*, 2005; Barboza & Parker, 2006) and wild (E. Jones, unpublished data from British Columbia; M. Oakley, unpublished data from Yukon; this study) populations.

Recognizing that the deposition and mobilization of fat varies with age (Dauphiné, 1976; Heard *et al.*, 1997), previous demands of reproduction (Chan-McLeod *et al.*, 1994), and across the winter season (Thomas & Kiliaan, 1998; Chan-McLeod *et al.*, 1999), ultrasonography can be used as a non-invasive technique in the field to assist in evaluating nutritional condition of caribou. Similar to data collected from carcass evaluations in previous studies on barren-ground caribou (e.g., Dauphiné, 1976; Thomas & Kiliaan, 1998), the non-pregnant woodland caribou in our sample had less rump fat than pregnant individuals. Although these data are within general thresholds of percent body fat needed for pregnancy in caribou (Crête *et al.*, 1993; Ouellet *et al.*, 1997), additional studies should quantify the environmental and physiological parameters that affect rates of fat and protein deposition and catabolism for individuals within a population. In addition to ultrasound measurements of rump fat, body condition scores [described in Gerhart *et al.* (1996*b*) and developed for elk by Cook *et al.* (2002)] and estimates of body protein would help to quantify maternal investment towards calf production and the ecological strategies used to address energetic and protein demands for reproduction and survival.

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Abstract

Woodland caribou management in Alberta: historical perspectives and future opportunities

Elston H. Dzus & Pat Cabezas

Alberta Caribou Committee, 15810-114 Avenue, Edmonton, AB Canada T5M 2Z4 (corresponding author: Elston.Dzus@alpac.ca).

Woodland caribou conservation has been the topic of much debate for the past few decades. By the late 1970s there was growing concern about declining woodland caribou populations and the interaction between industrial activities and woodland caribou. Initial concerns led to the closure of the licensed hunting season in 1981. Early confrontation between government and industry in the late 1980s transformed into a series of evolving collaborative ventures. Improving our understanding of the basic ecology of woodland caribou in Alberta was at the center of early research efforts; more recent studies have examined the effects of industrial activities on caribou and effectiveness of various mitigation factors. Despite having amassed an impressive body of information from a research and monitoring perspective, progress on implementing effective management actions has been less dramatic. Industry has endured significant costs implementing a variety of perceived conservation initiatives, but caribou populations continued to decline through the last few decades. While some parties feel more research is needed, there is growing consensus that changes to habitat as induced by human activities are important factors influencing current caribou declines. Predation is a proximate cause of most caribou mortality. Climate change mediated alterations to habitat and predator-prey interactions remain a key source of uncertainty relative to future caribou population trends. Management actions will need to deal with long term habitat changes associated with human land use and short term implications of increased predation.

In 2005, the provincial minister responsible for caribou conservation responded to the draft 2004 recovery plan and created the Alberta Caribou Committee (ACC). The goal of the ACC is to maintain and recover woodland caribou in Alberta's forest ecosystems while providing opportunities for resource development, following guidance provided by the Alberta Woodland Caribou Recovery Plan, as qualified by the Minister of Sustainable Resource Development. The current and future challenge involves conserving and recovering caribou populations and habitat through use of knowledge-based processes, applied through existing or other mechanisms, as deemed appropriate. As outlined in the ACC terms of reference, this complex challenge is to be achieved in an atmosphere of co-operation and trust amongst participants. The mandate of the ACC is to bring together the expertise and experience of its members under a consensus-based partnership for the purpose of: 1) providing thoughtful advice to government and, 2) implementing or supporting approved caribou population and habitat conservation and recovery programs. The ACC provides advice to government regarding policy and program matters, but does not create government policy or programs. Compared to previous multi-stakeholder committees dealing with caribou in Alberta, the ACC has an expanded membership that includes representatives from aboriginal organizations, industry (forestry and energy sector), environmental non-government organizations, the scientific community, and the government of Alberta. In addition to the expanded 'breadth' in committee membership and mandate scope, is an increased 'height' of influence in that the governance board provides advice to the Alberta government through the Deputy Minister of Sustainable Resource Development (the provincial department responsible for land and wildlife management). This new collaboration brings new optimism for translating knowledge to effective cumulative effects management alternatives. For more information on the Alberta Caribou Committee see: http://www.albertacariboucommittee.ca/

While the federal government is not represented on the ACC, there are a number of opportunities exist for engagement of federal government agencies and personnel in the evolving caribou conservation arena. As woodland caribou are listed as a threatened species, there is an obvious role for Environment Canada to develop a national recovery strategy and administer the Species At Risk Act (including facilitating a definition of critical habitat). Additional opportunities for federal involvement include the development of strategies specific to lands under federal jurisdiction and, where appropriate, participation on landscape teams to develop management strategies for herds whose range crosses provincial and/or federal boundaries.

Key words: boreal forest, conservation, industrial development, species at risk.

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An integrated assessment of Porcupine caribou seasonal distribution, movements, and habitat preferences for regional land use planning in northern Yukon Territory, Canada

John L. Ryder[1*], Phillipa McNeil[2], Jeff Hamm[1], Wendy A. Nixon[2], Don Russell[2] & Shawn R. Francis[1]

[1] Yukon Land Use Planning Council, 201-307 Jarvis Street, Whitehorse, YT, Y1A 2H3, Canada (*corresponding author: john@planyukon.ca).

[2] Environment Canada, Canadian Wildlife Service, 91780 Alaska Highway, Whitehorse, YT, Y1A 5B7, Canada.

