Proceedings of the Ninth
North American Caribou Workshop
Kuujjuaq, Québec, Canada
23-27 April, 2001

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and other Northern Ungulates

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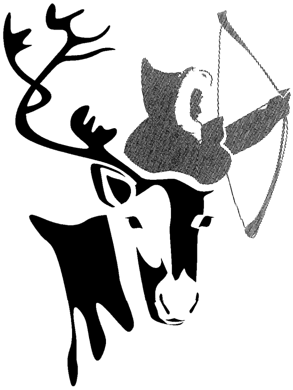

LE CARIBOU ET L'HOMME
CARIBOU AND MAN

Kuujjuaq, Québec, Canada, April 23 to 27, 2001

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Preface

For centuries the lives of North American native peoples have been closely tied to the caribou, or *Rangifer tarandus*. For many of these peoples, caribou are more than a vital food source, they are, simply put, a way of life. There is growing interest in the longstanding relationship between the caribou and human populations who share the same territory, or in what is called traditional environmental knowledge.

Caribou ecology and conservation status differ radically among ecotypes, whether migratory-tundra, sedentary-boreal, montane, or insular. While the migratory caribou ecotype has been generally abundant since the early 1980s throughout North America, the sedentary ecotype has recently experienced continent-wide low densities and decline. Nevertheless, even migratory caribou have not always been plentiful, and over the last century, their numbers have fluctuated dramatically. If we look at the caribou populations on the Northern Québec and Labrador Peninsula, abrupt declines in caribou populations have led to starvation among some native groups. Following a period of relative abundance in the late 19th century, caribou numbers on the peninsula became very low from early the 1900s to about 1960. However, in the 1970s, for reasons that remain unclear, the Québec-Labrador caribou numbers began to rise again. Today, two migratory herds—the George River Herd (referred to locally as the *Troupeau de la Rivière George*) and the Leaf River Herd (*Troupeau de la Rivière aux Feuilles*)—whose territories overlap in their yearly migration, together make up one of the largest group of free-ranging ungulates in the world. One million-strong, these caribou roam through the region's arctic tundra, taiga, and boreal forest and use an area of about one million square kilometres annually. Such caribou populations form a part of our global heritage.

In this context of such fluctuations in numbers, a central concern is the current and future state of these caribou populations. Besides satisfying the subsistence and cultural needs of the native people, caribou are essential to the viability of many northern outfitting businesses that employ both natives and non-natives. Other activities in this Arctic landscape include hydroelectric development, construction, mining, forestry, military training, and tourism. More than ever, there is a need to document and assess the effects of direct and indirect human intervention on the caribou.

The North American Caribou Workshop is held every two or three years. The purpose of the event is to bring together people interested in caribou to share their knowledge about the species in order to ensure its conservation. Previous North American Caribou Workshop locations, dates, and themes are listed below.

1st: Whitehorse, Yukon Territory, Sept. 28-29, 1983, **Caribou and Human Activity**
2nd: Val Morin, Québec, Oct. 17-20, 1984, **Caribou Management – Census Techniques – Status in Eastern Canada**
3rd: Chena Hot Springs, Alaska, Nov. 4-6, 1987, **Reproduction and Calf Survival**
4th: St. John's, Newfoundland, Oct. 31-Nov. 3, 1989
5th: Yellowknife, Northwest Territories, March 19-21, 1991, **Caribou Management in the 1990s: Incorporating Theory into Practice**
6th: Prince George, British Columbia, March 1-4, 1994
7th: Thunder Bay, Ontario, Aug. 19-21, 1996, **Putting Caribou Knowledge into Ecosystem Context**
8th: Whitehorse, Yukon Territory, April 20-24, 1998, **A Future for an Ancient Deer**

From April 23 to 27, 2001, more than 230 caribou experts migrated to the 9th North American Caribou Workshop, held at the tree-line in the Inuit town of Kuujjuaq, Nunavik, Québec. This community of about 1800 people near Ungava Bay was chosen over larger cities in southern Québec following a survey of potential workshop participants. Holding the conference in such a particularly appropriate location was made possible by the sustained efforts of the Organizing and Scientific Committees, by the help of the sponsors, and, above all, by the tremendous support of the people of Kuujjuaq. Keeping in mind the importance of caribou to the local people and the fact that development and other fast-growing human activities have today reached the North—for many southerners, the last frontier—the theme chosen for the 9th North American Caribou Workshop was also particularly appropriate: **Caribou and Man**.

Workshop participants were first welcomed in Montreal, where they attended a special viewing of the IMAX® film *Great North*, featuring caribou/reindeer and northern peoples and filmed in Québec, Labrador, and Sweden. The next day, they were flown by charter plane to Kuujjuaq to attend the workshop. The organizers performed many logistical miracles, and during the five days in Kuujjuaq, participants discussed current issues related to the caribou, shared the results of research efforts, and exchanged ideas on the latest information and technologies. Scientists felt very welcome in Kuujjuaq: when additional sleeping quarters were required for the event, people literally opened their homes to the visitors.

Hosted by the Hunting, Fishing and Trapping Coordinating Committee (HFTCC), this conference provided a unique opportunity to increase our understanding of the caribou and to encourage research and productive communication. Appropriately, translations were provided in English, French and Inuktittut in order to serve the diverse audience present at the workshop. Scientists and members of aboriginal communities shared their concerns and information about caribou biology and conservation. Each day began with a prayer by a local representative. Each session began with a presentation by an Inuit, Cree, Naskapi, or Innu elder; these elders hailed from throughout Northern Québec and Labrador, and their presentations described current and past experiences with caribou and wildlife. The organizers' main objective was to make the workshop informative and to encourage the exchange of information between all participants. Sharing common interests for the caribou's Eurasian relative, many reindeer experts, particularly from Russia, Norway, and Sweden, brought interesting discussions to the workshop.

The editors of this issue would like to thank the members of the Organizing Committee and the Scientific Committee, the members of the HFTCC, the workshop sponsors, and the people of Kuujjuaq for making the 9th North American Caribou Workshop a success, not only for its science and knowledge content but also for its cultural value. Special thanks must be extended to the 230 migrants (from all ecotypes) who travelled to Kuujjuaq from all over the world, proving that it is possible to organize a large conference in a small Arctic community. We would also like to thank the authors and reviewers for their efforts in producing these valuable proceedings, which provide a permanent record of the discussions that took place in Kuujjuaq and which will foster further exchange among scientists and caribou users alike.

Serge Couturier
Chairman, Scientific Committee and issue co-editor

Quentin van Ginhoven
Member of the Scientific Committee and issue co-editor

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- Daisy Watt, Kuujjuaq, Québec

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Session one

Caribou and Man, a Long-term Relationship

Inuit Elder's Story:

Johnny George Annanack, Kangiqsualujjuaq, Québec

Johnny George Annanack has lived his entire life in the heart of George River caribou country. Born in 1925 at Tasiujakuluk, a little north of the current community of Kangiqsualujjuaq, he remembers his family was always on the land hunting caribou in the Kangiqsualujjuaq area and into Labrador. Johnny has always been involved in his community and was a long-time culture teacher at the local Satuumavik school. A widower, he raised a large family with his wife of many years, Annie. Johnny is a respected elder and hunter who is well known for his knowledge of Inuit culture and traditions and is an important participant in the elder's conferences of the Avataq Cultural Institute.

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Rangifer and man: An ancient relationship

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Abstract: A long-term relationship between *Rangifer* and humans is documented in three case studies: the Canadian Barrenlands (8000 years ago to Historic period), Ice-Age France (11 000-19 000 years ago) and Mesolithic Russia (7000-10 000 years ago). Ancient human and herd migration occurred in all areas, based upon *Rangifer* remains and seasonal variations in tools along reconstructed migration routes, with few if any hunting camps outside the routes. An April peak of ancient human births is inferred from the historic record where we see births occurring nine months after peak nutritional states in herds and people. The origin of reindeer domestication and breeding in Eurasia is discussed.

Key words: Barrenlands, caribou, herd following, hunters, Magdalenian, Mesolithic, reindeer.

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Introduction

For most of the year, the Barrenlands are empty – devoid of movement from freeze up to breakup except for windblown snow. In spring, caribou come north from the forest to their calving ground. In late spring, the crash of ice pans and chimes of falling candle ice signal river breakup, followed by the calls of ducks, geese and other birds landing on their nesting grounds. In late summer, immense caribou herds of bulls, cows and calves return to the forest, forming a moving carpet, flowing over knolls, ravines and water. With them go wolves, scavengers, and the greatest predator of all – man. In autumn all disappear. The land returns to empty tundra save for some stragglers scurrying to avoid getting caught by the white death of winter.

For people that have lived on Earth, *Rangifer* was the most important game for more than a million years. It dominated numerically and geographically, and was used by people more intensively than any other animal. It was more important than North American or Ice-Age European wild cattle, bison, mammoth, mastodon or horse. It was more important than seals and whales in all the oceans; more important than red deer, black and white-tailed deer, moose and elk. It was more important than the great African herds of antelope, zebra and gazelle. It and its hunters occupied half the land north of the equator (Fig. 1). Its bond with man cannot be overemphasized when we consider the extensive circumpolar distribution of its tundra and woodland forms in the New and Old Worlds (Banfield, 1961; Spiess, 1979). Whether woodland or tundra, *Rangifer* could be hunted year-round by herd-followers. It yielded flesh like other animals, but both sexes provided better antler for tools, warmer fur for clothing and better sinew for sewing than other deer. Domestic reindeer also provided milk and transportation (Schefferus, 1674; Bogoras, 1904-9: 86, 90; Ingold, 1980: 107).

Ancient evidence

Earliest indications for caribou in North America include a 1.6 million year-old tooth from Fort Selkirk, Yukon, a 45 500 year-old cranial fragment from Sixtymile, Yukon, and a 40 600 year-old antler from the St. Antonin moraine near Rivière-du-Loup, Québec (C. R. Harington, pers. comm., 2001). Signs of the earliest interaction with man consist of a 11 300 year-old man-made antler punch from Hunker Creek near Dawson City, and a scatter of bone and

Fig. 1. World *Rangifer* hunters and herders (from Ingold, 1980: 286).

projectile points just below the plow zone at the Udora site in southern Ontario, estimated to date 10 000-10 550 years ago (Storck & Spiess, 1994). The earliest documented caribou hunt is at the stratified Migod site water crossing on the Dubawnt River in the Beverly range of the Barrenlands, dating 8000 years (Gordon, 1976). Here and at several locations on the Thelon River, two meter deep cultural levels have abundant bone and stone tools. The stratified nature of these sites confirms hunters and herd used the same water-crossings year after year. Subherds were hunted at smaller crossings up and down the range.

In the Bathurst range to the west, late prehistoric Copper Inuit even built domed huts from bull antler for drying meat in the ever-present wind (Gordon, 1986a,b,c; 1988). At Nadlok Island or *Crossing-place-of-deer*, about 3500 antlers were used to roof each of four huts (Fig. 2 & Gordon, 1995).

Old World reindeer are probably more recent than caribou (C. R. Harington, pers. comm., 2001), but hunted much earlier by Neanderthal almost one-half million years ago in Süssenborn, Germany (Banfield, 1961). Hunting continued through the Middle and Upper Palaeolithic, with intense dependence in the Magdalenian (Gordon, 1988b). It is uncertain when domestication of reindeer began. According to the *diffusion theory* reindeer domestication began east of the Urals and spread to other groups (Sirelius, 1916; Laufer 1917 (1974); Hatt, 1918; Aronsson, 1991) after wild herds spread from Siberia to Scandinavia. It proceeded gradually as hunters bonded with herds, taming small groups as lure animals and for riding and transport. The latter practices are still followed by forest and tundra Evenks, with heavy taiga reindeer breeding in the 18th century. To the west, Siberians used reindeer traction for sleds year-round, with 2-3 animals in winter and up to 5 in summer.

The evolution theory on the other hand argues for independent domestication in different areas (Wiklund, 1919; Mulk, 1994; Storli, 1994; 1996) based on the fact that reindeer are easily tamed, as

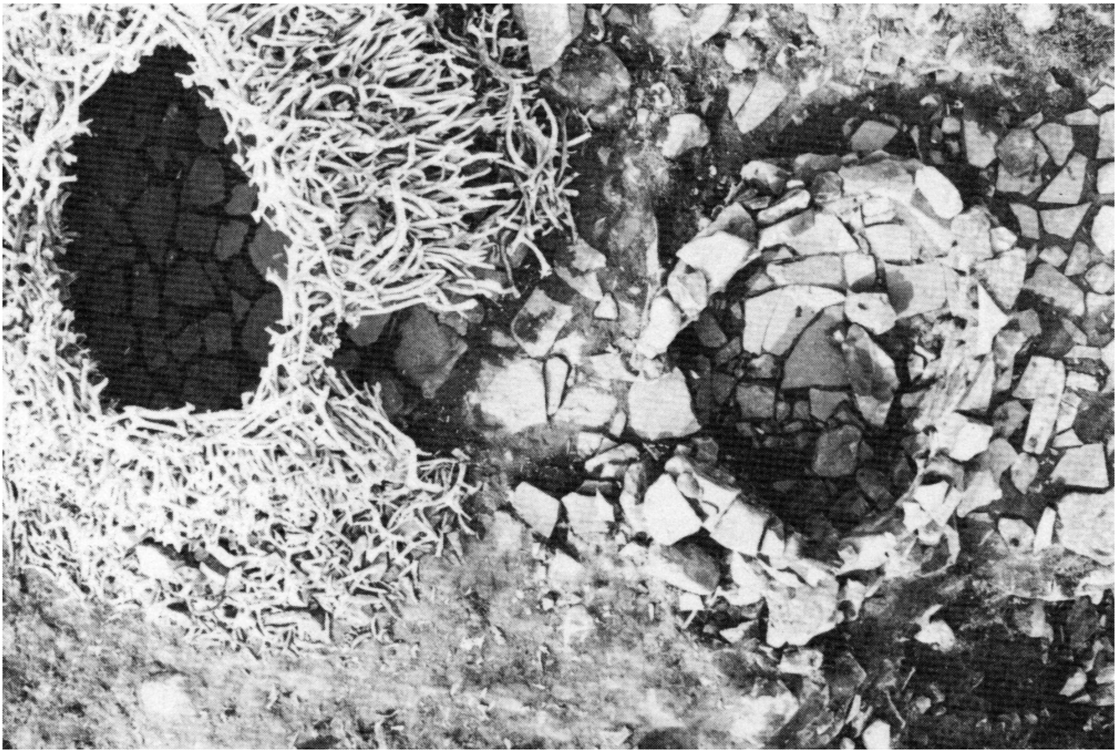


Fig. 2. Aerial view of the antler hut and semi-subterranean stone winter house at Nadlok water-crossing, Burnside River, N.W.T. A paved porch connects their opposing doors.

quickly experienced by different human groups. Domestication was probably separate from taming, but herd following led to herd control, with ready access to meat and milk a guarantee against starvation. Later hunters all but disappeared throughout Eurasia, while Nentsi, Koryaks, Chukchi and other herders survived (Baskin, 1999). Iron and Bronze Age petroglyphs and pictographs show the transition to domestication. North Eurasians domesticated the reindeer for transport, meat, milk, hides and medicine.

The Sayans of Buratia, Irkutsk, Tuva Republic and the Mongolian Aimag have likely been herders for several millenia, and may represent the origin of domestication (diffusion theory), moving their herds between taiga and tundra. Nonetheless, they were mainly nomadic hunter-gatherers rather than pastoralists. As their region is less than 800 kilometers in a herd range exceeding several thousand kilometers, they may have traded and inter-married, their languages and ancestry closely related to old Tuva. Now, all have experienced a 10-year exponential decline in herding (Plumley, 2000).

The *Rangifer*-human bond

Throughout the world, from Siberia (Popov, 1948) to arctic Québec (Fig. 3), *Rangifer*'s herding instinct and curiosity made easy harvesting. *Rangifer* could be driven into V-shaped drivelanes ending in a corral, net, snares, hidden hunters, lake or stonewall. In Greenland, terrain features, waving Inuit, rock piles and kayaks were heavily used (Grønnow *et al.*, 1983). In the Old World, corrals were semi-circular, as seen in a 6000 year-old engraving in North-Norway (Helskog, 1977). A typical model consists of cairns, snowblocks, brush and pole fences or pickets on one side of a V-shaped channel, the other side perhaps natural barriers like lakes, rivers or cliffs (Gordon, 1990: 297). Curious manlike shapes also lured *Rangifer*. Rather than repelling herds, stone cairns and inukshuit (stone men) attracted them, just like certain sounds. In 1973, I saw many flakes from quartzite hammer stones inside the walls of pockmarked sandstone hunting blinds between the Back and Thelon Rivers of the Barrenlands. When I made my own flakes by striking a hammer stone against the wall, I found its ringing sound attracted caribou up to a kilometer away (Gordon, 1974).

Modern seasonal movements vary due to overhunting, ground ice, forest fires and human settlement, but calving ground locations, like water-crossing sites, have also remained stable for centuries,

Fig. 3. Caribou drive in northern Québec. Drawn by Nua Kilupaq. Reproduced by permission of Saladin d'Anglure, Université Laval.

based on aerial survey and archaeological sites ending at the calving grounds (Gordon, 1975, 1990, 1996). Furthermore, calving ground sites contain tools from all Barrenland cultural periods, proving long-term association of people and herds. Herd following has been rejected by some historians focusing their research on rare fur trade accounts of random winter sub herd movement near forts. It is even rejected by some Dene villagers who avoid ancient crossings because they demand boats, long walks and waits. Instead, they fly to open areas near the tree line and rely on distant shooting of individuals. Nonetheless, hunters for many generations shared meat at water-crossing camps surrounded by smaller camps. One year while excavating 7 levels of the 6500 year-old KjNb-7 site, we watched the approach of a small Beverly sub herd crossing the Thelon River in the Game Sanctuary - a direct confirmation of herds returning to major crossings (Gordon, 1975 & Fig. 4). In other years, we witnessed animals from horizon to horizon funnel hourglasslike towards the crossings and swell again on the shore opposite.

Fig. 4. KjNb-7 excavation crew watching the approach of a Beverly caribou subherd (in center of picture) in the Thelon Game Sanctuary, N.W.T. in 1976.