Abstract: This study was undertaken to improve understanding of Porcupine caribou herd distribution, movements, and habitat preferences to assist with developing a regional land use plan for the North Yukon Planning Region, Yukon Territory. Three different methods were used to identify current and historical patterns of caribou distribution and habitat preferences within the region to prioritize conservation areas. Two of the approaches focused on incorporating information on caribou distribution and migrations from scientific and local knowledge, while the third focused on identifying and mapping habitats suitable for supporting caribou. Local knowledge dating back to the 1930s and two decades of satellite telemetry data confirmed that most of the planning region is used by the Porcupine caribou herd and highlighted areas of concentrated use. Maps of suitable winter habitat derived from expert opinion ratings of habitat use did not agree with the other information sources. The local knowledge and satellite telemetry analyses were used to identify spatially explicit priority areas for caribou conservation and the results were applied to develop conservation recommendations for a draft regional land use plan. The plan will be submitted to government approval bodies for review in the spring of 2007. The success in implementing conservation strategies for the Porcupine caribou herd will be reviewed and evaluated following adoption of a final approved plan.

Key words: concentrated use areas, conservation, cumulative effects, cumulative impacts, habitat suitability, home range, local knowledge, *Rangifer*, thresholds, traditional ecological knowledge, utilization density.

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Introduction

To fulfill its land use planning mandate under the terms of the Vuntut Gwitchin First Nation (VGFN) Final Agreement (Department of Indian Affairs and Northern Development, 1993), the North Yukon Planning Commission (NYPC) must develop and recommend a draft regional land use plan for the North Yukon Planning Region by the spring of 2007. The planning region is located in Canada's Yukon Territory, encompasses the traditional territory of the VGFN, and is approximately 55 500 km^2 in size (Fig. 1).

The NYPC is an independent body comprised of six publicly appointed members. Representation is equally split between VGFN and Yukon Government. Members are charged with developing regional land use goals, objectives, and management recommendations for submission to VGFN and Yukon Government for consideration and approval. Under Chapter 11 of the VGFN final agreement, "regional land use plans shall include recommendations for the use of land, water and other renewable and non-renewable resources in the planning region in a manner determined by the Regional Land Use Planning Commission" (Department of Indian Affairs and Northern Development, 1993).

Under the terms of the VGFN Final Agreement (Department of Indian Affairs and Northern Development, 1993) and the NYPC precise terms of reference (North Yukon Planning Commission, 2004), there

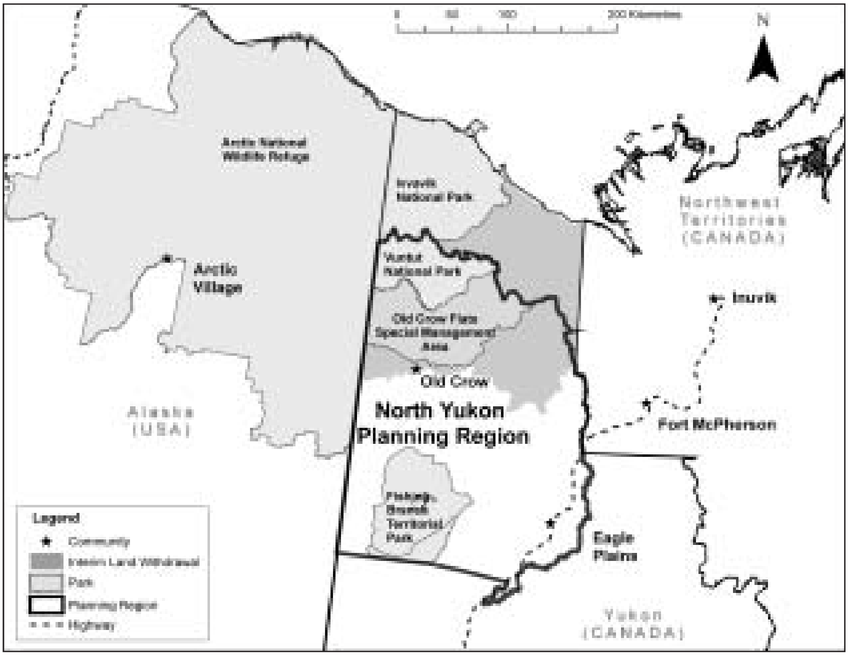

Fig. 1. Location of the North Yukon Planning Region (thick black outline) in northern Yukon Territory, Canada. Protected areas within the region include Vuntut National Park and Fishing Branch Territorial Park. A protected land designation for the Old Crow Flats Special Management Area (SMA) is in progress (March 2007). An additional protected area under interim land withdrawal is also shown.

are five general guiding principles that the Commission must follow during plan production: 1) recognize and promote the cultural values of Yukon Indian people, 2) promote and ensure sustainable development, 3) integrate decision-making, 4) recommend measures to minimize land-use conflicts, and 5) consider scientific and traditional (local) knowledge of resources equally. An additional important consideration for the Commission is to recommend tools and approaches to mitigate potential cumulative effects/impacts of multiple land use activities on resources.

VGFN settlement lands account for 7762 km^2 or 14% of the planning region (areas not shown). Most of the remaining non-settlement lands are managed by the Yukon Government. The only permanent community in the region is Old Crow with a population of approximately 270 residents (Yukon Department of Health and Social Services & Yukon Bureau of Statistics, 2005). There is also a small year-round service facility located at Eagle Plains along the Dempster Highway.

Much of the land in the region has existing protected area status or is under a land withdrawal order that prohibits exploration and development activities. The land withdrawal area is considered a protected area at present, but the order is for an unspecified time period and could be lifted in the future. The protected areas include Vuntut National Park, Fishing Branch (Ni'iilii'njik) Territorial Park, Old Crow Flats Special Management Area (OCF-SMA), and the land withdrawal area extending south and east of the OCF-SMA. The area delineated at the southern limit of Fishing Branch Territorial Park is designated as a Habitat Protection Area (HPA). This area is to be managed as a conservation unit to maintain ecological integrity, but it is not a protected area. The protected areas and HPA represent approximately 46% of the region's area. Outside these areas, the remaining settlement and non-settlement lands have undetermined management objectives. These are the areas of focus for NYPC activities.

A recurring issue of concern expressed at community consultations is the conservation of the Porcupine caribou herd across the region, given the potential for oil and gas exploration/development activities and the uncertain effects of climate change on caribou. Consequently, the NYPC, VGFN, Yukon Department of Environment, and other plan partners identified caribou as a resource of primary interest for further study in the context of producing a land use plan.

The Porcupine caribou are a tundra herd of Grant's caribou (*Rangifer tarandus granti*) that range from Northeastern Alaska to the Yukon/Northwest Territories border. The most recent population survey estimated the herd size at 123 000 animals, down from a 30 year high of 178 000 animals in 1989

(McNeil *et al.*, 2005). This herd has special cultural and ecological significance to First Nations and has been a high profile population internationally with ongoing proposals for hydrocarbon exploration and extraction on their calving grounds in Alaska (Griffith *et al.*, 2002).

Within the planning region, the community of Old Crow is one of the primary users of the herd and subsistence harvest remains strong (Berman *et al.*, 2004). Porcupine caribou are harvested during the fall, winter and spring periods along the Dempster Highway corridor by other communities and non-first nation hunters in the Yukon and Northwest Territories (Kofinas & Braund, 1998). Caribou primarily occupy the planning region during the fall migration, rut, winter, and spring migration seasons. The range of dates for these seasons has been reported elsewhere (Porcupine Caribou Technical Committee, 1993; McNeil *et al.*, 2005). The Porcupine Caribou Technical Committee (1993) assessed the relative importance of habitats to caribou during these seasons, according to six criteria, and concluded that these seasonal habitats were less important than the calving, post-calving, and early summer habitats. A detailed description and characteristics of the range are reported in Russell *et al.* (1993).

The identification and conservation of significant areas of use for the Porcupine caribou herd were considered regional priorities. To address the information needs of this requirement, the NYPC collected, analyzed, and interpreted spatially explicit scientific and local knowledge of caribou use of the region from 2004-2006. The need for and benefits of sharing and integrating scientific and local knowledge to improve resource decision-making have been well documented (Russell *et al.*, 2000; Huntington *et al.*, 2002; Danby *et al.*, 2003; Kelsey, 2003; Berman & Kofinas, 2004; Moller *et al.*, 2004; Ellis, 2005). This study was undertaken to achieve three objectives: 1) to integrate and compare various sources of data on caribou distribution to identify spatial patterns in seasonal habitat use, and presence/arrangement of suitable habitat, 2) to identify areas of conservation priority for caribou, and 3) to apply the information to develop and recommend conservation strategies in a draft regional land use plan, with emphasis on mitigation and management of potential cumulative impacts to caribou.

Material and methods

Three different methods were employed to identify current and historical caribou use areas. Two of the approaches focused on incorporating population-level information on caribou distribution and migration patterns in the four seasons when caribou primarily occur within the planning region: fall migration, rut, winter and spring migration. The population distribution information was obtained from local knowledge of significant caribou use areas and analyses of satellite telemetry data. The third approach focused on collaboratively developing expert opinion ratings of habitats suitable for supporting caribou during the winter season and applying the ratings to a habitat map of the region. Each method is described below.

Table 1. Seasonal definitions used for the Porcupine caribou herd.

Season	*Date*
Winter	December 1 to March 31
Spring Migration	April 1 to May 31
Calving	June 1 to June 10
Post-calving	June 11 to June 30
Early summer	July 1 to July 15
Mid to late summer	July 16 to August 7
Fall migration	August 8 to October 7
Rut	October 8 to November 30

Satellite telemetry analyses

In June 2005, the Canadian Wildlife Service and the NYPC analyzed a long-term (1985-2004) satellite telemetry dataset of collared Porcupine caribou cows to quantify seasonal habitat use and migrations of the herd, and to examine landscape level patterns of distribution. A detailed description of the satellite collar project can be found on the Taiga Net website (Taiga Net, 2006). The analysis identified general use areas, concentrated use areas and mean directional vectors for animal migrations between seasons.

The annual cycle was divided into eight seasons based upon caribou activities (Table 1; Porcupine Caribou Technical Committee, 1993). The dataset included an average of 11 collared animals per year with 68 different animals over the time period. Caribou locations for each season were limited to a maximum of 10 random samples per animal to ensure that no animal was over-represented (McNeil *et al.*, 2005). Of the 18 979 locations, 4306 were randomly sampled for this study with 450 to 650 locations per season. Utilization density grids were created for each season using fixed-kernel analysis procedures (Seaman *et al.*, 1998). General use areas, representing habitats where most of the satellite collared animals were found at low density, were derived from the 99% isopleth for each seasonal kernel analysis (Griffith *et al.*, 2002). Concentrated use areas, representing habitats occupied at a higher density of animals than other areas within the herd's range, were derived from the 60% isopleth. While the 50% isopleth has been used to denote concentrated use areas for the Porcupine caribou herd (Griffith *et al.*, 2002), the 60% isopleth was initially chosen to provide a conservative estimate. The 60% isopleth has recently been used to identify concentrated use areas for other caribou populations, as a result of exponential fit modelling (Schindler, 2005; Schindler, *pers. comm.*).