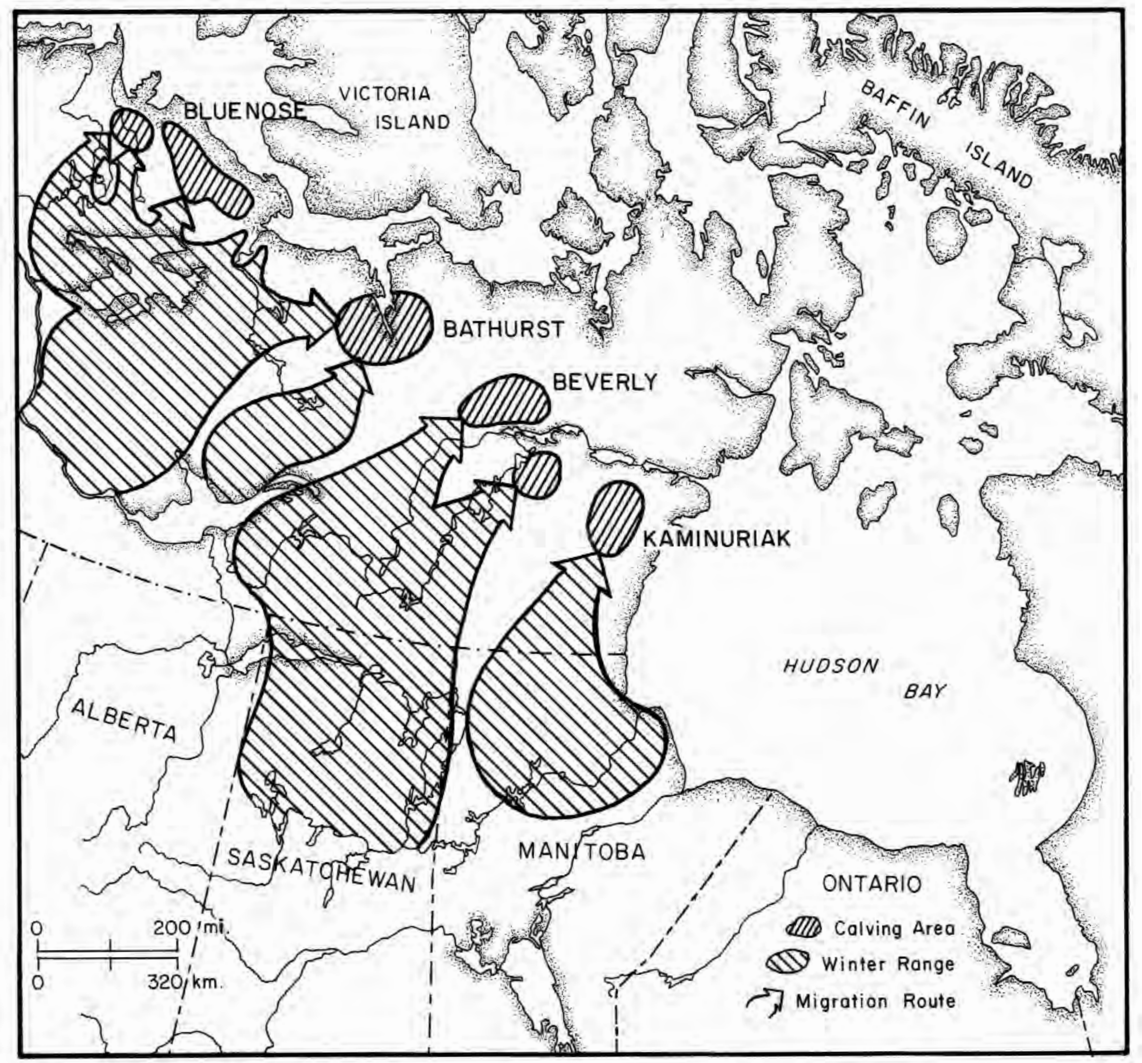


Fig. 5. Barrenland caribou ranges which overlapped Dene hunting ranges.

The tremendous influence migratory game has on hunters is apparent in Dene caribou hunters. Ethnologist J.G.E. Smith (1978) noted alignment of a Dene hunting band with each of the Bluenose, Bathurst, Beverly and Kaminuriak herds. Herd alignment and subsequent partial isolation has resulted in each hunting band having a different name and dialect of the main language. Migration routes and calving grounds are far apart, so contact between hunting bands and herds in adjacent ranges was limited, as shown by arrows in Fig. 5 (Gordon, 1975). Simultaneously, the Canadian Wildlife Service observed 94% discreteness in each herd by ear-tags (Parker, 1972). Combining Smith's and the wildlife studies with observations of differences in 3500-1500 year-old Pre-Dorset artifacts in all ranges, I proposed a discrete band-discrete herd association in the Barrenlands for the last 8000 years (Gordon, 1975). Wherever a herd crosses a river or lake in its annual migration, sites are dense with artifacts, bone and antler. This shows man as herd follower.

Rangifer *and man in the Canadian barrenlands*

A well-documented example of the man-*Rangifer* bond is in the Beverly caribou range, bordered on the south by the Churchill River of northern Saskatchewan, and west, north and east by Great Slave and Artillery Lakes and the Back and Dubawnt Rivers (Fig. 5). The forest where animals winter is south of the tree line in mainly Manitoba and Saskatchewan, spring migration to the calving ground are the two upward arrows, and autumn migration south approximately the same in reverse. Each spring, the Beverly herd leaves its forest and moves north to

Fig. 6. Small Inuit caribou drive in northern Québec. Reproduced by permission of Saladin d'Anglure, Université Laval, 2001.

calve. In early May, cow sub herds lead the herd northeast onto the tundra where they calve 400 kilometers north in high, dry and windy areas relatively free from man, wolf and insects. Bulls stop short of the calving ground but join southerly moving cows and calves in late summer to form the largest herd of the year. Sometimes, this giant herd splits temporarily into sub herds as it crosses rivers. In autumn, it moves south as one vast herd popular in film and story. At tree line, it divides and enters the forest, reappearing briefly to rut before returning. Habitual return to a calving ground may relate to a learned homing capacity and an evolutionary imprinting, which funnels herds past topographic features.

Directly associated with herd splitting are major and minor water crossing sites. These are few and tiny near the calving ground, as seen in Inuit hunters in another range (Fig. 6), concentrated at mid-migration like the Thelon sites, dense but small at tree line, and few, scattered and tiny in the forest. An example of *Rangifer*'s vulnerable position when it migrated across rivers and lakes to the southern forest comes from Rennie Lake, N.W.T. (Fig. 7). Advantageous positions for hunting are between north collecting and south dispersion spits. Swarming on the north spit of the Rennie Island crossing forced the herd to cross en masse, permitting heavy harvesting by hunters at 7 locations on land, and several in the water. As lances easily penetrate the kidneys or spinal cord with a single thrust delivered from a canoe or kayak, hunters quickly mortally wounded many animals, allowing them to float away for retrieval by women and children. For land hunting, a 7th harvest on the south dispersal spit of the crossing was minimal because most animals had run the gauntlet or been killed.

Stratified artifacts were used to identify and date the numerous surface tools. This allowed seasonal, temporal and locational comparison of 10 000 tools from 1000 sites within the Beverly range (Gordon, 1996; 1999). These can be used to study seasonally different activities.

Variation in tree line with climate had little effect on migration and calving ground location. But it had a profound effect on seasonal cultural expression due to available wood for tent poles, fires and tools. Comparing artifacts of each culture in relation to tree line, points, knives, chithos or hide softeners, cores, flakes, hammer stones, whetstones and push-planes are smaller in the forest. I suggest hunters were extending their useful life by resharpening, rather than using poor quality deeply snow-covered forest stone. Tools also changed seasonally. Tundra scrapers have convex bits and tapered handles while forest scrapers have serrated bits and rectangular handles for better cold-weather gripping and frozen hide scraping. Forest knives are also serrated for cutting frozen meat.

Rangifer *and people in ice-age France and Mesolithic Russia*

Throughout the Upper Paleolithic, reindeer was extensively hunted, dramatically so in the Magdalenian, where several dozen sites with extensive reindeer bone and teeth are depicted in southwest France (Fig. 8). This is the period when cave art reached its zenith 19 000-11 000 years ago, and when most game was reindeer.

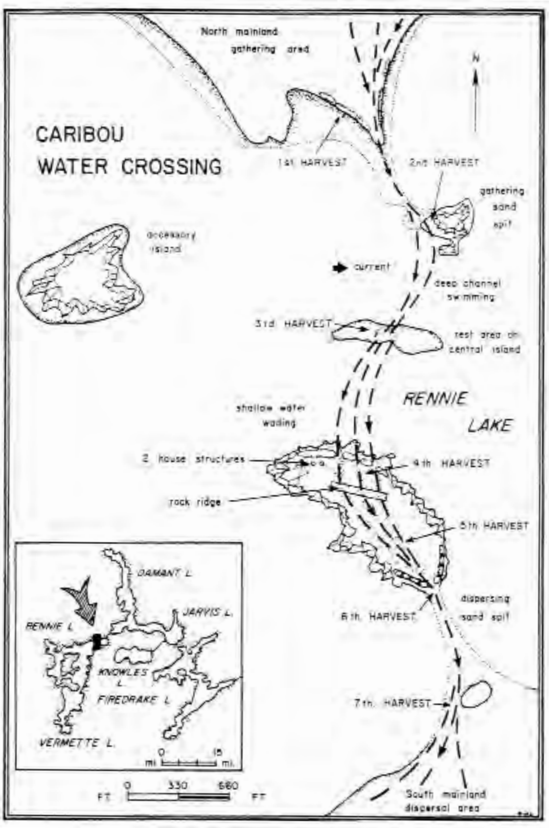


Fig. 7. Seven harvesting areas in the Rennie Lake caribou water-crossing, N.W.T. (from Gordon, 1977).

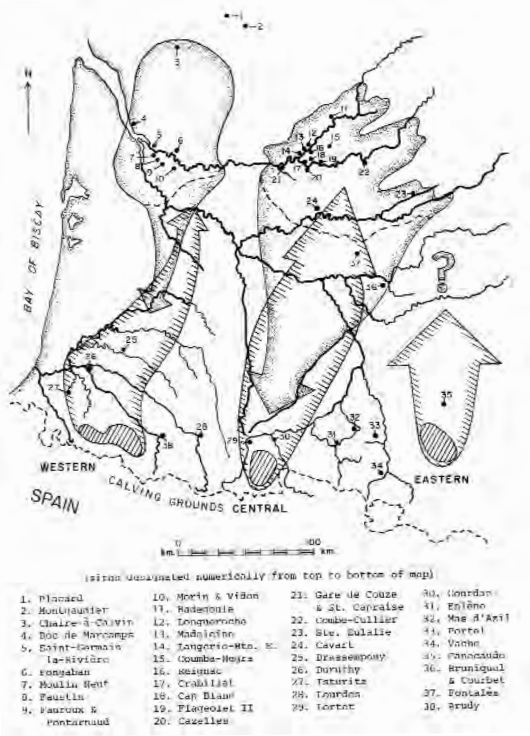


Fig. 8. Magdalenian reindeer hunting sites in three ranges in southwest France (from Gordon, 1986d; 1988b; 1988). Note: Positions of the Western, Central and Eastern Reindeer Ranges of Southwest France. Winter ranges are in Charente, Gironde and Dordogne, while summer calving grounds are in the Pyrenees 200 km south.

Reindeer are long since extinct here and we have no documented herd following, so my conclusions rest heavily on a technique taken from wildlife research, that of tooth sectioning (Miller, 1974; Gordon, 1982a,b). All mammals produce growth rings on their tooth roots visible using microscopic thin sections. Like tree-rings, they can be counted to determine age, but we perfected this technique to find season-of-death, and sometimes month-of-death by comparing outer and inner ring thickness (Fig. 9). A thin opaque ring forms in winter; a thick translucent ring in summer. To evaluate past herd following, I studied hundreds of reindeer teeth from dozens of sites. These allowed a reconstruction of a seasonal progression of kills across the land, showing 8 reindeer ranges, three of which are in southwest France (Gordon, 1989).

The biggest and densest site cluster includes Dordogne with its famous painted cave of Lascaux. More than 95% of the bone in Lascaux and neighbouring sites are reindeer, yet the wall paintings are other animals not living there. Tooth sections indicate the area was occupied in winter. Why did hunters depending on reindeer paint other animals in the long winter nights? Perhaps because they and their herd migrated several hundred kilometers south to the area where these other animals were hunted. Herd-followers were either appeasing the spirits of the other animals they hunted the previous summer or summoning the spirits of next summer's hunt. Nonetheless, they depicted these other animals realistically, as observant hunters do. They did not bother to paint common reindeer, the staple diet. After all, you seldom place a picture of a loaf of bread, a bowl of rice or a potato, all staples, on your wall. Most importantly, these paintings portray the spiritual side of the human-animal bond.

My third example of the human-animal bond is northern Eurasia, where hunters and herds spread from Scandinavia to Bering Strait (Flerov, 1952). At its center are historic Nganasan tribes of the Taimyr Peninsula of central Siberia near the Arctic Ocean (Fig. 1, centre right). As a preliminary test for herd following, I compared Sdobnikov's (1958) diagram of 300 year-old herd sightings with Dolgikh's (1962)

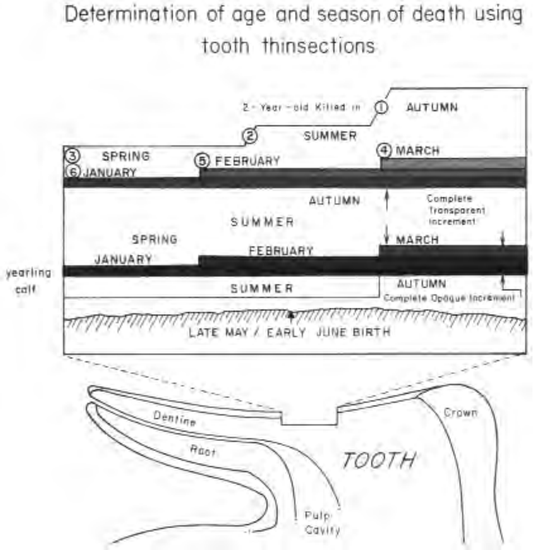


Fig. 9. Determining the season of *Rangifer* death using tooth thin sections (from Gordon, 1984; 1992).

and Popov's (1948) recent Nganasan band distributions. Their overlapping distributions indicate past herd following, with band and herd division like those of the Barrenlands.

With the ancestors of contemporary Chukchi and Sami and prehistoric Altai Mountain people of northern Eurasia, herd following is taken to a new level, that of actually controlling herds. Anthropological studies suggest domestication began in the south Altai *ca.* 5000 years ago (see pp. 16-17). Other studies trace its origin to 3000 year-old wild reindeer hunting, when hunters tethered tame deer to attract wild herds. Later, tame animals were used to pull sleds, and in some cultures, saddled and ridden. Eventually, people kept herds as a dependable source of food, hides and transport.

The Sami nomadism has underwent different phases over many centuries (Storli, 1994; 1996) and Hedman (2003) concludes that the reindeer herding and husbandry probably developed from the last part of the Iron Age. The development towards nomadic herds occurred in the 16th and 17th century (Mulk, 1994) when wild reindeer no longer were a threat and hunting had diminished and according to lists of taxation bigger nomadic herds (animals >100) were a reality from the mid-18th century (Arell, 1977). Reindeer herding was introduced to North America when Chukchi and Sami herders and Chukotkan reindeer were brought to Alaska in the late 19th century.

Turning west to the European side of the Urals to the Komi Republic and adjacent tundra of far northeast Europe, I reconstructed 7000-10 000 year-old reindeer migrations using Mesolithic site distribution and historically-documented herds migrating between tundra calving grounds and winter forest, while some hunters remained south of tree line (Gordon, 2003; 2004). Site locations and artifact trait clusters show ancient hunters followed the migrations of a Western and Eastern herd from the forest headwaters of the Pechora River to their coastal calving grounds (Fig. 10). These long migrations resemble those in the Barrenlands, Prairies and Ice-Age France. Again, tools differ seasonally in the 56 sites in both ranges.

Traits common to all herd-followers: Cultural Control

I have discussed advantages of herd following – year-round hunting over extended range with fresh food on the hoof, more natural resources and trade goods, and brief alliances with other hunters in winter for feasts and intermarriage. People were so dependent upon *Rangifer* that much of their behavior and cultural expression hinged on its movements. But there were limitations relating to constant migration needed to follow herds. The sick and aged were abandoned. Material goods like tools and tents had to be portable. Language divided into dialects.

Control is the catchword describing the relationship between animals and most people, but when we enter the world of the hunter dependent on animals, man's control was limited. Control was sometimes as simple as stone lines on the ground surface directing animals to hunting blinds. But control was also spiritual.

Spirituality

Spiritual influence of *Rangifer* on people appears in taboos, legends and art, including the aforementioned wall paintings. Early French specialists of Paleolithic cave art believed if the spirit or totem agreed, it was just a matter of the hunter finding the animal represented in the art (Breuil, 1952). The Dene did not offend spirits by mixing flesh of the land, air or water. Many origin beliefs surround *Rangifer* hunters.

An Inuit legend mentions once there were no caribou, but a man wanting them cut a great hole deep in the earth, and through it came many animals until the ground was almost covered. When the man thought there were enough, he closed the hole (Rasmussen, 1930).

A Caribou-Eater Dene legend mentions caribou arose from the Milky Way, descending in late summer, before spending the winter with the Dene in

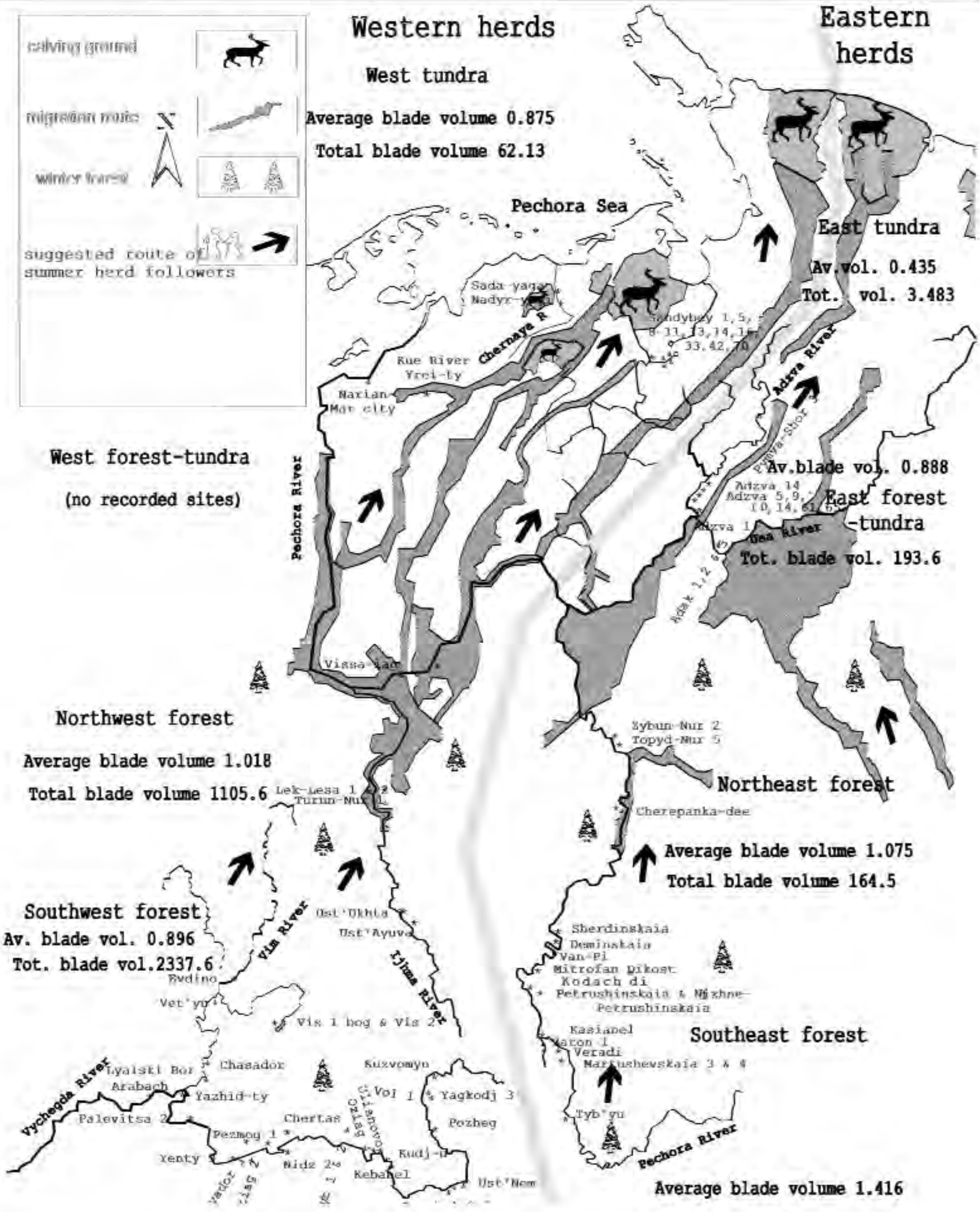


Fig. 10. Mesolithic Eastern and Western reindeer and hunter ranges in far northeast European Russia.

the forest. Another legend attributes the origin of caribou to the *Aurora Borealis*. In a Siberian Ugrian version of heavenly reindeer, Ostiak hunters followed them north as symbolized in the Big Dipper, which stole the sun. When mythical hunters, symbolized as the Bear, kill the reindeer, new days begin (Hámori, n.d.).

An Innu legend of Labrador mentions *Why the Fart Man, Matshishkapeu, is more Powerful than the Caribou Master*, told by Greg Penashue, Sheshatshiu, 1987: "Long ago, the Master of the Caribou was stingy and would not give them to the Innu, who began to starve. Using the shaman tent, the Innu asked *Matshishkapeu* to assist them. He went to Caribou Master and asked him to release the herd, but Caribou Master refused. *Matshishkapeu* then told him that if he did not relent, he would be punished. He refused, so *Matshiskapeu* made him constipated; so much so he was in danger of dying. He couldn't fart or shit. Finally, he acceded to the Fart Man's request to provide caribou to the Innu, and as a result, was

Fig. 11. Dene mothers and babies in summer, judging by their clothing. Courtesy of Father P. Duchaussois, Oblate Archives Photograph 44, Yellowknife. (Photo undated but *ca.* early 1920s)

cured. This explains why Fart Man is the most powerful Innu spirit, even more so than Caribou Master."

A Naskapi legend of Labrador also concerns Caribou Master: Between Ungava and Hudson Bay is a place where no Indians go because there are pure white mountains of neither snow, ice, nor rock, but of caribou hair in the shape of a house. Many thousands of caribou live in a valley under the control of a white man dressed in black, sometimes with a beard. He is Caribou Master and will not permit anyone to come within 150 miles, the punishment being death. The few Indians who did and lived say caribou enter and leave each year, passing between two high mountains 15 miles apart. Here, hair on the ground is a yard deep, with migration paths through a layer of waist-deep cast antler (Speck, 1935: 84).

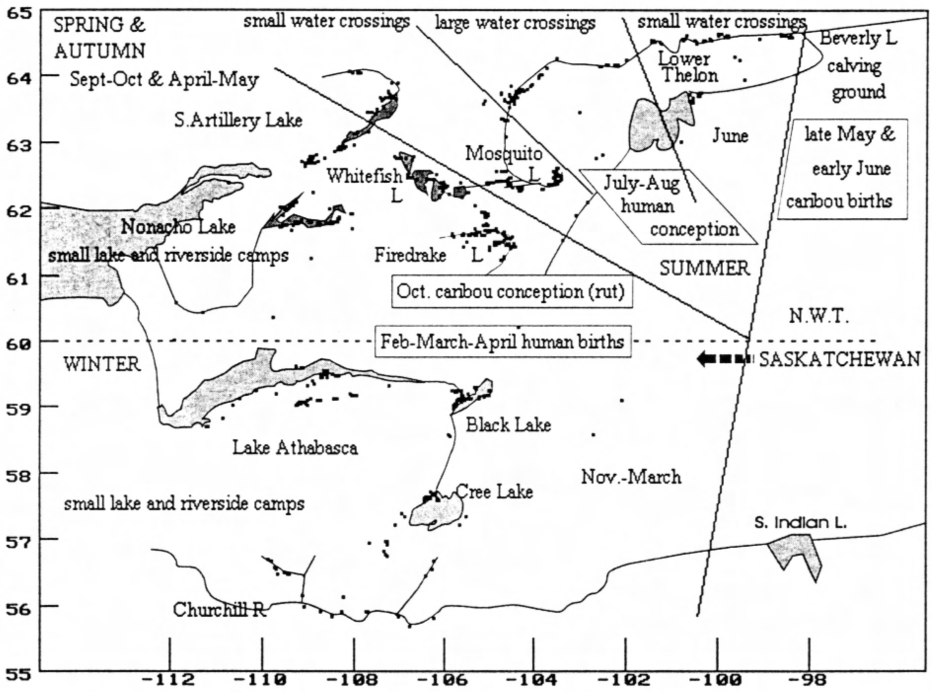
In Eurasia, Plumley (2000) suggests the earliest petroglyphs showing a transition from hunted to domesticated *Rangifer* depict an animal imbued with a northern spirit that can reach the high gods, the "upper worlds" of the shaman.

From the Baltic to Bering Strait, *Rangifer* had an indirect role in spirituality by eating the fly agaric mushroom, *Amanita muscaria*, which has the hallucinogen muscimole, plus other toxins. Ostiak, Yukagir, Kamchadal and Inuit shamans and Koryak and Chukchi men drank its urine and milk and ate its meat, inducing a trance with the spirits (Bogoras, 1904-09: 205-207). Toxins are normally more potent in the urine, but are filtered by the reindeer kidneys. On the Chukchi's Pegtymel River in northeast Siberia, human-mushroom spirits are depicted in small petroglyphs dated to the Bronze Age by Dikov (1979: 159).

Leaving the spirit world depicting the human-herd bond, we must not forget that people must obey and adapt to natural laws, just like animals. The most important law of survival is that based on food supply. Hunters must adapt to the migration cycle of the caribou. In so doing, it determines the human life cycle, birth, maturation, conception of new life, and death.

Human seasonal nutrition and birth spacing

Rangifer regulates human conception through its seasonal availability and seasonal fat content. A women



Distribution of Beverly sites by month and season.

Fig. 12. One thousand and two Beverly caribou hunting camps (dots) by month and season (from Gordon, 1996, figs. 11.5 and pp. 15-16).

with 12% body fat can conceive, but cannot carry a child; 18% is satisfactory (Frisch, 1988; Rosetta, 1992). Different seasonal nutrition is most apparent in northern hunting cultures, where other food is absent. A high birth peak from January to March among Greenland Inuit is attributed to high nutrition nine months earlier (Cook, 1894a,b; 1897). Sexual intercourse was year-round in Copper Inuit, yet winter births dominate (Jenness, 1922). Heavy spring birthrate occurred in 3700 Labrador Inuit in 1778-1940. Turn-of-century Polar Inuit women did not menstruate over winter (Cook, *op. cit.*), while 1950-60s breast-feeding Inuit women had very few periods.

For people with sharp seasonal food shortage, like inland *Rangifer* hunters, birthing is a late winter-early spring event (Fig. 11). This is in accord with hundreds of 19th and early 20th century Caribou-Eater Dene birth dates showing 4 of 5 babies born from February to April with an April peak (Gordon, 1996). This translates to a very steep conception peak in July/August on the tundra, when *Rangifer* fat was plentiful in both bulls and cows, which were killed by the hundreds. The Dene cycle of July/August conception meshes with the *Rangifer* yearly cycle, just as it undoubtedly did for all hunters and herd followers. The timing of births relates more to female nutrition than frequency of intercourse or hours of sunlight.

In June, Dene families followed the migration route northeast past Nonacho, Whitefish, Firedrake and Mosquito Lakes (Fig. 12). Some descended the Dubawnt and Thelon Rivers to the calving ground but most remained at the big water crossings in the Thelon Game Sanctuary to harvest caribou from the immense summer herds. Here, women conceived while processing fat and meat.

Warm summers lessened human energy requirements. New skin clothing and shelter were not so necessary at the time when skins were in poor shape and mothers were preoccupied with drying meat. High nutrition came when mothers were breast-feeding.

November rut was a nutritional drain on caribou. Back fat decreased and the meat of bulls was tainted. The fat of cows and calves sustained people. Over winter, available animal fat and subsequent nutrition decreased. In the Beverly range, women gave birth in small camps around Athabasca, Black and Cree Lakes in late winter and early spring, when nutrition was lowest. But there were advantages to spring births. Children had a summer to grow and strengthen for the following winter, just like caribou calves.

Malnutrition resulted in later puberty, earlier menopause and fewer children. Dene women lactated for 3 to 4 years, rarely having more than five children in 20 reproductive years.

Conclusions

The human-*Rangifer* bond is evident in the Canadian Barrenlands, Siberia, northern Europe and Ice-Age France. It was long term, balanced and successful. For 98% of our existence as anatomically modern man, we adjusted to movement of *Rangifer* and honoured its spirit. Our reproductive cycle was bound to it. Contact was governed by range, and resulted in distinct language, tools, trade goods and art.

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The Norwegian system for wild reindeer management – major development since the 19th century

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Abstract: In the 19th century the hunting of wild reindeer was relatively unrestricted in Norway. This, combined with a more efficient hunting, caused a severe reduction in the number of wild reindeer at the turn of the century. The national authorities responded by stricter hunting control, and in 1930 hunting quotas related to the size of the wild reindeer areas were introduced. The Ministry of Agriculture decided the number of licences, and the number of wild reindeer increased. During the 1950s a major controversy between the Ministry and local people arose in the Snøhetta area. People there increased their power over the wild reindeer management by organising a "Wild Reindeer Board" (WRB). This inspired people in other districts to organise similar boards. These WRBs had no formal power according to the law, but became important managers of the herds. An official organisation for each wild reindeer area, the Wild Reindeer Committee (WRC), was introduced in 1988. Since the WRCs are official institutions, legal power is decentralised to them.

Key words: co-management, common pool resources, *Rangifer tarandus*, Rondane, Snøhetta.

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The Norwegian wild reindeer areas

At the middle of the 1990s Norway had 26 wild reindeer areas (Fig. 1). Potentially the wild reindeer may use larger areas but human impacts have fragmented and reduced the size of the mountain areas suitable for wild reindeer. In northern Norway the wild reindeer was extinct in the 19th century. The management goal for the number of wild reindeer in each area varies substantially today. In small wild reindeer areas the goal is 40-150 individuals, whereas the goal for the largest area, Hardangervidda, is 10 000 individuals. The annual number of wild reindeer legally killed by hunting in Norway since 1889 is illustrated in Fig. 2. Generally, the hunting increased substantially in the 1950s, reflecting better management and an increased number of wild reindeer. In this article the general development of the wild reindeer management in Norway is supplemented by describing the development in the Rondane and Snøhetta wild reindeer areas.

Historical development of wild reindeer management in Norway

According to Middle Age laws of Frostating court and King Magnus Lagabøter's code of laws there were rules concerning the mutual organising of pitfalls in order to avoid trappers from disturbing one another (Reimers, 1989). An organised management of the wild reindeer herds does not seem to have existed. From the 18th century, official policy in Norway was to kill as many large predators as possible in order to maximise the conditions for domesticated animals and "useful" wildlife. The rapidly decreasing populations of carnivores created favourable conditions for wild reindeer but better guns, an increased human population and an infrastructure opening the mountain areas caused overexploitation of the wild herds.

As a countermeasure, the Norwegian State introduced from the second half of the 19th century new acts and regulations of hunting. The acts would reg-

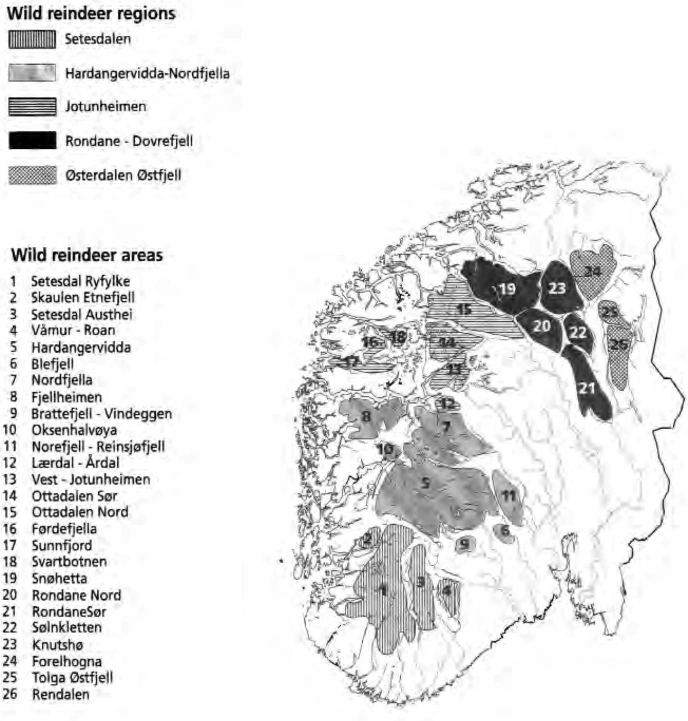

Fig. 1. Wild reindeer regions and wild reindeer areas in southern Norway in the mid 1990s (Jordhøy *et al.*, 1996).

ulate the time for hunting, abandoned killing calves, restricted type of rifles permitted, etc. In 1902 - 1906 all wild reindeer hunting in Norway was prohibited. These efforts had some effects but did not lead up to a stable wild reindeer population, one reason being that every Norwegian citizen was allowed to hunt in the large nationally owned mountain areas of southern Norway. The Mountain Act from 1920 limited the number of hunters; in distinct commons hunters from the nearby communities had priority but there was no limitation upon the *number* of reindeer to be hunted. In addition, the division of a large area into many small commons produced a co-ordination problem.

In 1930, the authorities introduced quotas and only a specified number of wild reindeer related to the size of the mountain area were allowed hunted. Even the owners of the mountain areas had to apply for license to hunt. Thereafter the number of wild reindeer gradually increased. Paradoxically, the Ministry of Agriculture (MA) did not know the number of wild reindeer in each mountain area; instead they used the size of the areas as an indication of the number of reindeer.

The Hunting Act of 1951 defined a national hierarchy consisting of wild life managers in the local authority districts and at the national level. Contrary to the management of other big game species, the local authority districts did not get any formal power for deciding the quotas of wild reindeer. The management of the wild reindeer became an issue for the land owners and the MA. A strong national administration in co-ordinating the management was needed, because the herds often crossed the borders of local districts and counties (Christensen, 1967). But as time passed, local influence upon the quotas was demanded. This development is illustrated by the conflicts in the Snøhetta area in the 1950s and early 1960s. According to the owners of the ground the MA did not allow for high enough quotas. Locals based their assessments upon some censuses but mostly upon observations of what they judged as many wild reindeer and over-used pastures. They also thought the size of the wild reindeer decreased and that the wild reindeer fed on plants not ordinarily eaten. The Ministry argued that the herd was not too large, and that the quota was the correct one (Heitkøtter, 1981; Hansen, 1987; Jordhøy, 2001). This was a classical controversy between local people and national authorities.

As a response, in 1961 the land owners in the Snøhetta area organised the first local Wild Reindeer Board (WRB) increasing their power and influence relative to the MA, and the quotas increased considerably. After some years, a better balance between herd size and its resources was achieved. The WRB in Snøhetta inspired people in other wild reindeer areas, and similar boards emerged during the 1960s, although the new organisation had no formal power according to the Hunting Act.

The achievements of the WRB have been closely investigated in the Rondane area (Bråtå, 2001). In 1967, the largest owners of land there, the Mountain Boards (MB), agreed to found a *formal* WRB for improving the management of the wild reindeer. The MBs were the most important local actors and had co-operated about management since the early 1950s. In 1956 the MBs in Rondane initiated the first national park in Norway and continued as important actors until it was established in 1962. An

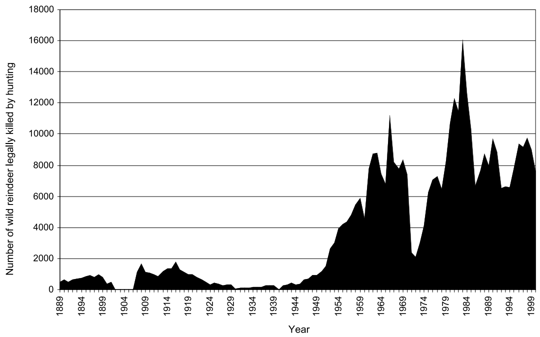

Fig. 2. The number of wild reindeer legally killed by hunting in Norway 1889-2000 (Source: Statistics Norway).