Migration patterns were considered supplementary information to the identification of concentrated use areas. General migration pathways between seasons were derived for fall migration through to spring migration. For each animal, point to point linear migration vectors were created between the last location in one season's concentrated use area and the first location in the following season's concentrated use area. Animals had to be present in both concentrated use areas, across seasons, to be included for analysis. Individual migration vectors were then subjectively assigned to a general migration path, based on travel direction and geographic locations of departure and arrival. For example, if two animals generally traveled in a south to north direction between Old Crow and Old Crow Flats, across seasons, they would both be assigned to this migration path. Based on this subjective assignment, a mean directional vector was computed for each general migration path.

Local knowledge workshop

In November 2004, the NYPC hosted two interactive community workshops in Old Crow, YT, with Vuntut Gwitchin elders and other community residents to document local sources of information on wildlife use of the region. Both workshops were public sessions, and residents collectively shared their historical and current knowledge of caribou distribution. A total of 18 workshop participants (13 male/5 female) and 11 support staff participated in the workshops. All participants were current or former hunters of varying ages. Approximately two-thirds of the participants were young or middle-aged adults, and the rest were elders. Local knowledge of general caribou distribution spanned from at least the 1930s to present. Many stories told at the workshop reflected a historical knowledge base much older than this period. Information on caribou distribution across various portions of the region and for various life functions (general range, breeding area, migration corridor, and mineral lick) was obtained. Participants provided locational information for the months of August through to May, corresponding to the fall migration, rut, winter, and spring migration periods. Temporal trends in caribou distribution were not obtained. Support staff delineated important caribou areas and migration routes on 1:250 000 scale paper maps. This information was subsequently digitized and attributed in ArcGIS v. 9.1 (ESRI Inc., Redlands, California, USA), a geographical information system.

Habitat suitability workshops

At the November 2004 workshop, participants expressed an interest in assessing the winter habitat use of Porcupine caribou. Residents were familiar with and comfortable in rating caribou use of winter habitats only. As a result, two habitat suitability workshops were held in January 2005 with biologists and community residents to collaboratively rate various habitats for their winter value to caribou. This expert opinion based approach, referred to as a Delphi process, aims to develop consensus between experts over several rounds of deliberation on the assumption that combining the expertise of several individuals will provide more reliable results than consulting one or two individuals (MacMillan & Marshall, 2006).

At the outset of the workshops, participants developed a common definition and understanding of the winter season. Definitions of seasons were discussed and decided upon by Old Crow residents and biologists. For caribou, the winter period was defined as November 1st to March 31st, differing from the Porcupine Caribou Technical Committee definition of December 1st to March 31st (Porcupine Caribou Technical Committee, 1993).

In early January 2005, the Yukon Department of Environment held a habitat suitability mapping workshop in Whitehorse, YT. Three biologists with expert knowledge of the habitat use and requirements of Porcupine caribou rated the relative value of various winter habitat types within the region. Reference photos of 28 unique habitat types (summer images) depicting various vegetation communities, elevation gradients, and physical characteristics were shown to participants who then collectively rated the habitats for their relative winter importance to caribou. The habitat types represented the range of habitat features found throughout the region. Participants were asked to classify the value of habitats into one of four categories (0=lowest; 1=low; 2=moderate; 3=high).

A subsequent habitat suitability workshop was held in late January 2005 with Old Crow residents. The workshop was a public session and most attendees were also present at the wildlife workshops in November 2004. Workshop participants were shown the same representative photographs of various habitat types. Participants were likewise asked to rate the habitat types for their relative value to caribou. A total of 17 Old Crow residents and 5 support staff participated.

Habitat suitability ratings from both workshops were combined to produce one composite rating for each habitat type. Habitat ratings were compiled in a database and the values were linked to a biophysical habitat map (v. May 2006) of the planning region. The biophysical map showed the same 28 habitat types with their ratings and the spatial arrangement and location of each habitat in the region. The ratings and coverage were spatially comprehensive within the region, and there were no missing values.

The biophysical map was derived through a predictive ecosystem modeling process. Three primary layers of mapped information were used to create the biophysical map of the region: 1) vegetation cover data (25m resolution) from Earth Observation for Sustainable Development Landsat interpretation (Natural Resources Canada, 2000), 2) a 90m digital elevation model (DEM) of the Yukon Territory, and 3) a 1:250 000 scale vector map showing regional terrain features. A relative soil moisture model was derived from the DEM, providing a reasonable approximation of ecosite conditions stratified by elevation and terrain features. Regional terrain mapping refers to a method of delineating and describing regional terrain conditions that are ecologically relevant (i.e. influence the distribution, structure and productivity of vegetation communities). Regional terrain features are similar to surficial geology and included pediment slopes, major stream valleys, glaciolacustrine basins, bedrock, plateaus, and mountains in the region. A description of the biophysical mapping methodology is available at the NYPC website (North Yukon Planning Commission, 2006). The biophysical map was reviewed for adequacy and accuracy in its representation of habitat types, and was found to be adequate for the purpose of regional habitat characterization (Cryo Geographic & Makonis Consulting, 2006).

A preliminary habitat map with the ratings was shown to participants in April 2005 for review, refinement, and further discussion. The ratings for specific habitats were adjusted where required, based on a consensus decision by the participants. A final map of winter habitat suitability for Porcupine caribou was then produced.

Maps showing caribou concentrated use areas, migration patterns, important areas from local knowledge sources, and winter habitat suitability were overlaid and visually compared in ArcGIS v.9.1 to identify priority areas for caribou conservation. Conservation priorities were subjectively determined by Commission members through collective interpretation of this information. A rigorous statistical analyses and comparison of the spatial trends in the data was not considered appropriate given the varying quality, resolution, and scale of the data.