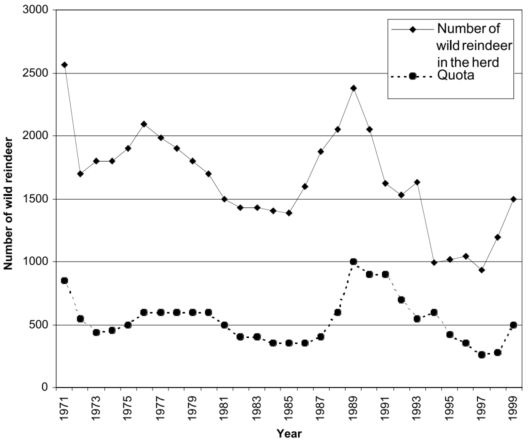

Fig. 3. The number of wild reindeer and the quota in the northern part of the Rondane region 1971-1999.

important reason for their initiative was to protect the important wild reindeer areas and migration routes against increased human exploitation.

An important theme for the MBs in Rondane in the second half of the 1950s was, by the means of censuses, to obtain processed knowledge (Friedmann, 1973, 1987; Polanyi, 1976, 1978; Rolf, 1989; Flyvbjerg, 1992) about the number of wild reindeer. The count was not initiated by the Ministry who decided the quotas but by local people deeply concerned with what seemed to be too high quotas. The first census was carried out in 1960. Subsequent counts were carried out in 1962, 1964, 1967 and thereafter annually. Through the organising of a formal WRB in Rondane in 1967, a systematic effort began in order to obtain an overview of the quotas and number of wild reindeer killed by hunting in the area. Such detailed processed knowledge existed in the Ministry but was only published later in a summarised version by the Statistics of Norway. However the WRB needed the knowledge earlier and more detailed for keeping control with each owner's hunting in the Rondane area. To better control the management private landowners in 1970 were invited to join the WRB, and they became active members. This expansion increased the need for precise information at the right time of the year.

The WRB in Rondane managed to extend the quotas in 1968, and have generally achieved the quotas they applied for to the national authorities. In 1970 the first WRB was divided into three WRBs. Fig. 3 shows that the quotas in the northern part of the Rondane area are closely related to the number of wild reindeer in the censuses. The number of animals in the herd was adapted to the local goals. During the 1970s the WRB in Rondane, and probably several other WRBs, became the real managers of the wild reindeer in many areas. Still, the WRBs had no formal power according to the Hunting Act. From the 1970s, the national authorities and the Rondane North WRB developed a good relationship. The relationship to the Directorate for Wildlife Management, established in 1965, was an example of co-management to the best of the common pool resource.

Despite good co-operation, in some wild reindeer areas it became a problem for the national authorities during the 1970s that no official wild reindeer institutions adapted to the size of each area existed. The new Wild Reindeer Committees (WRC) proposed at the first half of the 1980s, were supposed to be the missing link in the national hierarchy of wildlife institutions, and would consist of officially elected representatives from each local authority district in a wild reindeer area. Several members of the existing Rondane North WRB opposed this proposal.

Notwithstanding the criticism, official WRCs for each wild reindeer area were introduced in 1988. The existing WRBs were supposed to continue as clearly defined organisations for the owners of the land and to have the daily responsibility for the management of the wild reindeer areas, whereas the new committees were supposed to be supervisors. As the WRCs were formally defined in the Wildlife Act and linked to the hierarchy of administrative organisations, power was decentralised to them from the Directorate for Nature Management. The WRCs were supposed to decide upon e.g. the quota for each wild reindeer area. Local officials were given formal power and as part of the official power hierarchy the WRCs had an official responsibility for the state of the resource system, one of their duties was to make assessments of proposed human impact in the wild reindeer areas.

A presupposition for official and decentralised decisions, for example quotas, was the existence of management plans for each wild reindeer area and processed knowledge was a necessity for such plans. The landowners in a WRB, were obliged to elaborate a plan which the WRC was supposed to approve or reject. At the beginning of the 1990s the Directorate for Nature Management thought that the basic biological questions of wild reindeer were solved; research funding was directed to other topics and annual counts in each herd were not considered necessary. Instead a coordinated program for scientific monitoring of herds was introduced. Based upon e.g. the management plans for the wild reindeer areas, the grants for management were supposed to be directed to wild reindeer areas with specific problems (Jaren, 1991).

Explaining the described development

The wild reindeer, an open resource

In order to control the overexploitation before and after 1900, the wild reindeer became a theme for what Max Weber (1995) called an official jurisdictional area, and gradually the theme for a bureaucracy. The efforts to control the hunting of wild reindeer can be understood as part of a broader process of rationalisation increasing the control of nature and society. The Mountain Act of 1920 is a part of this process because a modernised Norway needed defined property rules.

The power of the national institutions applied in the years preceding 1930 did not create sustainable use of the wild reindeer. One important reason was the absence of limitations upon the number of wild reindeer to be hunted. In fact, the wild reindeer was an open resource. That, and its migratory behaviour, disposed for the "tragedy of the commons". It was rational for the hunters to shoot as many wild reindeer as possible when they had the opportunity (Olson 1965; Hardin 1968, 1998; Berkes, 1998). Aggregation in flocks may also give an impression of many wild reindeer, independent of the total population. These aspects, which the reindeer share with other migratory species, make it difficult to manage the wild reindeer (Buck, 1989; Gibbs & Bromley, 1989; Feeny *et al.*, 1990; Berkes, 1998).

National institution fix the quotas

When the MA in 1930 introduced quotas as a mean to reduce overexploitation, a nationally situated institution was assigned all power in the wild reindeer management. Some authors appraise nationally centralised power as the only possible way to manage common pool resources (Ophuls, 1973). Others appraise it as being one of several solutions, including privatisation and managed commons (Berkes & Taghi Farvar, 1989; Ostrom, 1990). When quotas are based upon the size of a wild reindeer area, the quotas relied upon quantitative and objective knowledge ideal for a bureaucratic organisation (Weber, 1995). The introduction of quotas prevented overharvest but a weak point was that the number of wild reindeer in the mountain areas was unknown.

The Hunting Act in 1951 implied that the wild reindeer became managed within a clearly shaped hierarchy. Still, the local authority districts had no formal power regarding its management. The advantage of all power assigned to the national level was one institution being responsible for the wild reindeer management across administrative borders. The drawback was the total reliance upon the judgements of the bureaucrats in the MA (Lütken & Rom, 1959).

The Snøhetta case illustrates problems associated with a centralised wild reindeer management, and how the nationally based power was challenged when the owners of the land organised themselves. The organising of the land owners is interesting, because they at the same time kept their position in the national system, and by organising an arena outside the system, violated its basic assumptions. Disagreements between national authorities and the owners of the land, as in Snøhetta, are frequent in wild reindeer and caribou management (Freeman, 1989; Andersen & Rowell, 1991; Thomas & Schaefer, 1991). Different types of knowledge may influence those relations because local people often use personal knowledge (Friedmann, 1973, 1987; Polanyi, 1976, 1978; Rolf, 1989) based upon own observations, whereas national agencies are inclined to favour processed knowledge.

If the bureaucracy relies upon processed knowledge (Weber, 1995) one should anticipate that the MA increased its efforts to obtain the best possible knowledge for action but in the 1950s and early 1960s, the Ministry did not initiate a quantification of the wild reindeer in Rondane. The decisions of the MA in those years are characterised by a limited rationality caused by "cognitive limits" (Forester, 1989; March & Simon 1993) aiming at a "good enough", and not necessarily the "best", wild reindeer management. Almost unchanged quotas in the northern part of Rondane in 1952 - 1967 supports the indication that national actors do not necessarily seek an optimal wild reindeer management.

According to Ostrom (1990) precise information is a necessity for centralised management. It was however non-existing in the Rondane area until the MBs in 1960 made the first count and thereby reduced uncertainty (Ostrom, 1990). It was also the MBs that by the means of observations and context dependent processed knowledge documented an asymmetrical distribution of wild reindeer in the Rondane area in the 1970s. The quotas had prevented an overexploitation of the herd as an area unit but not prevented overexploitation in most parts of the area. A centralised and national actor with much power but without knowledge on the real distribution of the animals was not able to manage them properly. This illustrates the assertion by Grima & Berkes (1989), that national decisions not being influenced by the knowledge of local people and their concern for the well being of the resources (Berkes & Taghi Farvar, 1989; Ostrom, 1990), can be a problem.

Processed knowledge and wild reindeer management

Annual censuses became crucial for the Rondane North WRB when applying to the national authorities for quotas. The owners of the land also engaged experts in order to increase the local knowledge about the pasture. In that way professional processed knowledge was integrated with the personal knowledge of the local mountain rangers, *cf.* Johnson (1992). "A skilful pooling and blending of scientific knowledge and local time-and place knowledge" (Ostrom, 1990: 34) reduced the uncertainty in the local management. A good relationship between scientists and local managers evolved from the 1970s due to the involvement of the mountain rangers in the practical scientific fieldwork. Mutual trust is important for successful integration of processed knowledge into local management, but is difficult to obtain (Freeman, 1989; Thomas & Schaefer, 1991; Johnson, 1992; Weeks & Packard, 1997). Still, it became one of the characteristics for the wild reindeer management in Rondane from onwards the 1970s because the owners of the land needed processed knowledge illustrating that "traditional environmental knowledge" and western scientific knowledge were not two excluding forms of knowledge.

Censuses are based upon quantification, which is basic for statistics. Statistics imply that a population is transferred from an undefined mass of individuals to a collection of individuals characterised by certain parameters (Foucault, 1999). By the means of quantification, the wild reindeer in Rondane became a collection of individuals. Statistics, and the categories upon which it is based, increased the option for controlling the wild reindeer resource (Hacking, 1991). Quantified quotas illustrate the assertions that power is not necessarily something negative since quotas can hinder overexploitation (Foucault, 1999).

The initiatives of the MBs in Rondane in the 1950s have some similarity to Canadian Dene Indians and Cree Indians efforts to increase their knowledge about the caribou. Also the Indian tribes collected synchronic and diachronic data about the wild reindeer or caribou and their distribution in the landscape. On the other hand the MBs wanted quantitative knowledge about the total number of wild reindeer and the hunting success whereas the Indian tribes based their action upon qualitative data (Smith, 1978; Thomas & Schaefer, 1991; Berkes, 1998). Such use of qualitative and quantitative data illustrates a basic difference between "native systems" and systems influenced by western science (Freeman, 1985).

Foundation of a formal reindeer board in Rondane

The development towards a formal WRB in 1967 is in accordance with the optimism in group theory that individuals with a common interest voluntarily advance such interests (Ostrom, 1990). Others have been doubtful about the ability of achieving such an organisation. Unless the number of individuals is quite small, or unless there is coercion to make individuals act in a common interest, rational, self-interested individuals will not act to achieve their common or group interests (Olson, 1965). Despite Olson's scepticism the MBs in Rondane gradually organised during the 1950s and 1960s, probably because the process of organising started with so few "individuals" (the MBs), that mutual trust between the members was established. They developed a social capital, which is basic for developing institutions for common pool resource management (Coleman, 1990; Ostrom, 1995). The organising was important because it gave more power to local people and thereby local control of the wild reindeer herds.

Conflicts concerning the quotas were moved more to the level of the wild reindeer area; in the period 1930 - 1967 the quotas, and disagreements, were primarily a theme for the MA and each land owner. When establishing the WRB local actors had to agree before applying to the national authorities for quotas. Possible conflicts had to be solved locally. Due to the fact that the landowners received a quota equal to their share of the total area, few conflicts between them should exist. But still in the early 1970s the landowners disagreed about the total quota for the northern part of Rondane. One reason was that the sustainable number of wild reindeer was interpreted in the separate context of each landowner. This illustrates that the acceptable limit for resource use has a biological and a social dimension (Gjølme-Andersen, 1993; Cozzens & Woodhouse, 1995; Gjessing, 1998). Despite some disagreement, the shareholders usually agreed upon the quotas inquired at the national authorities.

Because the Rondane North WRB, and elsewhere was not defined in the Hunting Act, the landowners themselves decided the rules for the board. Such discussions generally increase in complexity with the number of actors involved, as does the risk for an unsuccessful group activity (Olson, 1965). The Rondane North MBs judged the advantage of having a mutual agreement for a bigger wild reindeer area as being greater than the disadvantage of including private landowners, because the risk of free-raiding was reduced (Gibbs & Bromley, 1989; Ostrom, 1990). Since the landowners themselves defined the rules for the WRB, the definition of the rules became complicated, and the ones having most of the land achieved more formal power. That power was sometimes expressed openly, although generally speaking, open conflicts were not the case. The question of non-decisions due to the fact that the weaker landowners may have avoided conflicts, then arises, but is hard to investigate.

Official Wild Reindeer Committees and increased use of planning

The largest, and most powerful, landowners in Rondane North were especially reluctant to the new and official WRC in Rondane in the mid 1980s because in the WRC the power would be equally divided between the local authority districts. In the existing WRB the power was distributed according to each landowners share of the wild reindeer area. A conflict between representation and power based upon a symmetrical and an asymmetrical representation of the resource system emerged (Knight, 1992; Ostrom, 1995). Despite the resistance the WRCs were introduced, and the WRBs were subordinated to them.

An interesting question is why the national authorities wanted official WRCs, as long as the WRBs existed. Official documents tell the committees were needed since there were no official bodies at the level of the wild reindeer area. This can be interpreted as a tendency for hierarchies to develop a perfect structure. The introduction of the WRCs coincided with a general tendency of decentralisation; therefore is also the possibility that the national authorities wanted a regional official body because it paved the ground for decentralisation of power to the areas and an official framework for including the advantages of knowledge, goals and values held by local people.

Planning was an important pre-condition for the decentralisation of formal power because management plans approved by the WRCs bound the future decisions of the landowners. Still the management plans would be monitored every year in order to check the relationship between the plan and the reality. The emphasis on management plans coincided with a general belief in planning (Ministry of Environment 1991, 1996; Emmelin & Kleven, 1999). Processed knowledge became an important pre-condition for demanding management plans since it was anticipated that science had unravelled the basic relationships for the development of wild reindeer herds, and it was easy to gather such processed knowledge. An additional advantage of processed knowledge was that it could be communicated formally and critically examined to a larger extent than personal knowledge (Friedmann, 1973). The possibility of critical examination of the plans, because they were based upon processed knowledge, paved the ground for decentralising their approval to the WRCs. There seems to be a strong linkage between an increased body of processed knowledge, planning and decentralisation.

Conclusion

Historically the management of the wild reindeer becomes an issue for an official jurisdictional area with an official bureaucracy. This is caused by a tendency to solve the negative effects of modernisation and overexploitation by the means of technocratic management (Rabinov, 1991). The power situated in this structure has been especially evident since 1930 when the national state introduced quotas for wild reindeer hunting. This decision prevented overexploitation, but at least in the Snøhetta area, it turned into a problem because quotas were too low. The reason was that the Ministry possessing the power lacked knowledge about local conditions or did not accept the personal knowledge of the landowners. The landowners in many mountain areas in the 1960s organised influential boards for wild reindeer management, adapted to the size of the wild reindeer area. The WRBs based their management upon local values, personal knowledge, and processed knowledge but were voluntary and had no official power according to the law. The WRCs, introduced in 1988, were supposed to keep up with the advantages of a management based on local values and the advantages of the hierarchy. Essential for the decentralisation was the elaboration of management plans for each wild reindeer area. The plans were based upon scientific knowledge and locally produced personal and processed knowledge. An increased amount of processed knowledge produced for a local context, had increased the power of the landowners. But in order to be used, the knowledge had to be acceptable for those possessing the power.

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River crossings as principal points of human/reindeer relationship in Eurasia

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Abstract: Since prehistoric time, indigenous peoples throughout Eurasia have hunted reindeer from boats when the animals were swimming across rivers. A number of landscape peculiarities and reindeer behavior features determine the phenomena of mass reindeer river crossings at a few points. Hunting at river crossings occurs predominantly in the autumn season along migration routes of tundra and forest-tundra populations. In the past, many of the well-known river crossings were in private possession by indigenous families (Anonymous, 1945). In northern Russia, since the 1970s, the reindeer river crossings became the place of commercial slaughter of reindeer. The state hunting husbandry "Taymyrsky" was established, it received licenses for hunting and then totally regulated who was permitted to hunt reindeer and where (Sarkin, 1977). Step by step, most of the indigenous peoples have been forced out of their traditional hunting locations by aggressive non-indigenous newcomers and became unemployed. Large-scale commercial hunting has led to overexploitation and the decline of reindeer populations in Yakutia and Taymyr. The sustainable use of migratory reindeer populations, as well as renaissance of hunting economies, are possible if exclusive use of some of the reindeer river crossings are returned to indigenous communities as their property, with others to be used by urban hunters and commercial enterprises under the improved state regulations and enforcement.

Key words: behavior, indigenous people, *Rangifer tarandus*, sustainable use.

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Introduction

Since prehistoric time, indigenous peoples throughout Eurasia have known that reindeer use a few river crossings year after year. The fact is that reindeer have used some localities for very long periods. In Taymyr, 8 km from Katyryk settlement on Kheta River (Fig. 1) there is a reindeer river crossing that is said to have been functioning for 3200 years (Khlobystin, 1998). In that place, Khlobystin excavated an ancient settlement, which specialized in reindeer stabbing, at the river crossing. In the past, mass slaughters in river crossings were a significant part of national economies and hunting culture (Khlobystin, 1996). Many well-known crossings were in private possession of some families (Popov, 1948). When reindeer changed their use of crossing points, it led to severe famine and even the perishing of entire settlements (Argentov, 1857; Vdovin, 1965).

In the past thirty years, the large-scale commercial hunting on river crossings has forced out indigenous hunting husbandry. In Russia we meet urgent problems in the relationship of human and wild reindeer – a strong decline of wild reindeer populations caused crashes of commercial hunting and unemployment of indigenous people because urban hunters and commercial enterprises occupied their economical niche. In this paper, I demonstrate that fidelity of migratory reindeer to the river crossings provides a great possibility of exploitation, management, and study of reindeer populations.