Results

The satellite telemetry data confirmed that the Porcupine caribou herd uses the North Yukon Planning Region extensively. General use areas (99% isopleths) during all seasons covered 96% of the planning region (Fig. 2). Within the region, the concentrated use areas occupied a total area of 19 224 km^2, representing approximately 35% of the total planning region area. Approximately 55% of the total concentrated use area in the planning region is present in the existing Parks, Old Crow Flats SMA, Fishing Branch HPA, and the region under land withdrawal. The concentrated use area within the planning region represents 33% of the total range-wide fall migration/rut season concentrated use area of the herd, 36% of the winter season, and 13% of the spring migration season, respectively.

General migration patterns of the herd show that animals converged on the North Slope of the Yukon Territory and Alaska during the spring migration period, en route to the calving grounds. During the fall migration to rut period, the herd displayed large variability in directional migrations between habitat patches (not shown). In general, fall migration occurs as a southward movement of animals into the Richardson and Ogilvie mountain ranges. Between the rut and winter periods, caribou move more locally across habitat patches within these same mountain ranges.

The local knowledge map also confirmed that Porcupine caribou currently are, and have historically been, distributed across the region (Fig. 3). Several north-south migration corridors were identified through the Richardson Mountains, the perimeter of Old Crow Flats, and the central portion of the planning region. Numerous localized important caribou range areas were identified, particularly around the Old Crow Flats, and several regional mountain ranges south of Old Crow (i.e. Sharp Mountain, western Richardson Mountains). All polygons represent individual or collective knowledge of caribou distributions from workshop participants. Some of the polygons overlap where the same areas were identified by multiple participants. Most of the caribou distribution data from the community wildlife workshops were recorded for areas near Old Crow, during the winter season when caribou are present and harvested near the community.

The winter habitat suitability map (Fig. 4) reveals a predominance of high quality winter habitat in the southern portions of the planning region, particularly in the southeast. The northern portion of the range was classified as low to lowest quality winter habitat, while the Richardson Mountains along the eastern edge of the planning region were identified as moderate winter habitat. Approximately

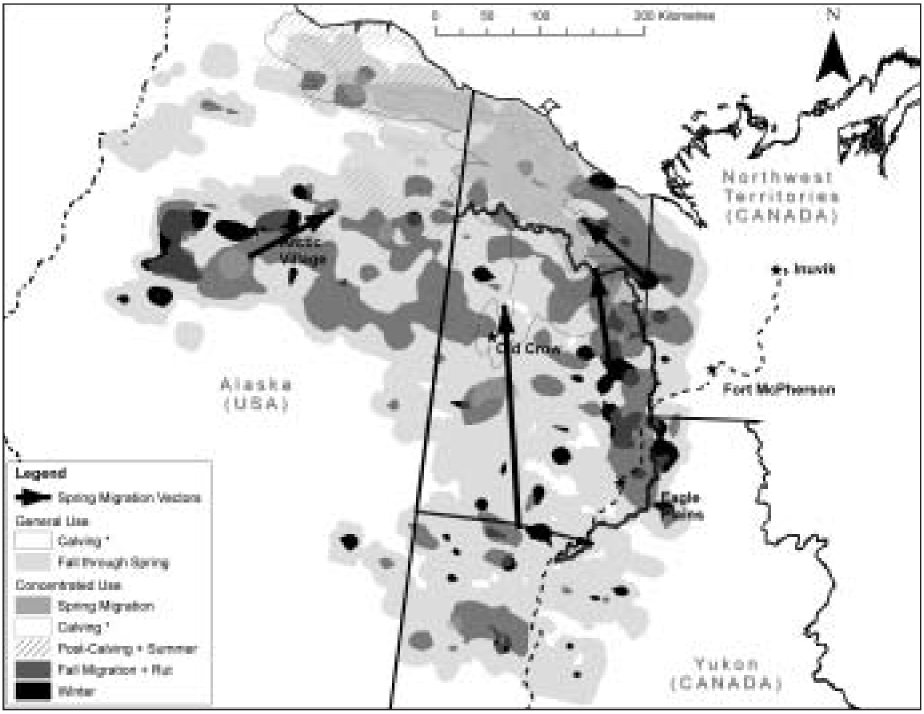

Fig. 2. General (99% isopleths) and concentrated use areas (60% isopleths) of the Porcupine caribou herd by season. Mean directional vectors (black arrows) show migration pathways between winter and spring migration seasons. * Calving areas shown as per Griffith *et al.* (2002).

47% of the planning region area was rated as moderate to high quality winter habitat (35% and 12% for each class, respectively). Within the winter concentrated use areas in the planning region, approximately 54% of the occupied habitat was rated as moderate to high quality (41% and 13% for each class, respectively).

Discussion

Two decades of satellite telemetry data and local knowledge dating back to the 1930s confirmed that most of the planning region is used by the Porcupine caribou herd at some time during their annual cycle, but primarily during fall migration, rut, winter, and spring migration seasons. Caribou are also found in the extreme northern portion of the region during the calving and mid/late summer seasons.

Several areas of the planning region had overlapping concentrated use areas across these seasons, suggesting a higher intensity of use. The analysis of caribou migration and distribution showed that the Richardson Mountain range is a consistently important area for the herd during fall, winter and spring. The northern portion of the Richardson range has been a consistent concentrated use area during summer. In contrast, the Eagle Plains basin has received less use by the herd, consistent with findings dating back to the 1970s (Russell *et al.*, 1992). Probable factors and explanations for these observed patterns have been reported (Russell *et al.*, 1993; Russell, 2000).

Concentrated calving areas within the region have been documented, but calving in the region is infrequent. Most calving occurs on the North Slope of Alaska in the Arctic National Wildlife Refuge (ANWR) (Griffith *et al.*, 2002). Concentrated use areas during the calving and mid/late summer seasons are contained within the existing protected areas, Old Crow Flats SMA, and the region under land withdrawal. Limited use of the planning region was observed during the post-calving and early summer seasons. During these seasons, satellite collared animals have been found concentrated along the North Slope of Alaska in the Arctic National Wildlife Refuge (ANWR) (Griffith *et al.*, 2002; McNeil *et al.*, 2005).

In general, good agreement between the important areas identified from local knowledge sources and the concentrated use areas derived from satellite telemetry analyses was revealed, with the exception of the Richardson Mountain range. This finding was not surprising as VGFN residents have not extensively occupied the Richardson Mountain range in recent times (post 1930). The community knowledge of distribution is best for the winter season when animals are harvested

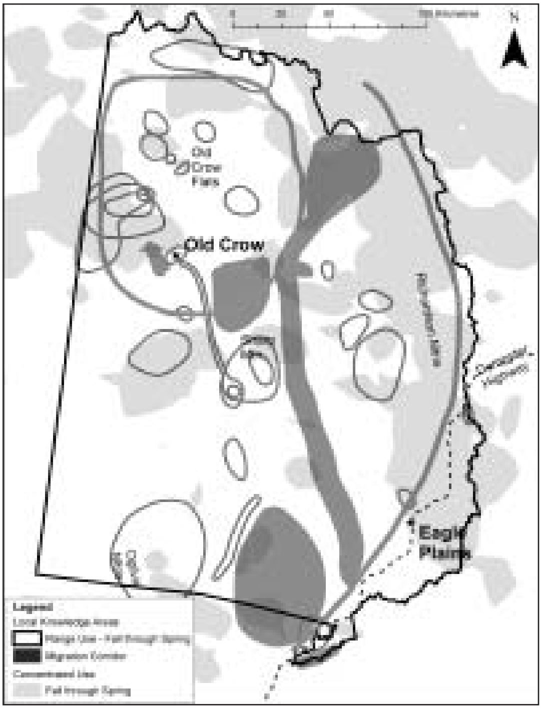

Fig. 3. Overlay of local knowledge and concentrated use areas for fall, winter and spring migration seasons. Important caribou range areas within the North Yukon Planning Region from August to May, as indicated by Old Crow residents, are shown as polygons (dark grey outline). Migration corridors (dark grey shading) and concentrated use areas (light grey shading) are also shown.

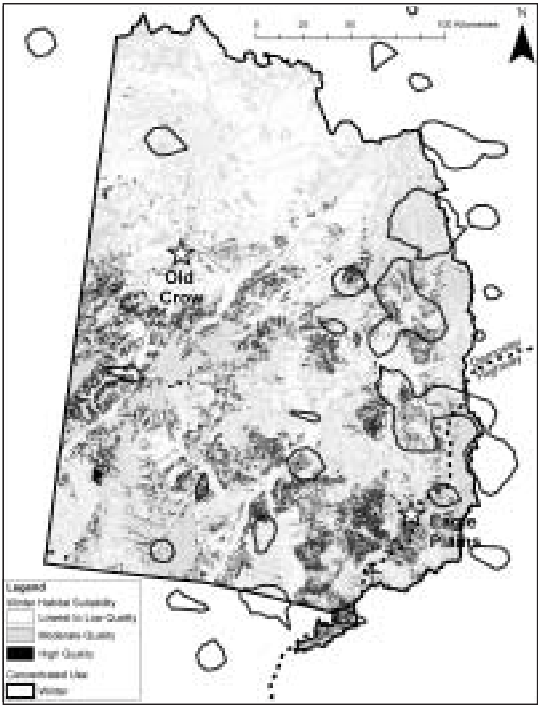

Fig. 4. Overlay of concentrated use areas and habitat suitability map for the winter season. Concentrated use areas (thick black outline), high quality habitat (black shading), moderate quality habitat (light grey shading), and lowest to low quality habitat (no shading) are shown.

near the community. There are local knowledge gaps for many areas that are no longer visited, have not been visited in recent times, or are only visited on a seasonal basis. The local and scientific information sources validated each other for areas that local residents are familiar with, and displayed complementary patterns of animal use of the landscape. Satellite telemetry analyses highlighted priority areas (e.g. Richardson Mountains), while local knowledge was useful to link patches of concentrated use areas via identified traditional migration corridors.

Based on our assessment, we recommend that local knowledge be used as a primary source of information for planning purposes around the vicinity of Old Crow. Local knowledge of caribou hunting areas from past research (Berman & Kofinas, 2004) has also been used to confirm the identification of important areas for Old Crow residents. The satellite telemetry analyses can be used to fill gaps in knowledge for areas that are not frequently visited by local residents.

Habitat suitability mapping derived from expert opinion did not agree with the other information sources. A poor agreement between the winter habitat suitability map and actual distribution of animals was observed, likely owing to several factors that were not considered. Workshop participants noted that caribou occupation of suitable habitats is dependent upon many factors not considered here, including, but not limited to: snow depth/resistance, predation risk, competition for resources, weather, wind, insect harassment, timing of seasonal cycles (i.e. spring green-up), presence of mineral licks, fire history, recent burn intensity, individual/group behaviours, and anthropogenic disturbance.