Stabbings of reindeer on river crossings in the past

Between a great diversity of hunting methods, stabbing reindeer by spears while animals were crossing rivers is well known in the history of indigenous peoples throughout Eurasia (Naumov, 1933; Washburn & Lankaster, 1968; Spiess, 1979). Stabbing at

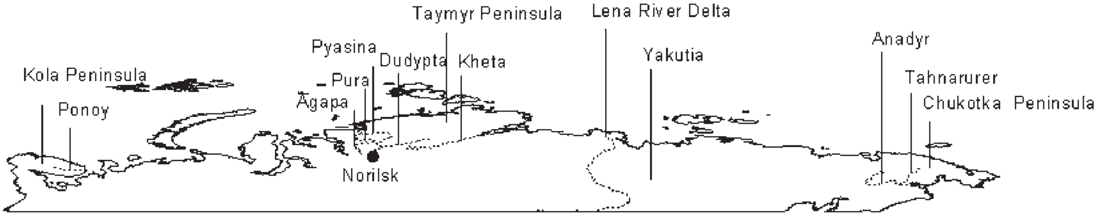

Fig. 1. Kheta river.

river crossings was the only method that provided a sufficient food supply guaranteeing survival of hunter's families over a year. There is much evidence on how productive such hunting was. During a half-hour period, the best hunters could kill up to 70 reindeer using only spears. They stabbed, aiming to damage an animal's liver, which kept the animals strong enough to reach a shore where assistants killed the animals and skinned them. Usually, there were small bands (up to 12 humans), which slaughtered up to 200 animals per a hunt. In fortunate years, each family stored up to 50 carcasses, which was enough to survive through a winter (Popov, 1948; Gurvich, 1982). In the past, many well-known crossings were in possession of indigenous communities. For example, in the basin of Pysina River where later the State hunting husbandry "Taymyrsky" was established right of hunting belonged to a nomadic community of Nganasans. In 1933, it consisted of 75 families from 5 genera, totaling 267 humans (Anonymous, 1945; Baskin, 2002). The family ownership of a crossing was determined by common law (Popov, 1948; Argentov, 1957; Vdovin, 1965).

Mass reindeer river crossings localities and reindeer behaviour

In the Kola Peninsula and Western Siberia, few localities are known to have reindeer spearing at river crossings during the last centuries. In Chukotka, a well-known place of stabbing reindeer was located at the confluence of the Anadyr and Tahnarurer Rivers (Fig. 1). Starting from the summer grounds, reindeer can select different directions in their southerly migration. In autumn, reindeer herds migrated from the tundra to mountain taiga, and hunters were on the lookout for them on the southern bank of Anadyr River. In the past, indigenous communities arranged a reconnaissance, trying to predict directions of reindeer migrations. In Chukotka, mass river crossings of reindeer were known not only in tundra and forest-tundra but also in the taiga regions. Autumn migrations were the only suitable time for hunting on river crossings because in spring reindeer often crossed the rivers along ice (Argentov, 1857).

In Yakutia, the well-known places of reindeer river crossings are located along the Olenekskaya Protoka Channel, a western branch of the Lena River Delta (Fig. 1). The reindeer population spends the summer in the Lena River Delta, where it finds plenty of food, cold winds and absence of insect harassment. In August and September, animals migrate southwest. The western bank is slightly elevated; dozens of hunting teams waited for the animals there.

In Taymyr, 24 locations of reindeer stabbing by indigenous people were situated along the Pyasina River and its tributaries (Fig. 1) (Popov, 1948). The mass river crossings of reindeer occupy fairly long parts of the river. For example, in modern days when commercial slaughtering is arranged, hunting teams occupy 10-20 km along the river, using observers that signal by radio about an approaching reindeer group and then use motor boats to the points where hunt can be organized (Sarkin, 1977). Obviously, past hunters used canoes and needed to recognize the places of reindeer-river crossing more precisely so as to be in the good place at the right time.

Other behavioral details are also very important for hunting success. Reindeer are very vulnerable in water. Although their speed in water is about 5.5 km/hour (Michurin, 1965) humans on light boats were able to reach the animals. Then, the hunters circled around a herd to keep animals together in solid mass and prevent their escape after a leader. Even in modern times, hunters using motorboats and rifles are able to kill a maximum of 70% of the animals of the group crossing the river.

Reindeer are often not able to see more than 200 m, especially in foggy conditions, and hence, cannot see the hunters and boats on the other side of the river. However, hunters use different precautions not to disturb the reindeer before they are in water and have reached the middle of the river. Humans must keep absolute silence, hide themselves and their boats. Special attention is taken for leaders of reindeer herds. Human experience confirms that if the leader of a herd is not disturbed, nor its group, the next groups will follow behind to cross the river without disturbance; if a leader has started to cross a river, the other animals will follow it in spite of danger (Savelev, 1977).

Commercial slaughtering

In the past thirty years, large-scale commercial slaughtering on river crossings has replaced indigenous hunting (Sarkin, 1977; Zabrodin & Pavlov, 1983). In that time, indigenous peoples using the crossings were based only on common law that was not recognized by the authorities. Since the State-hunting husbandry "Taymyrsky" was established, it had received the hunting grounds including the crossings, to conduct its activities. The local indigenous people were involved in the harvest as hunters but soon were pushed out by newcomers because the harvest was very profitable. In Yakutia since the 1970s, commercial hunting has been arranged at crossings and hunters-butchers have even tried to use electrical shock method. Hunters have stretched a wire connected with engine to kill reindeer by electricity when they came out from water. During last years, the migratory population declined drastically. The size of this herd has fallen to 800 animals (Safronov *et al.*, 1999).

In Taymyr up to the 1960s, indigenous people practiced subsistence hunting on river crossings. However, before the 1970s, Russian hunting regulations banned hunting on river crossings because animals in this position were considered extremely vulnerable. Since the 1960s, scientists have recognized a great increase of reindeer numbers in Taymyr. When the question was raised on how to arrange the most productive hunting, scientists proposed the use an ancient method of slaughtering at river crossings. Since 1970, the ban on slaughtering at river crossings has been canceled. The Taymyr State Game Husbandry Department was established. Up to 500 hunters participated in the slaughters. Practically, all appropriate locations of crossings on the Pyasina River and its tributaries Dudypta, Agapa, Pura (Fig. 1) have been occupied by hunters. The Pyasina River is a good waterway from an industrial zone of Norilsk. A ship-refrigerator was used to collect the meat. During 25 years, about 1.5 million of reindeer were harvested there (Pavlov *et al.*, 1993). In 1993, as reindeer did not return to these river crossings, a crash in hunting husbandry was observed. In later years the harvest has declined to 15 000 per year.

Management and conservation

In recent years in northern Russia, a market for venison and river crossing hunting has been revived. In mining settlements, the cost of venison is 2.5 US$ per kg, which makes commercial hunting profitable. A significant demand for velvet antlers also exists. However, northern Russia's present conditions: no roads and only a few settlements, makes hunting at reindeer river crossings a reliable and productive method of the economy.

The concentration of hunter's interest around a few localities gives a chance to improve management of the reindeer harvest. There is a responsibility to protect rights of indigenous hunters as a means of ensuring their livelihood. Because they are not able to compete with urban hunters, the only way is to return a few of reindeer river crossings as communal property to groups of indigenous hunters. At present, indigenous hunters only practice subsistence hunting. Becoming owners of the river crossings may revive commercial hunting. Several large industrial companies have expressed a readiness to support indigenous people in this endeavor and assist these hunters in transportation of their products to towns and mining settlements.

A portion of river crossings will be opened to other people from towns and for other commercial hunting operations. However, it is necessary to develop regulations to avoid large impacts on reindeer populations and migratory routes.

One proposed approach to protecting reindeer populations from over-exploitation is to establish hunting regulations that limits hunting to certain days in the week. Some reindeer-river crossings have been used for hundreds of years and are good candidates for protection.

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Session two

Traditional Ecological Knowledge and Scientific Information: Using the Best of Both Worlds

Naskapi Elder's Story:

John Shecanapish, Kawawachikamach, Québec

John Shecanapish was born on March 12, 1920 in Fort McKenzie, Québec. He was a hunter and trapper until he started working for the Iron Ore Company of Canada in Schefferville in 1957. He worked for the company until it ceased its operations in Schefferville in 1982. He served on the Naskapi Band Council for 20 years and was Chief from 1958 to 1960. He is the father of eight daughters and five sons. He started hunting caribou when he was 20 years old and still does today, at the age of 81.

Mr. Shecanapish has noticed a decline in the number of caribou in recent years and wants to share his observations with the participants. He also wants to hear what others have to say concerning the George River Herd. Governments have to take into account the latest information to decide on their intervention.

Towards a protocol for community monitoring of caribou body condition

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Abstract: Effective ecological monitoring is central to the sustainability of subsistence resources of indigenous communities. For caribou, Arctic indigenous people's most important terrestrial subsistence resource, body condition is a useful measure because it integrates many ecological factors that influence caribou productivity and is recognized by biologists and hunters as meaningful. We draw on experience working with indigenous communities to develop a body condition monitoring protocol for harvested animals. Local indigenous knowledge provides a broad set of caribou health indicators and explanations of how environmental conditions may affect body condition. Scientific research on caribou body condition provides a basis to develop a simple dichotomous key that includes back fat, intestinal fat, kidney fat and marrow-fat, as measures of body fat, which in autumn to early winter correlates with the likelihood of pregnancy. The dichotomous key was formulated on "expert knowledge" and validated against field estimates of body composition. We compare local indigenous knowledge indicators with hunter documented data based on the dichotomous key. The potential contribution of community body condition monitoring can be realized through the continued comparative analysis of datasets. Better communication among hunters and scientists, and refinement of data collection and analysis methods are recommended. Results suggest that specific local knowledge may become generalized and integrated between regions if the dichotomous key is used as a generalized (semi-quantitative) index and complemented with other science and community-based assessments.

Key words: local knowledge, traditional ecological knowledge (TEK).

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Introduction

There is a need to advance the methods of Rangifer monitoring to address the potential impacts of global change (i.e. climate change, industrial development, culture change) and build cooperative programs of resource management that involve agency managers, indigenous and non-indigenous resource users, and research scientists (Russell et al., 2000). The objective of this paper is to move that effort forward by exploring the potential of a Rangifer monitoring program based on body condition assessments of caribou harvested by indigenous hunters. We present three dimensions of the problem by examining local and traditional knowledge perspectives on caribou body condition, introducing a research-based analysis of caribou body condition that produces a simple dichotomous key for assessing caribou body condition, and exploring practical and theoretical challenges associated with implementation and synthesis of a community-based body condition monitoring program.

The material of this paper is drawn primarily from three experiments in caribou body condition monitoring involving local communities and graduate research on body condition of caribou (Adamczewski, 1987; Allaye-Chan, 1991; Gerhart, 1995). The Caribou Traditional Knowledge Project of the Western Arctic Herd in Alaska, undertaken in coop-

Table 1. What Old Crow, Fort McPherson, and Aklavik hunters perceive as the best source of information on body condition, caribou migration, and the Porcupine herd's population.

Body condition	n=105	*Migration*	n=106	*Population*	n=114
local hunters	38%	elders	37%	biologists	15%
self	13%	don't know, its a mystery	12%	PCMB member by name	14%
elders	10%	PCMB member by name	10%	A wildlife officer	12%
				Hunter's local organization	12%
				PCMB	11%

eration with hunters of Kotzebue and Kiana, Alaska; the Arctic Borderlands Ecological Knowledge Co-op (Kofinas et al., 2002a) which involves Porcupine Caribou user communities of Alaska, Northwest Territories, and Yukon; and the Łútsël K'é Study of the Bathurst Caribou Herd, undertaken with Łútsël K'é hunters and the Lands, Wildlife, and Environment Committee of that community contributed indigenous knowledge. Transactions of the Body Condition Monitoring Technical Workshop, held in Whitehorse, Yukon on February 16-20, 2000, provided scientific expert knowledge on body compositions (Kofinas et al., 2002b). The workshop recommended that community-based systems for monitoring caribou that track individual and herd well-being, detect change in environmental conditions, and contribute to the co-managed assessment of possible futures be established (ibid.). This community monitoring objective is a component of the new circumpolar monitoring initiative of the Conservation of Arctic Flora and Fauna (CAFF) working group, which seeks to draw on local and scientific knowledge to develop a broad set of indicators of Human-Rangifer Systems that will track change and allow for comparison between regions. This goal addresses the current necessity to move beyond broad and abstract discussions about the definition and value of traditional ecological knowledge, and towards the implementation of management systems that benefit from local knowledge as well as the more conventional approaches to the science of resource management (Stevenson, 1996; Berkes, 1999; Elkin, 1999; Berkes et al., 2000; Usher, 2000).

Rationale for exploring the potential of community monitoring of caribou body condition

Several factors motivate us to explore if and how community caribou monitoring of body condition can be undertaken. On the individual animal level, research findings show that caribou body condition is an important indicator of environmental conditions (Dauphiné, 1976; Reimers et al., 1982, 1983), integrating weather conditions, forage quality, and the reproductive history of a cow (Cameron et al., 1993; Chan-McLeod et al., 1995, 1999; Gerhart et al., 1996, 1997; Russell & White 2000). In autumn to early winter, body weight and condition of female caribou contributes to the likelihood the individual will become pregnant (Cameron et al., 1993, 2000) and the embryo retained (Russell et al., 1998). However body condition of calving females is indicative of the over winter effects and also correlates with milk production (R. White unpubl.), which is important to calf survival (Griffith et al., 2002). How individual cow caribou body condition relates to herd level productivity is less well understood. We hypothesize that a measurable decrease in herd fecundity resulting from a change in climate conditions and/or forage quality would be reflected in body condition monitoring and a general decreases in body condition could be the harbinger of change.

Traditional indigenous caribou hunters have a strong knowledge base in the area of caribou body condition and many indigenous hunters perceive themselves to be most knowledgeable in this area of caribou health and condition (Table 1). When asked to identify the best information sources on caribou body condition, caribou population levels, and causes of caribou migration patterns, most Porcupine Caribou hunters interviewed (n=105) perceived themselves as the best source of information on caribou body condition, with elders perceived as the knowledge holders on migration, and biologists, co-management board members, and wildlife officers as the best information sources on herd population (Kofinas, 1998: 262).

We suggest that hunters' monitoring of caribou body condition may serve to resolve some of the problems associated with agency-based body condition monitoring. While offering good precision in their assessments, agency-based caribou body condition monitoring programs are typically limited in sample size and plagued with costly field logistics

Table 2. Gwich'in, Iñupiaq, and Chipewyan language examples reflecting traditional knowledge of caribou body condition. (Sources: Gwich'in - Mr. Roy Moses of Old Crow Yukon; Dënesúłine (Chipewyan) - Łútsël K'é elders.

Gwich'in	
–Chikkyi	(New-born calf)
–Vutzuih njo	(Cow without calf in winter)
–Dazho k' eilik	(Small-antlered bull; two years old; considered a trouble maker)
Iñupiaq	
–Kulavagruitchiak	(Very old, skinny cow)
–Nuggailak	(Cow without calf)
–Tunusisak	(Hard covering of small stomach)
Dënesúłine (Chipewyan)	
–Tsi	(Unborn calf/ fetus)
–Besdzi?azé	(Calf less than one year old)
–Ts'udaí	(Young cow yet to breed)
–Dãbe	(Mature breeding cow)
–Déyath?azé	(Young 2-year old bull)
–Besdzichogh	(Mature 4-5-year old bull)
–Yáguzé	(Prime 6+-year old with the large rack of antlers).

that result in incomplete data. Between-year and between-population estimates of summer habitat condition can be assessed from the early winter of spring calves (see Valkenburg report p. 11 in Kofinas et al., 2002b), but the collection of calves as a method is regarded as unacceptable to many traditional hunters. We sought a method that addresses the problem of sample size and field cost that are often associated with agency-based monitoring methods, methods that are typically not compatible with community harvesting practices because of their high demand in technical sampling expertise or involve too long handling time to implement in a widespread community monitoring program. Hunter harvests of caribou, on the other hand, represent a potentially enormous sample size. For example the annual harvest estimates of Bathurst caribou are 14 000 to 18 000 animals and the Western Arctic caribou approximately 25 000 animals. The potential of using hunter harvest data can be seen from the array of publications addressing environmental concerns over Norwegian red deer populations, where 2000 to 5000 individual measures contribute annually to a database since the 1960s (Langvatn & Albon, 1986; Mysterud et al., 2001).

Therein lies our challenge – to develop a body-condition monitoring program that benefits from large numbers of harvests using sufficient warning indications of change, and which is comparable with the knowledge systems and harvesting practices of local indigenous hunters.

Local and traditional knowledge of caribou body condition

Indigenous hunters of caribou traditionally have been acutely aware of caribou body condition as an important indicator of meat quality and overall animal health. Traditional knowledge on caribou body condition is embedded in the language of indigenous northern caribou hunters, as is the case with Gwich'in (language of Athabascan or Dëne people of northeastern Alaska and the Western Canadian Arctic), Iñupiaq (language of Iñupiat or Eskimo of Alaska), and Dënesúłine (also referred to as Chipewyan language of the Dëne people of Northwest Territories, Canada, Table 2). For example, the Dënesúłine term for cows which have yet to breed and are usually in better condition than the other animals, is ts'udaí. Ts'udaí are generally targeted in spring. Nał?ás is a general term used to describe caribou migrating north to the calving grounds in spring. (Note that "?" is a full glottal stop in Dënesúłine) ?enįł?ás refers to caribou returning from the north. These are usually small caribou (yearlings) or "running caribou" which are first to arrive ahead of the cows. The people would say, "The caribou are coming" during this time. Nelyá is an expression used for bulls in the fall, which have returned south and are in good condition having built up fat reserves over summer. Ts'énajá or thenájá refers to the skinny bulls, which have finished and survived the rutting period. If at all possible, these bulls will not be harvested because of their poor condition and meat is considered tainted from rutting.

A hunter's assessment of caribou body condition is generally undertaken with a set of visual indicators when selecting an animal for harvest, and in the post-mortem phase, when ensuring that the harvested animal is fit for human consumption. Łútsël K'é hunters were asked for their description of preferred animals. In the pre-harvest assessment of a female caribou, a hunter generally looks for what they colloquially describe as a "pretty" animal. The characteristics that define this type of animal are: (i) large antler size, the shape, and the abundance of points; (ii) the manner in which the animal moves (i.e. "walks with a swagger"); (iii) straightness of the back and a fullness through the abdominal and rump regions. Hunters target "short" cows which is a reference to the length of the cow rather than its

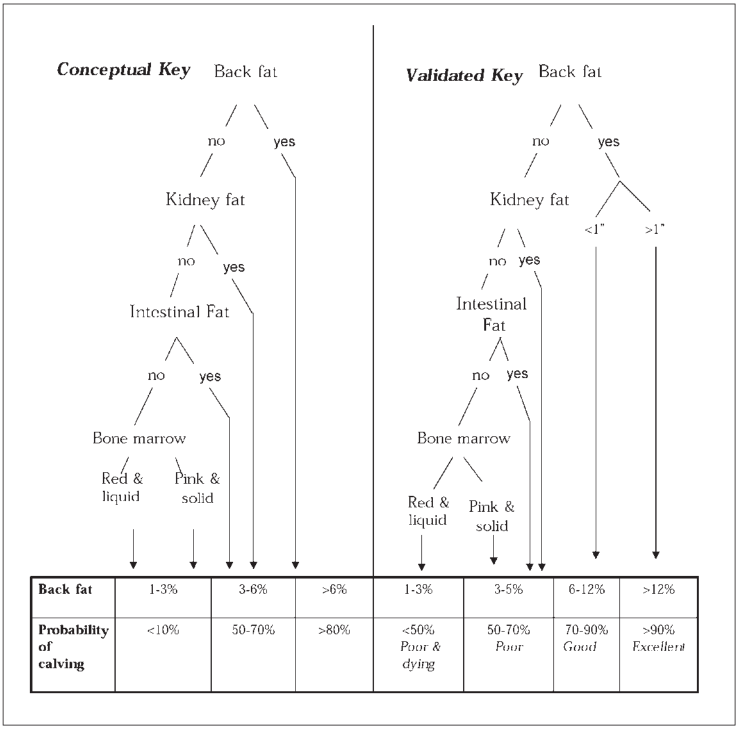
Table 3. Indicators of good caribou body condition and overall health, and reported by indigenous Porcupine Caribou hunters (Kofinas 1998: 166).

Indicators hunters look for when selecting caribou	• Size of rump • Gait or waddle of walk • Whiteness of mane • Size of rack • Symmetry and overall shape of rack • Number of configurations or points on rack • Size and shape of shovel • Grayness of rack • Social role of individual in group • Posture of animals when moving
Post mortem indicators of caribou health	• Quantity of "backfat" (i.e. rump) • Quantity of stomach fat • Color of marrow • Tone and color of lungs (e.g., lungs stuck to chest indicate poor health) • Color of kidneys and liver • Absence of pus bags on kidneys • Absence of "water" in muscles ("water being produced when animals is worked) • Contents of stomach (e.g., grass-filled indicate may be sick animals) • Presence of parasitic larvae in kidneys

height. A fat cow gives the impression it is shorter in length; (iv) the coloration of the hide. Hunters target those cows with prominent white stripes along their sides and under-bellies. A prominent mane is also indicates a better quality animal and; (v) the length of tail protruding from the rump. If the cow has a lot of rump fat the tail has the appearance of being short. Porcupine Caribou hunters of Old Crow, Aklavik, and Fort McPherson hunters were asked to list the indicators used visually to assess animals before shooting. (Table 3) Lútsël K'é and Inupiaq hunters of Kiana and Kotzebue use indicators similar to those of the Dënesúłine. The majority (87%) of surveyed hunters in Łútsël K'é (n=30) use antler size and formation to assess the body condition of a live female caribou. Fullness of rump and abdomen (43%) and hide coloration (33%) were the next most common assessment characteristics used by the hunters. Porcupine Caribou hunters also reported post-mortem indicators of "good" caribou. (Table 3) Of these indicators, Łútsël K'é hunters noted the quantity of brisket fat, back fat, kidney fat, stomach and intestinal fat, and to a lesser extent the color of marrow. Levels of parasitism in organs and flesh tissue were also assessed by Porcupine Caribou and the Łútsël K'é hunters.

Hunters provided explanations for what they perceive to be seasonal, annual, and special variability in caribou body condition. As would be expected, hunters stated their awareness of seasonal variability (e.g., "Bulls in the fall are the best," "Cows are best in spring."), with some also noting patterns of variability within a single season. For example, Kotzebue and Kiana hunters of the Western Arctic herd find that caribou migrating in August, and after the initial groups have passed their hunting grounds, tend to be fatter than the first migrants, with some hunters speculating that the difference is because later animals have more time to forage on calving grounds.

Hunters gave mixed reports regarding their perceptions of year-to-year variability in caribou body condition. Of over 100 Kiana, Kotzebue, Old Crow, Fort McPherson, Aklavik, and Łútsël K'é hunters interviewed, less than half stated that they noticed year-to-year variation in body condition, although several elders commented on decadal changes and year-to-year trends in body condition. Hunters did mention spatial variability in the body condition of groups of caribou. For example, in 2000, hunters of Łútsël K'é observed that caribou south of the community around Nonacho Lake were in better condition than the ones towards McKinley Point and Yellowknife. Disturbance from hunters and traffic,



Back fat	1-3%	3-6%	>6%	1-3%	3-5%	6-12%	>12%
Probability of calving	<10%	50-70%	>80%	<50% *Poor & dying*	50-70% *Poor*	70-90% *Good*	>90% *Excellent*

Fig. 1. Development of the Dichotomous Key to predict body condition in Caribou. Conceptual key as based on the presence and absence of fat in caribou (proposed by R. G. White, 2000, see Kofinas et al., 2001). The conceptual key was validated against datasets of body composition (Fig. 2) and modified to make linear the response noted in the Validated Key.

pollution, and poor quality of feed were theorized as the causes for the poorer body condition of the animals in the Yellowknife/McKinley Point area. Kotzebue hunters provided reports of spatial variability, attributing the difference to the effects of hunting activities in easily accessible areas and groups of caribou in other locations being harassed by wolves. Hunters also talked about variability among individual caribou. As an elder of Kiana stated, "Caribou are like people, some are just fatter than others." No discussions by hunters documented in our research indicated explicit knowledge of the relationship between body condition and pregnancy success, although it was clear from the hunters that pregnant cows encountering difficult travel conditions (deep or ice snows) to calving grounds would be less likely to be successful in raising a calf.

In summary, these findings support the assertion that community hunters bring a unique and rich knowledge base to a body conditions monitoring program.

Dichotomous Key for the assessment of body condition

In developing our monitoring protocol, we needed a sampling method of assessing body condition that would be easily employable by community hunters as a part of their regular subsistence harvesting. Drawing on the gestalt impressions and expert knowledge (e.g. Ringberg et al., 1981a,b), a dichotomous key assessing body fat in areas of caribou commonly observed by hunters was developed (Fig. 1). The key uses the presence or absence of back fat, intestinal fat, kidney fat and femur marrow fat in a hierarchical decision tree leading to each animal being classified into body-fat categories, with those categories corresponding to a relationship between fat levels and the animal's overall percentage of body fat. For cows harvested in fall to early winter, this relationship is extended to predict the probability that the cow was pregnant (Gerhart et al., 1997).

We validated the dichotomous key with two data sets (Chan-McLeod et al., 1995; Gerhart et al., 1996) that had the closest approximation to individual observations of reproductive condition, body fat level and measured (or deduced) values for variables in the dichotomous key. We conducted a Pearson correlation analysis to determine within what fat

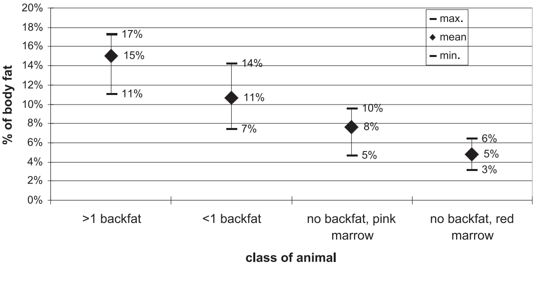


Fig. 2. Validation of Body Condition Class Structure using PCH Data

Table 4. Determinants of community monitoring effectiveness.

- Desire of community/hunters to participate
- Compatibility with hunting
- Sensitivity to cultural values
- Use of hunters' existing methods and knowledge
- Cost (labor and material)
- Amount of special training required
- Extent to which continuity of individuals is needed
- Contributions to regional monitoring
- Capability of providing a physical assessment of harvested animals while providing annual trend information on the population as a whole
- Extent to which the system is predictive
- Compatibility with the existing local systems of community members and local biologists' methods
- Contributions/additions to assessing food quality for communities (i.e. human health implications relating to the consumption of meat)

ranges each of these fat depots were dynamic (Fig. 2). Femur marrow fat was linearly related to whole body fat below about 9 % body fat ($r=0.80$, $P<0.0001$). Back fat was uniform below 9% body fat but linearly related above 9% ($r=0.77$, $P<0.0001$). Intestinal fat ($r=0.80$, $P<0.0001$) and kidney fat ($r=0.70$, $P<0.0001$) were linear throughout the range of body fats in the sample. A SAS program was developed to classify individuals into four body-fat categories using the dichotomous key approach (Fig. 2). In order to refine the body fat estimates we found it necessary to include the additional criterion of the presence of back fat greater than 1 inch in depth.

Hunters' Questionnaire

The success of a hunter-based body condition monitoring program would be determined by many factors (Table 4). After discussing the body condition monitoring program with local hunters in the initial phases of the project in Kiana and Kotzebue, we came to the conclusion that on-site assessments of animals would not be undertaken unless hunters were specially trained and hired to undertake the work. In an attempt to obtain the greatest harvest sample size as possible from the communities, we designed a questionnaire based on recall, which included variables in the Dichotomous Key plus an additional set of variables that place the key into a broader context. The questionnaire asks hunters about fat levels (i.e. Dichotomous Key measures), sex, lactation, pregnancy, reason for targeting animals, abnormalities/unusual observations, general location of harvest, date of harvest, other noteworthy environmental conditions. The questionnaire also asks hunters to make a general assessment, which is their own overall evaluation of each animal harvested. Terms for the general assessment were developed by Phil Lyver, who worked with Lútsël K'é hunters to identify ordinal measures that rank-order caribou condition using familiar words of hunters -- "skinny," "not so bad," "fat," "really fat." We later modified the questionnaire to include photographs of organs with and without fat. Other questions have been added periodically to address specific issues, such as perceived long-term changes and general concerns about caribou health.

Local associates of the Kotzebue IRA and the Kiana Traditional Council have administered the questionnaire since 1999. Hunters report on each form up to 5 animals per hunt (the legal daily limit for rural hunters in that region of Alaska), and are required to make their report within 7 days of harvesting the animals. Hunters were provided an honorarium of US$ 50 per form (i.e. per hunt) regardless of the number of animals harvested.

Since initiating the Western Arctic Project, the condition of over 450 individual animals has been documented, with the majority of the data collected during the fall. Initial data collection efforts have been focused on modifying the questionnaire and educating local hunters to its use. After several years of implementation, a group of hunters in each community are now aware of the program. They consciously keep a lookout for the indicators included in the questionnaire and seek out local research associates in order to report their findings immediately after their hunts. In Lútsël K'é, and with the Arctic Borderlands Ecological Knowledge Co-op program a different method has been followed. Hunters are asked to make a general assessment of all animals harvested at the end of the season. In the Lútsël K'é study, Lyver and locally trained people have accompanied local hunters in the field during hunts and asked them to provide their impression of each animal (i.e. skinny, not so bad, fat, really fat) harvested. Assessments of female caribou body condition made by hunters in the field were similar to hunters' general impressions at the end of the 2000 ($\chi^2=3.772$, d.f.= 3, $P=0.293$) and 2001 ($\chi^2=1.414$, d.f.= 2, $P=0.493$) seasons (Fig. 3a, b). The number of degrees of freedom was less in 2001 because the "really fat" category was omitted from the analysis. No hunters reported female caribou in this body condition category in interviews and only 1 female caribou was designated as "really fat" by hunters in the field.

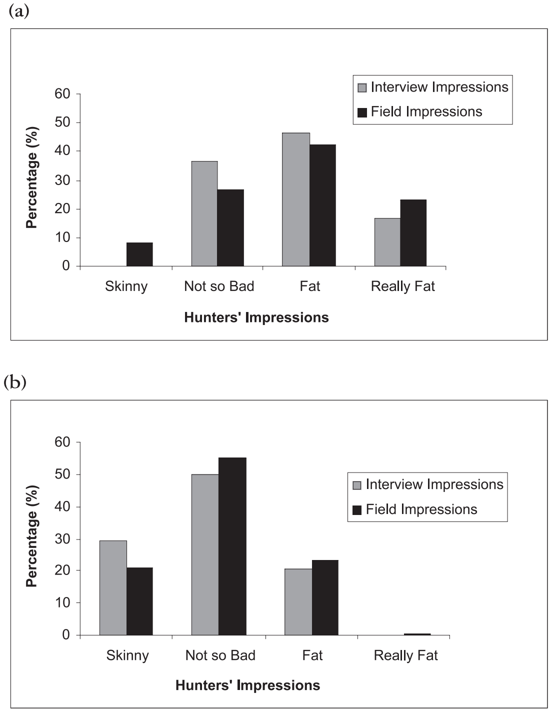


Fig. 3 Łútsël K'é hunters' impressions of female caribou body condition recorded in interviews at the end of each season, and for each animal harvested while in the field during spring (a) 2000 (n=30 hunter interview responses; n=87 field impressions), and (b) 2001 (n=44 hunter interview responses; n=176 field impressions).

Discussion

Our experience developing and implementing a protocol for community monitoring of caribou body condition has provided insights into both the potential and challenges associated with such an endeavour. From the outset, we worked on the assumption that a detailed and highly precise system of body condition assessment, as proposed by Chan-Mcloed et al. (1995), is not practical for hunters undertaking a body condition monitoring program while completing regular subsistence activities. We recognized that it would be difficult, if not impossible, to obtain individual reports on each animal harvested. Rather, we relied on hunters' memory recall and in some cases, hunters' recall of the season's harvest as a whole, rather than individual animals. Aware of the tradeoffs between a highly precise assessment method and one that is compatible with traditional hunting, which still offers a meaningful contribution to caribou monitoring and assessment, we sought a workable balance point. For example, a comparison between hunters' impressions of caribou body condition immediately after they cut-up an animal in the field and in interviews at the end of the spring hunting period were not dissimilar (Fig. 3a,b). This indicates that hunters' impressions of body condition could be recorded in short interviews at the end of a season reducing time and monetary costs immensely, and the imposition to hunters.

In all three of the monitoring programs, community hunters have been interested in participating. Not only do local hunters see value in the caribou monitoring program, they view their participation as an important means to include community understandings of caribou ecology in future management considerations. It is essential that the hunters understand and accept the reasons why the assessment is important if the program is to persist in the long-term. At the local level, the strong endorsement and good continuity in participation by local administrators and research associates has been key to these programs' success. It was evident from two of the programs that having one or a number of local people trained and employed to collect data from the hunters was advantageous. Their employment facilitated immediate access to the hunters, provided an opportunity for employment and capacity building within the community, a means to surmount barriers between the researcher and hunters. Moreover, these people's role provided important feedback to the program from hunters and the wider community. There has, however, been hesitation and resistance in participation by some hunters. Initially, problems arose when Kiana and Kotzebue hunters were asked to harvest and report on cows in the autumn. These problems highlight the need for flexibility in protocol, especially in the early phases of the monitoring program's development; we subsequently modified the protocol to include all animals harvested.

Regional variation in caribou physiology can also create differences in monitoring regimes between programs. In the Łútsël K'é study, it may be possible to monitor Bathurst female caribou in the spring when hunters specifically target these animals because a similar body condition-pregnancy relationship exists in Beverly caribou (Thomas & Kiliaan, 1998). However, that relationship has not been tested for the Porcupine and other herds in the spring, although there is an established relationship for the autumn (Cameron et al., 1994., Gerhart et al., 1995), when hunters prefer to harvest bulls. A modification to include bull caribou in the monitoring program, in turn, creates a demand for researchers to understand more clearly the seasonal weight (i.e. fat/protein) dynamics of bulls and the implications of seasonal condition of bulls to the population as a whole.

Hunters' unwillingness to participant has been because of concern for how monitoring findings may affect subsistence harvesting. These concerns have been most acute in Alaska (as compared to Canada), where indigenous hunters do not have specified harvesting rights to caribou hunting or formal caribou co-management arrangements, and consequently feel vulnerable to the actions of resource management. As corroborated with many other co-management experiences, an effective community-based monitoring protocol is dependent on the trust of resource users who are involved in the process. Communities need to understand why the assessments are being conducted and feel that they are in control of the information generated. As well, participating local communities need to be aware of how findings may be used to benefit caribou and their community.

These critical logistical challenges add to the basic science questions regarding the appropriate contribution of community-based body condition monitoring. Participants of our Technical Workshop debated whether body condition monitoring of caribou should be regarded as predictive, as suggested in the relationships of Dicotomous Key (Fig. 1), or whether it should simply serve as part of regular status reporting (Kofinas et al., 2002b). Several associated confounding issues follow from hunters' reports on the high spatial variability of body condition as well as biologists' understanding of these conditions (Thomas & Kiliaan, 1998), including weaning strategies of cows (Russell & White, 2000). These issues raise the applied research question of how a body condition monitoring program can account for variability between various areas within the range of a herd. In one effort to address this problem, the Traditional Knowledge Project of the Western Arctic herd has invited additional communities to be partners, thus providing a broader geographic scope and an opportunity to integrate monitoring results from several regions. These methodological questions raise the greater issue of whether monitoring body condition of caribou is sensitive enough to be indicative of change at the population level. In short, this is a problem of scale -- moving from an understanding of individual animal physiology to herd-level population dynamics (see Langvatn & Albon, 1986). To resolve this issue, we suggest research that examines on-going body condition monitoring results during periods of population increase and decline. Further analysis of data collected by the Yukon Renewable Resources Porcupine Caribou monitoring program (D. Cooley, unpubl. obs.) offers such an opportunity, given the last decade of population changes for the Porcupine Herd (Griffith et al., 2002).

Another potentially confounding aspect of the community-based monitoring system is hunters' bias for harvesting the best quality animals available. Many local hunters reported that being selective is a skill of the most experienced and that only a few of today's hunters have that ability. We suggest that hunter bias is not a problem in the protocol sampling, given that hunters' selection criteria are consistent. It should be remembered that a community-based monitoring technique may not offer an absolute body condition assessment, but rather a relative evaluation between years.