An additional consideration is that the habitat suitability ratings reported here are based on expert opinion and subjective interpretations of habitat use from summer reference images. It is possible there was some misinterpretation of the reference images in the context of producing the winter suitability map. Owing to these factors and possible issues with the workshop methodology, the map of suitable habitat was not used for identifying caribou conservation priorities.

A particularly important factor that should be considered in future iterations of a habitat suitability map is snow characteristics. We speculate that in deep snow years, snow characteristics (i.e. depth, density, and resistance) are the most important variables likely to predict winter caribou distribution, whereas the presence of suitable vegetation underneath the snow would determine winter habitat suitability in shallow snow years. Caribou may be limited by availability of forage that is inaccessible because of snow cover (Cronin *et al.*, 1998). The southeastern portion of the Porcupine caribou range was identified as having very high quality habitat but it is also an area where deep snow is prevalent (Russell *et al.*, 1993). Johnson *et al.* (2001) found that woodland caribou shifted foraging areas when snow depth, density, and hardness limited access to terrestrial lichens. There is a need for good quality snow mapping, ideally via cost-effective remote sensing to assess patterns of snow conditions throughout the range.

An important consideration for caribou in a land use planning context is the maintenance of migration routes as connections between concentrated use areas and across seasons, particularly for long-distance migrants such as barren-ground caribou. A recent study indicated that long-distance migrants have poor long-term prospects due to anthropogenic impacts and that migration corridors should be conserved (Berger, 2004).

In general, the results reported here are consistent with published findings on the herd's distribution (Russell *et al.*, 1992, 1993). While we identify distribution patterns collectively over the past half-century, there may be habitats used by caribou over longer time scales that are not reflected in these analyses. For instance, areas that were subjected to forest fires within the past 50 years may become more important as lichens recover. Our analysis may have been influenced by short-term changes such as fire history, snowfall and decadal climate patterns. Hinkes *et al.* (2005) reported erratic migrations, range shifts, and changes in migratory behaviours of a barren-ground caribou herd in Alaska and concluded that 20-25 years of monitoring individual caribou herds is too short a time to fully understand the role of movement in caribou ecology. This conclusion was corroborated by several elders at the Old Crow workshop, who commented that changes in caribou use of the landscape required long-term studies on the order of 100 years. Such findings highlight the importance of long-term monitoring to identify changing patterns in caribou distribution.

To address the objectives for this study, we restricted our interpretations and conclusions to the local knowledge and satellite telemetry analyses to recommend regional caribou conservation priorities. The application of the findings toward the development of management direction and recommendations in a draft regional land use plan is discussed below.

Implications for land use planning

Within the planning region, the factors most likely to impact the herd in the near future (5-20 year time horizon) are oil and gas exploration and development and the effects of climate change. The cumulative effects of these factors may be greater than each factor in isolation, particularly when new areas are accessed for development, providing opportunities for additional harvest and anthropogenic disturbance. In Alaska, tundra caribou have shown a particular sensitivity to disturbances associated with hydrocarbon development activities (Nellemann & Cameron, 1998; Cameron *et al.*, 2005). The potential positive and negative effects of climate change on the Porcupine herd have been reported (Kruse *et al.*, 2004; McNeil *et al.*, 2005). Seasonal distribution may deviate from historical and current observed patterns if climate change, development, and harvest pressures concurrently alter the landscape.

Given these potential uncertainties, and the fact that approximately half of the planning region already has protected area, SMA, or conservation land withdrawal status, the NYPC is proposing to use cumulative impact thresholds (limits of acceptable change) as a tool to manage the remaining landscape. This approach is typically referred to as a "flexibly prescriptive" approach to land use planning, in that it provides guidelines, objectives, and stated desirable outcomes for specific land management units without differentiating "acceptable" and "unacceptable" land uses in specific areas. Such an approach would be in addition to the general guidelines and required operating procedures (i.e. seasonal timing windows to mitigate disturbance to caribou concentrated use areas and migration corridors) that form much of the content of existing land-use plans from other jurisdictions. Threshold-based approaches to conserve caribou have recently been proposed or approved for two adjacent land use planning regions in the Northwest Territories and Alaska, consistent with a flexibly-prescriptive planning model (Northeast Alaska Petroleum Reserve, Alaska, and DehCho, NWT) (U.S. Department of the Interior, Bureau of Land Management, 2005; DehCho Land Use Planning Committee, 2006).

A recommended approach by the NYPC is to set limits of acceptable change for two terrestrial indicators: allowable cumulative impact (area of direct surface disturbance) and linear feature density (km/

km²). A considerable body of research has indicated that these two selected indicators are: 1) easily measured, 2) have demonstrated ecological significance (relevant to caribou conservation), 3) are cost effective to measure and track, 4) are easily understood, 5) are common to most land use activities, and 6) can be actively managed (e.g. Duinker, 2000; Dyer *et al.*, 2001; Environment Directorate, Northern Affairs Program, 2002; Cameron *et al.*, 2005). An additional consideration is that the tracking of the indicators is a politically feasible recommendation that can be relatively easily implemented through existing development review processes. The allowable thresholds for these indicators would be applied to specific land management units. At present, the Commission is proposing two land use designations to apply to the land management units in the region: (a) Protected Area and (b) Integrated Management Area (IMA).

As described above, exploration and development activities are prohibited in protected areas and these were not considered for thresholds. The thresholds would apply to the IMA, which currently have four recommended levels (zones) of desired conservation focus and associated thresholds: I) highest conservation focus, II) high conservation focus, III) moderate conservation focus, and IV) low conservation focus. The levels of conservation within the IMA were determined subjectively by NYPC through overlays of various wildlife/fish and cultural/heritage data, with emphasis on identified caribou and wetland values. For caribou, the conservation priority emphasis was on areas with overlapping concentrated use areas across seasons, overlapping local knowledge areas, and major migration corridors necessary to maintain connectivity between significant areas and seasons. A description of identified ecological and cultural resources that were considered during this process is available (North Yukon Planning Commission, 2006).