Conclusion

The development and implementation of community-based monitoring of caribou body conditions represents a departure from a previous paradigm in which hunters only supply data on harvest numbers, and towards an effort to engage local communities in dialogue about caribou ecology. Community monitoring of caribou body conditions is not an ideal approach in its precision to measure individual animals, but it does offer the opportunity to engage hunters in a monitoring program that generates a large sample of animals and meaningful results. Clearly, there is much work to be done to realize the full benefits of community-based body condition monitoring. Given the prospects for global change (i.e. climate changes, industrial development, new infrastructure, etc.), its possible effects on caribou, and the increasing restrictions in agency funding, it is important to advance this approach to body condition monitoring. The potential success of this monitoring will be realized through further comparative analysis of datasets, better communication among hunters and scientists, and the refinement of data collection and analysis methods.

Acknowledgements

Many people made important contributions to this paper. They include community members and caribou hunters of Kiana, Kotzebue, Old Crow, Fort McPherson, Aklavik and Łútsël K'é; Alex Whiting and Victor Karman, Kotzebue, IRA; Vera Morris and Charlene Hadley, Kiana Traditional Council; Łútsël K'é Lands Wildlife and Environment Committee; Jan Adamczewski, Government of the Yukon; Ray Cameron, University of Alaska, Fairbanks; Dorothy Cooley, Government of the Yukon; Jim Dau, Alaska Department of Fish and Game; Rick Farnell, Government of the Yukon; Anne Gunn, Government of the Northwest Territories; Brad Griffith, University of Alaska Fairbanks; Loralee Laberge, Government of the Yukon; Brent Patterson, Government of Nunavut; Craig Nicolson, University of Massachusetts;. A special thank you is given to Karen Gerhart and Anne Chan-McCloud for use of body condition data to validate the dichotomous key. Funding for this paper has been made possible through a grant from the Arctic Social Science Program of the National Science Foundation / Office of Polar Programs Award # OPP-9709971. This paper was improved by Bruce Forbes and one anonymous reviewer.

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The Ninth North American Caribou Workshop,
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Brief communication

First Nations communications and support program

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The Institute for Environmental Monitoring and Research (IEMR) was established in 1995 in response to a recommendation by an independent environmental assessment panel, appointed by the federal government to review an Environmental Impact Statement on military flight training based out of Goose-Bay (Labrador). These activities are available for countries that are part of NATO (North-Atlantic treaty Organization). IEMR's main objectives is to conduct multi-disciplinary scientific research on the Labrador and north-eastern Québec ecosystems affected by the military low-level flying program, an area of over 130 000 km^2 (Fig. 1).

Two of the IEMR mandates are to foster a trust amongst all native and non-native groups affected by the military training program and to implicate aboriginal communities in research. Through these mandates, the IEMR has created its communication program with the following objectives:

- To promote understanding of concerns expressed by the aboriginal communities and of traditional environmental knowledge (TEK) by IEMR researchers, non-aboriginal members of the IEMR board members, and the IEMR's Scientific Review Committee (SRC), which is an advisory group of recognized scientists to the board members;
- To allow the incorporation of TEK into IEMR research work;
- To ensure information exchange and facilitation between the SRC, IEMR researchers and First Nations experts (mostly elders) and foster a prop-

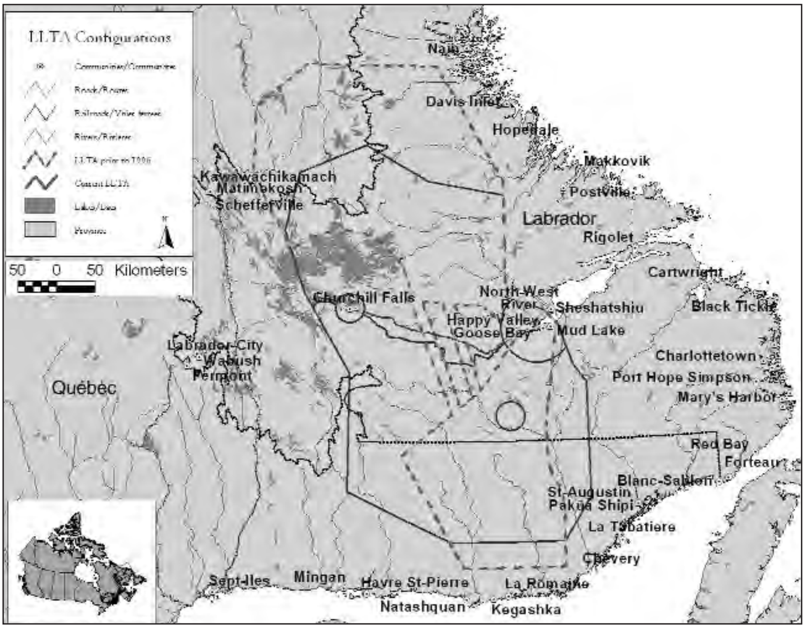

Fig. 1. Location showing military low-level training area and communities visited by the Institute of Environmental Monitoring and Research communication program

er understanding of research methodologies and the results obtained.

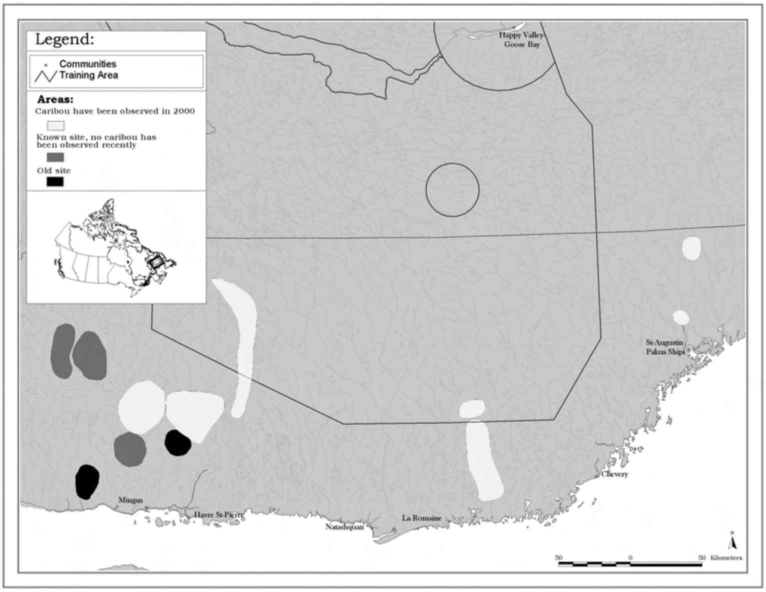

Fig. 2. Areas of high potential for the woodland caribou, identified by the experts committees of Mingan, La Romaine and Pakua-Shipi in fall 2000 (adapted from D'Astous, 2001).

Through its communication program, which started in 1998, the IEMR has appointed a liaison officer to visit the communities that are situated in the surrounding of the military training area (Fig. 1). These communities are represented by the Innu Nation of Labrador and Mamit Innuat and by the Naskapi Nation of Québec. Visits are conducted in average two times per year. Ding each visit, the liaison officer meets with a committee of four native experts recognized for their knowledge of the territory and the wildlife. One exception is the Naskapi Band of Kawawachikamach where the band council prefers the participation of eight experts within the same budget.

Topics of discussion include the presentation of current IEMR research, methodology used in research (radio-collaring, caribou capturing, etc.), aerial surveys of caribou and waterfowl and impact studies of military over flights on wildlife. During these discussions with native experts, the liaison officer records elements of native observations on several subjects such as caribou physical condition, migration patterns and habitat quality. An example of TEK that can be recorded is the map showing location of woodland caribou observation and good potential habitats to be consulted by the IEMR for future survey (Fig. 2). Meetings include regularly the participation of IEMR researchers, ensuring direct contact between researchers and aboriginal experts. The Institute also ensures participation of aboriginal human resources in field studies. These participants are, after the fieldwork, invited to share their experience and comments with the aboriginal experts at the next meetings with the liaison officer.

Concerns and suggestions brought up by experts during the meetings are later shared with members of SRC and non-aboriginal board members of the IEMR. Subsequent visits to the communities provide a reply from the IEMR, thus assuring a proper flow of information.

Since the beginning of this communication program in 1998, the aboriginals have shared a great deal with the liaison officer and help change the perception that aboriginal and ono-aboriginal have in regards to each other. It is now of primary importance to consolidate the communication process between the liaison officer, the Institute and the researchers it hires. In the opinion of the author, this communication program has reached a turning point. The Institute must henceforth require its scientists to demonstrate more openness in their work methods, particularly with regards to the handling of animals and the use of telemetric collars. As example, this can be realize in part by putting pressure on companies who are building the collars to improve them in regard of the animals comfort or by creating education program on environment for younger members of native community.

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Session three

Caribou and Human Activity: Industrial Development, Hunting and Commercialization

Cree Elder's Story:

Thomas Coon, Cree Trappers Association, Mistissini, Québec

Thomas Coon was involved in the negotiations that led to the signing of the James Bay Agreement right from the beginning as a representative for Mistissini. He later became involved in the Cree Regional Authority as the Director of the Traditional Pursuit Agency, where much of his time was dedicated to protecting the Canadian fur trapping industry. He is currently the President of the Cree Trapper Association.

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Of reindeer and man, modern and Neanderthal: A creation story founded on a historic perspective on how to conserve wildlife, woodland caribou in particular

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Abstract: A review of successful systems of wildlife conservation, the North American included, suggests that broad public support and determined effort by volunteers is essential for wildlife conservation. Since North American wildlife conservation is the only large-scale system of sustainable natural resource use, and exemplifies the great economic and cultural benefits of a renewable resource held in common, its lessons may be profitably applied to Rangifer conservation. Animals that have value are surrounded by myths that tell of their relationship to humans. In our Anglo-American culture reindeer and caribou are rather deficient in this respect. However, reindeer feature prominently in the rise of modern humans and the demise of Neanderthal man early in the Upper Paleolithic. The colonization by humans of the periglacial environments during the last glaciation depended on the rich periglacial megafauna, Rangifer included. Archeological sites of the European Upper Paleolithic show that reindeer were the most important food source. The Upper Paleolithic, characterized by exceptional physical development and health of people, as well as by the first flowering of art, extended from Spain to Crimea with surprisingly little cultural change for some 25 000 years. While the cave paintings express an infatuation with dangerous game (woolly mammoth, woolly rhino, steppe wisent, giant deer, cave lions, bears etc), the archeological sites indicate that reindeer was the staple food. Reindeer play a minor role in cave art. Neither this art, nor archeological sites, show any evidence of warfare. It is hypothesized that during a mid-glacial interstadial modern people entered Europe having developed a highly successful system of hunting reindeer using interception based on the discovery of chronologic time. This led to a first flowering of culture based on a rich economy, but also to additional hunting mortality of the periglacial mega-herbivores that Neanderthal people depended on. That would explain the slow decline into extinction of the previously invincible Neanderthal people. Therefore, modern humans owe much of what they are to reindeer. We need to reciprocate. What is urgently required is a foundation formed by volunteers for the conservation of caribou, similar to the Rocky Mountain Elk Foundation, focusing on the severely endangered woodland caribou.

Key words: caribou conservation, cave art, extinction, megafauna, Rangifer tarandus, Upper Paleolithic.

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Successful conservation models

A review of the conservation of migratory caribou and reindeer (Rangifer tarandus) and its unquestionable successes, indicates that conservation of these animals follows the principles of successful conservation of other species. However, this only highlights the fact that, by contrast, woodland type caribou and reindeer, with the exception of Newfoundland caribou, have not prospered and that some unique populations are in imminent danger of extinction. As my basis of comparison I have used first the North American model of wildlife conservation that arose in the past 80 years, as it not only led to the return of wildlife continentally, but is remarkable in other ways as well. It shows how to hold and manage a renewable natural resource in public trust so as to defeat Garrett Hardin's Tragedy of the Commons (Hardin, 1968), that the resource is being used not merely in a sustainable fashion, but has expanded and multiplied, that a public resource can generate through the private sector remarkable wealth and employment, that some markets in wildlife actually do foster conservation, while others - in particular the sale of dead wildlife - are highly detrimental, and while wildlife conservation is linked to a broad-based public support, it is but a fragment of that public which supports wildlife substantially in return for the use of that resource. Put less delicately, wildlife has blossomed because hunters volunteered great effort and finances in order to see wildlife prosper (Geist, 1981; 1995; Geist et al., 2001). The following paper is thus a discourse on the much vaunted "human factors" in wildlife conservation.

Using the North American conservation model one can delineate the conditions for successful conservation, and in so doing discover that these appear to be universals. For conservation of a species to be successful there needs to be an organized, politically potent clientele promoting that species. That clientele is instrumental in generating systems to monitor and investigate said species, it fosters common belief about the species that stimulate, entertain and unify the clientele, it insures just and fair distribution of spoils generated by the resource, it functions in an open and democratic process that reinforces the clientele member's status, generates innovation, maintains and augments useful traditions, and enshrines and celebrates its successes symbolically. You may notice that these factors apply to such grass-roots conservation organizations as Ducks Unlimited, or The Rocky Mountain Elk Foundation, Foundation for North American Wild Sheep, the Wild Turkey Federation and others, but also to current societal structures - aboriginal and modern - that support migratory barren ground caribou in North America and migratory reindeer in Eurasia. There is the grass-roots clientele of hunters, users of caribou and reindeer that are most anxious to see these animals prosper. These users are organized to see that there is monitoring, research as well as open discussions of management, and the translation of their concerns into effective political action. Moreover, some of these users are not merely rationally or economically involved with reindeer or caribou, but have a deep emotional bond to these animals, maintain a tradition of myths and celebrate the culture that thrives about migratory Rangifer. These animals are thus far more than a source of livelihood or economics, but are a source of ongoing cultural identity, entertainment, education, the very societal glue of communities that hunt migratory caribou or reindeer. Formal gatherings to discuss Rangifer biology and management are an expression of this grass root concern and signify the importance this animal has to people living in arctic landscape

While the above is valid for migratory caribou and reindeer, it is not for most forest or woodland forms, be they Eurasian or North American. The woodland forms are the usually large-bodied races on the southern rim of Rangifer's continental distribution here and in Asia. The societal factors that do apply to elk (*Cervus elaphus canadensis*) via the Rocky Mountain Elk Foundation or to mountain sheep (*Ovis dalli*, *Ovis canadensis*) via the Foundation for North American Wild Sheep, have no counter part for woodland caribou. Why are elk so captivating to so many persons, but woodland caribou are not? Is it the scenic splendor of mountains which frames elk, as opposed to gloomy tamarack and black spruce bogs that hide woodland caribou, as my son Karl, a wildlife artist, suggests? Is it that herds of migratory caribou pouring across the television screen obliterate concern for the dying woodland forms? It is significant in this context that elk or mountain sheep have little role in the livelihood of most members of the respective elk and sheep conservation organization. Yet there is much passion for these animals, even by those that have little hope, if any, of someday hunting elk or sheep. Instead, members celebrate their identity with other like-minded via well-attended meetings to raise funds for conservation, share journals and news letters, support arts and crafts symbolizing elk and sheep, weave together tall tales of shared experiences and become active politically in diverse ways. In a recent book the Foundation for North American Wild Sheep and the Boone & Crockett Club celebrated a quarter century of success in mountain sheep conservation, in which wild sheep populations across North America increased by nearly 50 percent (Toweill & Geist, 1999).

Please note this success is based on private effort without recourse to coercive or punitive legislation. It was done without noticeable national or international publicity or public incitement, in short, quite different from activities associated with conventional environmental movements. Yet these quiet private efforts were eminently successful as seen by the increase in distribution and numbers of elk and wild sheep. Could this be duplicated for woodland caribou? There are no clubs organized to specifically rehabilitate woodland caribou in mainland North America, although the Newfoundland caribou, a colorful woodland form by convergence, is thriving. It does so due to the dedicated support of Newfoundland's citizen. The Newfoundland caribou is a subspecies quite distinct in pelage characteristics from other caribou. Put in other words: placing woodland caribou on an endangered species list might have some benefits, but having an organized citizen group root aggressively for woodland caribou would be much better.

Pitfalls in caribou taxonomy

A brief excursion into caribou taxonomy is essential at this point. The common term Woodland Caribou encompasses a collection of diverse boreal forest (taiga) and mountain-welling caribou, as, unfortunately does the taxonomic name Rangifer tarandus caribou Gmelin 1788, as used by Banfield (1961). The common and scientific name have been applied not only to the usually large, dark caribou with minimal display coat markings and their diagnostic short antlers, but also to sedentary populations of barren-ground caribou (R. t. groenlandicus Linnaeus 1767) that happen to have achieved large body size, to the colorful Newfoundland caribou (R. t. terraenovae Bangs 1896), to the migratory Labrador caribou (R. t. caboti Allen 1914), and to the big Osborn's caribou (R. t. osborni Allen 1902) of north-western British Columbia . Banfield (1961) lumped caribou of the same skull length into the same subspecies (see Geist, 1998: 319-326). If one confines the terms Woodland caribou or R. t. caribou to just the dark, southern form with its diagnostic pelage and antler form, then one realizes how few Woodland Caribou are left and how critical it is to find ways to uphold their numbers. In Eurasia three subspecies have at least some woodland characteristics, the European forest reindeer R. t. fennicus Lonnberg 1909, the Siberian forest reindeer R. t. valentinae Flerov 1933 and the far-eastern Okhotsk reindeer R. t. phylarchus Hollister 1912, which, judging from its nuptial coat, is a true caribou and not a reindeer (Heptner et al., 1988; Geist, 1998: 326-328).

Modern man and reindeer: A modern creation story

Essential to conservation are positive myths that celebrate the animal. What positive myths exist in general in North America about caribou? Rudolf the Red-Nosed Reindeer and his fellow reindeer pulling Santa's sleigh at Christmas time, comes closest. However, even here there is erosion. Quite often one sees today white-tailed deer (Odocoileus virginianus), antlered "Bambies", replace the reindeer. White-tailed deer with their smaller, more-baby-like faces and big eyes have become, increasingly, the symbolic deer of North America and even Europe (Geist, 2001). We have considerable mythology about horses, dogs, cats - even pigs! Currently, there is little mythology or public knowledge about caribou and reindeer, excepting in aboriginal and northern communities that depend on caribou for sustenance. There is little celebration of caribou or reindeer in arts and crafts, as there is of elk, deer or even mountain sheep. There are but a few songs, poems or popular books dedicated to caribou or reindeer and even such are invariably about the migratory barren ground forms (Calef, 1981; Russell, 1998). There are no annual conventions dedicated to caribou that draw thousands of urban-based lay persons for attendance as is the case for elk, mountain sheep or turkeys.