For each zone from I-IV, threshold tolerance limits would increase. For example, an IMA categorized as zone I would have the lowest threshold. All exploration, development, and tourism activities would be considered equal opportunities within the IMA, subject to usual permitting processes, general operating procedures and guidelines, and the condition that a threshold is not to be exceeded in a given zone if the activity is approved. For the current status of an IMA to be effectively monitored, the indicators must be tracked, reported and periodically updated/revised as new data become available.

Based primarily on the assessment of the caribou data reported here, and various other wildlife/fish, wetlands, and cultural/heritage data, the NYPC's proposed land management units and designations for the region are shown in Fig. 5. A consensus-based decision making process with Commission members and other stakeholders on appropriate zoning and level of conservation focus was used in the proposal. Thirteen distinct units are delineated and the level of conservation focus for each is shown. The areas shown as highest conservation focus contain the region's identified significant wetland complexes (Yukon Department of Environment, unpublished data). These are sensitive permafrost terrain areas that support a variety of wetland-dependent organisms, and are culturally important to VGFN residents. One additional protected area is proposed for the Whitefish wetlands complex, a culturally and ecologically significant and sensitive area, on land owned by VGFN (located in the centre of the highest conservation focus IMA west of the Richardson Mountains). The areas shown as high conservation focus

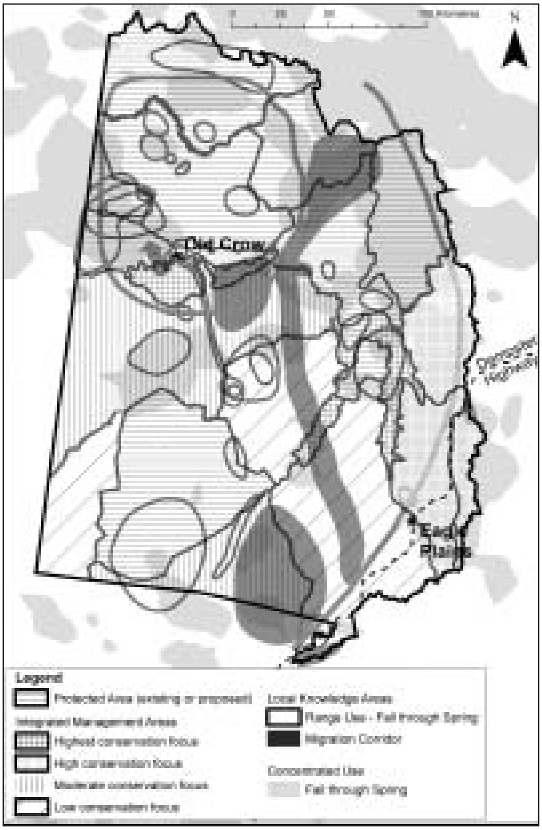

Fig. 5. Proposed land designations and zones overlayed with local knowledge and concentrated use areas for fall, winter and spring migration seasons. Existing and proposed protected areas are shown (horizontal hatch). Integrated Management Areas show proposed highest conservation focus (square hatch), high conservation focus (stippled), moderate conservation focus (vertical hatch), and low conservation focus (diagonal hatch).

had overlapping seasonal caribou concentrated use, in addition to other ecological and cultural values (Richardson Mountains).

The highest and high conservation focus zones (zones I and II) and the new protected area proposal captured 61% of the remaining caribou concentrated use areas outside the existing protected areas, Old Crow Flats SMA, Fishing Branch HPA, and the region under land withdrawal. If the concentrated use areas contained within existing and proposed protected areas and zones I and II are included, 82% of the herd's concentrated use areas would have protected area or conservation management designations under this proposal. All observed calving areas, both concentrated and general use, would also be captured under this scenario.

Flexibly-prescriptive planning models appear to hold the best promise to meet stakeholder needs in our planning region, but to be effective must contain quantitative statements about desired future states. Under the guiding principles that the Commission must follow, thresholds are appropriate tools to balance regional economic/development opportunities with the desire to ensure that current and potentially future important areas for Porcupine caribou, other wildlife/fish, and cultural/heritage resources have adequate conservation measures. Such an approach would involve monitoring, tracking, reporting, and evaluating the terrestrial disturbance indicators noted above. Where thresholds are being reached, additional monitoring of other ecological indicators would be required to determine if undesirable impacts to fish and wildlife populations or habitats ensue.

While the precise details of specific land designation units and acceptable thresholds have yet to be agreed upon or approved, and recognizing that threshold limits may be based on subjective determinations, the analysis and integration of scientific and local knowledge of Porcupine caribou herd distribution will play a crucial role in determining land use management recommendations and in NYPC's development and recommendation of a draft land use plan in the spring of 2007.

The success in implementing a thresholds approach to land management decision-making, and the usefulness and acceptance of the threshold metrics themselves, will be evaluated periodically following adoption of a final land use plan. Threshold implementation also provides quantitative criteria to assist assessment boards and regulatory authorities to establish potential project-level contributions to significant cumulative environmental and socio-economic impacts, thereby providing increased certainty and transparency in the assessment process. As better information on disturbance thresholds and potential impacts to caribou becomes available through additional research, the acceptable limits would be adjusted at the next planning cycle, using an adaptive management style approach to refine the values.

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