Excepting northern communities, North American society does not celebrate caribou or reindeer. However, we ought to! The reindeer may well have been the very best friend we ever had, and even more noteworthy, reindeer may have been essential to the rise and success of modern humans. Without reindeer Neanderthal might still be alive and well in Europe and modern culture may have never arisen. Buried deep in the studies of diverse scholarly disciplines are data and insights that show just how important the Eurasian version of caribou, the reindeer, once was to us in our struggle to survive and thrive. It happened during a critical formative period of modern humans, during the early Upper Paleolithic, late in the Pleistocene, when we gained the upper hand and displaced the once invincible Neanderthal man. Yet there is no evidence for warfare. Neanderthal people faded slowly into extinction over many millennia, just as we only slowly colonized all of ice age Europe. Reindeer appear to be the key-species that made our ascent possible and shaped us towards creating the modern world we live in. It's a tale based on interdigitating caribou biology with periglacial ecology and archeology.

An enlightened veterinarian once quipped that a perfectly balanced ration for a cat, was a mouse. What, one may ask, might it be for humans? Despite the popular "out of Africa hypothesis" of human origin, the answer appears to be a reindeer or caribou. Reindeer, are not merely the staple food of people living in cold circumpolar climates, but were the chief food of the European Upper Paleolithic (Bouchud, 1975; David, 1985; see Geist, 1998: 335-336). That is, the aboriginal Ice Age ancestors of Europeans were tied closely to a food economy dominated by reindeer, and that for some 30 000 years during the latter half of the last, the Würm Glaciation. Reindeer are thus not only "in the genes" of northern Europeans, Asians and North Americans, but very much "in the genes" of all those who descended from the Eurasian Cro-magnid populations of the late Pleistocene. The following is based on my book (Geist, 1978) and on an excellent summary article on Neanderthal man in Der Spiegel (Schult, 2000), unless otherwise cited.

The Upper Paleolithic was a crucial and remarkable period of both, human history and evolution. Here people reached a degree of luxurious physical development unequaled since. It was a period of great cultural activity as well as stability over a huge geographic area, as reflected in the nature of its vibrant art and artifacts, and in the lack of evidence for warfare (in sharp contrast to the following Mesolithic and subsequent periods). There were many unique attributes: for instance, we expect colonizing populations of large mammals exploiting virgin habitats to grow into luxury phenotypes. That is, normally, a passing phenomenon, because with population growth and the occupation of available habitat, body size soon shrinks, as resources are reduced by intra-specific competition. However, humans in the Upper Paleolithic appear to be exempt from that rule. They show superlative physical development not only when they enter Europe about 40 000 years ago, but for millennia after millennia till the close of the glacial period about 12 000 years ago. Not only are individuals tall, with rugged athletic bodies and bones free of diseases, but they also achieve brain sizes about a quarter greater than ours. Brain size in large mammals tends to shrink with domestication and poor nutrition.

The Upper Paleolithic was the first age of Art flourishing as evidenced by cave paintings, carvings, sculptures and decorations of clothing and self. It displayed in the Venus Cult a conspicuous focus on woman as expressed in carvings, personal adornments, cave sculptures and pebble art. There is nothing remotely comparable in earlier cultures or in contemporary Neanderthal artifacts. Music, as an idea, was already developed as evidenced by bone flutes and whistles, and so was apparently symbolism, as evidenced by abstract signs that accompany Upper Paleolithic cave art.

We can decipher some of that culture by applying our modern knowledge of how to grow large, athletic human bodies. Some of that is found not in anthropology, but in Animal Science, an agricultural discipline which focuses on how to manipulate the growth of live stock environmentally. Their findings reflect also on human biology. The athletic bodies, but above all the large cortex of the brain indicate a luxurious ontogenetic development, luxurious not only in food, but in conditions that had to be deliberately maintained in order that children might achieve the physical development they did. Out of necessity, the focus had to be on generating conditions fostering motherhood, from before conception towards - and that's crucial - a long lactation period to support the child's growth. This must have been followed by an ontogeny made deliberately rich in physical and intellectual activity. Since lactation is here a critical factor, every effort had to be applied to keep mothers in a contented state, as stress quickly terminates milk production. The emphasis on highly developed bodies and brains can only be achieved by a conspicuous manipulation of reproduction, with a knowledgeable emphasis on individual development and welfare. Excellent physical and mental development was probably a precondition for the demanding athletic and intellectual challenges mastered routinely by our ice age ancestors. The Venus Cult appears a logical outgrowth of extreme concern about the state of female partners, in the demanding role of giving birth and nurturing children of high physical and intellectual abilities, and this insured the continuity of the tribe under very hard living conditions. Emphasis was thus on individuals as irreplaceable, precious carriers of tribal life, not on massive reproduction - as in agricultural cultures, which by necessity are linked to warfare and high mortality. In the Upper Paleolithic attention was heaped on an individual to foster its abilities, not on maximizing tribal numbers. However, with great value placed on each individual, warfare becomes unthinkable - particularly against physically superior neighbors such as Neanderthal man.

Cave art shows us some of these demands, namely, mastery with primitive weapons over large, powerful, intelligent creatures that populated the late Pleistocene megafauna. Cave art is a record of achievements, occasional bragging (Geist, 1978: 322-323; Guthrie, 1999). There is infatuation with the megafauna and dangerous hunts, but no evidence of bragging about warfare. Meanwhile, the bulk of the food came from reindeer.

Moreover, our modern Cro-magnoid ancestors did not appear within a landscape unoccupied by humans, quite the contrary. They appeared in Europe despite the presence of Neanderthal people. They slowly, ever so slowly replaced Neanderthal people as these shrank in distribution over some five to seven millennia and went finally extinct about 28 000 years ago. There is no evidence that the "take over" by Cro-magnoids was hostile, as there is no evidence for warfare, neither in the archeological record nor in the copious, expressive cave art. Overlap of Neanderthal's Mousterian and Cro-Magnon's Upper Paleolithic artifacts are exceptional. Neanderthal and Cro-Magnon remained segregated. This displacement of Neanderthal man is most remarkable, as in earlier millennia Neanderthal dominated modern people and displaced them as well as confined them geographically. Thus at the beginning of the last, the Würm glaciation, about 80 000 years ago, Mousterian tool kits replace pre-Aurignacian tool kits in the Mediterranean basin. In short, Neanderthal replaces us and confines us in North Africa. However, at the first glacial maximum about 60 000 BP and maximum desertification in Africa, modern people skirted around Neanderthal to the south and east and break out through the Levant, the eastern Mediterranean, to colonize southern Asia and Australia. That left Neanderthal in control of Europe for as long as glacial conditions lasted. During glaciations Neanderthal appeared invincible.

However, a long interstadial erupted about 40 000 years BP, which marked the entrance of modern people into Europe - despite Neanderthal. The onset of interstadial or interglacial conditions is a very difficult time for humans. Neanderthal would have been affected. While this interstadial ebbed and flowed modern people formed a wedge between the continental ice sheath to the north, and the alpine glaciers to the south. This wedge of modern people slowly expanded west and south, and Neanderthal slowly shrank in distribution around mountain ranges, and finally suffered extinction. This left modern humans as the sole occupants of Europe with the return to full glacial conditions in the second half of the Würm Glaciation.

Neanderthal man was very different from us. When placing the idiosyncrasies of its morphology into the ecology and behavior of its preferred prey, the largest-bodied as well as the hairiest of the periglacial megafauna, then it appears the Neanderthal hunted in a unique and dangerous way. He specialized in close-quarter confrontation hunting, in which only two hunters needed to cooperate. Parasitizing its prey's proclivity to confront predators, hunter A lures the prey into an attack. Hunter B attaches himself to the prey's hair distracting it from A. While B hangs onto the bucking, whirling beast, hunter A kills the prey with hand-held weapons (Geist, 1978; 1981). This hypothesis explains not only much of the characteristic morphology of Neanderthal, but also of its weapon, its frequent bone breakages and its pattern of bone breakages, which followed that of rodeo cowboys. Neanderthal men had to be enormously strong, quick, exceedingly agile and utterly death-defiant, but also very kind, generous and caring to companions to allow recovery from bone breakages. Moreover, during the early Würm Glaciation Neanderthal man changes progressively, enhancing its anatomical characteristic. That suggests that its mode of hunting selected severely for highly competent confrontation hunters. This would indicate, for instance, that hybridization with modern people was unlikely, as it lowered crucial physical abilities in the hybrid, making it impossible for it to safely match the hunting abilities of pure Neanderthal men. Hybrids would lead short lives and be poor providers. Archeological evidence suggests that Neanderthal People dismembered large prey and probably froze or buried it in large chunks. Confrontation hunting paid off, in that it minimized the need for dangerous hunting, by producing large masses of meat from large prey at set periods. Neanderthal probably lived from kill to kill. However, that must have limited Neanderthal man to the best existing wintering areas of the megafauna where prey densities were sufficient to insure living from kill to kill. Neanderthal people apparently lived at much lower density than did Cro-Magnon people, as well as in smaller social groups.

How can one account for this gradual displacement of Neanderthal by Cro-Magnon people, as well as for the superlative physical development of Cromagnoids, despite competition by Neanderthal people for the wildlife resources of Europe? One can make a case that the reindeer played a key role in the explanation. Without reindeer, Neanderthal would probably be still around and there would probably have been no remarkable Upper Paleolithic, and probably no modern world.

Reindeer are central to explaining how modern man displaced Neanderthal man without the need for overt warfare. Reindeer and caribou are favored by interglacial conditions when tundra and alpine plant communities expand at the expense of periglacial loess-steppe, which shrinks in response to glacial withdrawal. As the loess-steppe shrinks, so does its associated megafauna of large grazers, such as mammoth (Mammuthus primigenius), rhino (Coelodonta antiqutatis), bison (Bison priscuis), horses (Equus przewalskii) and giant deer (Megaloceros giganteus). That is, the primary food of Neanderthal man, the mega-herbivores of the periglacial loess steppes, shrinks in abundance and geographic distribution. However, reindeer become more abundant.

Cro-Magnon had developed a new way to harvest reindeer. These were taken in interception hunts, killed in excess, and the excess converted into stored foods. The ability to intercept reindeer depended on linking reindeer migrations to chronologic time. Such is apparently expressed in lunar calendars, as were carried about in the form of the "baton de commandement" from reindeer antlers (Marshack, 1972). The discovery and use of chronologic time was an enormous innovation, which was probably derived from two sources: (1) an ancient origin of modern-type people in the deserts of North Africa, and therefore exposure and challenges of clear night skies, inviting observation. Modern people arise from archaic populations during the enormous Penultimate or Riss glaciations beginning about 225 000 years ago, a glaciation that during its maxima must have turned most of Africa into a desert. (2) Interstadials bring some deglaciation and thus the rise of ocean shore-lines above the continental shelves, creating large expanses of shallow, productive seas. This would lead to coastal boat technology and a general need for navigation. Given the ability to keep calendar-time chronologically, one can apply such to predicting reindeer migrations, as such move by chronologic time. Given the ability to predict reindeer migrations, one can plan ahead, kill in excess of current need and conserve the rest for future use.

This requires the ability to conserve meat and fat. Many Upper Paleolithic sites appear to be meat-processing sites. These are characterized by large accumulations of small, thin blades, such as would be required carving meat thinly in order to dry and smoke it. Cro-magnoids, as already noted, appear to have their origins in deserts. They were, therefore, students of the movements of heavenly bodies, as well as the conservation of food through desiccation, long before they settled in the rich, periglacial regions of glacial Europe. These technical innovations probably led to their domination of Neanderthal despite the latter's superior strength, agility and speed.

Being able to kill an excess of reindeer, and thereby securing adequate food for the long term, Cro-magnoids were free to indulge in recreation and fancies. One of these was to hunt truly dangerous game. In short, while they ate reindeer, they dreamt of challenging woolly mammoth, woolly rhino, bison, bears (*Ursus arctos*), lions (*Panthera leo*), giant stags etc. Migratory tundra reindeer were clearly identified as such by the archeological record, and by reindeer images in cave art. Other smaller-bodied hoofed mammals were also taken, ibex (*Capra ibex*) and chamois (*Rupicapra rubicapra*) in colder climatic periods, red deer (*Cervus elaphus*), aurochs (*Bos primigenius*) and horses in warmer periods. However, cave art suggests that hunters were dreaming of much more dangerous, demanding game. With their food secured they were free to hunt the remnants of the periglacial megafauna - that Neanderthal probably depended on.

With the coming of Cro-Magnon people to Europe about 40 000 years ago, woolly mammoth and the giant deer decreased in abundance and eventually went extinct (Lister, 1994; 1995). Both had co-existed with Neanderthal man for tens of thousands of years as one of its prey species. If Cro-Magnon as well as Neanderthal man made inroads into the populations of the slow-to-reproduce megafauna, at a period when this fauna was declining due to a warming climate, then it would push Neanderthal increasingly towards the mountain fronts where the alpine glaciers there. Right up against the glacial fronts were the winter ranges of the megafauna as illustrated today by the periglacial ecology of caribou in Greenland (Meldgaard, 1986). Cold temperatures at the glacial front insure powdery snow throughout winter, snow soft enough to be scraped from forage. During warm cycles much of the winter forage, except at the glacial fronts, may be iced over by sudden melts and becomes unavailable to wintering mega-herbivores. We expect their populations to decline. It is thus likely that while reindeer were the staple food of the Upper Paleolithic, it allowed modern hunters to focus on more glamorous, but declining species (giant deer, mammoth, woolly rhino, steppe bison, horses) and deplete them further, essentially robbing Neanderthal people of their food supply.

The above is currently a mere hypothesis, but a hopeful one. New findings might disprove or support it. In the meantime it may serve as an example of how a wildlife species may gain relevance for a broader public. Without reindeer, human history in Eurasia would have been very different. Neanderthal people might have survived and we might not be here.

Where do we go?

Our history shows two principle approaches to wildlife conservation, a monopolistic one and a populist one. In the former a small group within society holds exclusive rights to some of the wildlife resource from which it draws benefits and which it in turn protects and fosters. The populist model, however, makes all citizens *de facto* owner of the resource, and these delegate management authority through their political leadership. The monopolistic model was most common in the history of wildlife in Europe, and entailed the exclusive right to wildlife by an elite. This model informs us that exclusive monopolies over wildlife lead to severe repercussions by the excluded, and to a public dislike of wildlife, which in Europe has never been eliminated. The monopolistic model, but in limited form, has also a history in North America, such as the Hudson's Bay monopoly on beavers, or the division of a landscape into exclusive trapping or guiding territories, as practiced in British Columbia (Ball, 1985). The best example of the populist model is the modern system of wildlife conservation in North America (Geist, 1995; Geist et al., 2001). It is an exceedingly successful model which in less than a century returned wildlife to North America from the edge of extinction. It is similar to the native model of moose (*Alces alces*) management among Labrador Cree. It is this model which has pregnant lessons for all management of natural resources, woodland caribou included.

What can one learn form history? One learns that caribou conservation thrives by a broad, but organized public support. Currently, caribou do not enjoy the support or attention that elk, deer, wild sheep, turkeys and grouse have over much of this continent. Only migratory caribou and reindeer in the north enjoy great local support, but this does not extend to the declining remnants of the woodland forms, here and in Eurasia. It is admirable to have meetings such as we have here with a strong mix of native stakeholders, managers and scientists. However, it is imperative to reach beyond and make caribou relevant continentally and vivid stories why caribou and reindeer are important to us are relevant in this context. There is need for a broadly based Caribou Foundation that can act effectively in the political arena - irrespective of endangered species legislation. In particular we need a foundation for the endangered woodland caribou and reindeer. The larger question being is how to make this happen.

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Effectiveness of spatial mitigation for the George River Caribou Herd within the military training area of Labrador and Québec

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Abstract: The George River Caribou (Rangifer tarandus) Herd (GRCH) regularly migrates through the military Low Level Training Area (LLTA) used for jet training out of 5 Wing Goose Bay, Labrador. Potential disturbance to caribou by military aircraft has been mitigated through the reconfiguration of the LLTA in 1996 away from the traditional migration routes and the establishment of closure areas based on the locations of ≥20 adults fitted with satellite telemetry collars. In 2000 and 2001, we conducted seven aerial surveys to examine the caribou distribution and abundance within the northern portion and adjacent area of the LLTA during post-calving, summer dispersal, pre-rut and late winter. We flew transects to examine approximately 10% of areas traditionally used during each period. The timing and direction of caribou movements through this region were similar to that observed in the 1990s. Collared caribou were a good indicator of movements of the GRCH through the LLTA. Closure areas based on the location of satellite collars and direction of movement, were found to enclose the majority of caribou observed within the LLTA. Most GRCH activity now occurs outside the LLTA as a result of reconfiguration.

Key words: habitat, Labrador, Nunavik, population ecology, range fidelity, Rangifer tarandus, spatial, telemetry.

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Introduction

Areas of critical importance to the George River Caribou Herd (GRCH) have been identified within the boundaries of the area originally proposed for the Low Level Training Area (LLTA) out of 5 Wing Goose Bay (DND, 1994; RRCS, 1995; Harrington, 1996). The GRCH migrated through the former LLTA during the summer and early fall periods for calving, post-calving and the rut. Aerial surveys by the Department of National Defence (DND) reported large aggregations (100 000 or more in one year) within the previous LLTA in 1990 and 1991 (RRCS, 1992). Wetland and other open areas characteristic of these areas of occupation, are important habitats providing forage for lactating females and growing calves and/or relief from biting insects during this period (Crête et al., 1990; Walsh et al., 1992). Consequently, the GRCH was identified by the Department of National Defence as a Valued Ecosystem Component in the Environmental Impact Statement (EIS) on Military Flying Activities in Labrador and Quebec (DND, 1994). Following an extensive public review, DND proposed a mitigation program to address potential impacts on the GRCH.

Mitigation is based on spatial separation of military training aircraft from caribou within the LLTA. Since migrating caribou may continue to occupy the current LLTA during the flight training season, DND reconfigured the boundaries of the LLTA in 1996 away from areas frequented by the GRCH during most of the April through October training period. A second initiative was to implement an annual monitoring program of satellite collared caribou to indicate herd movements and distribution (Table 1). Locations from at least 20 satellite-collared female caribou are received at 5 Wing Goose Bay every four

Table 1. DND (1994) avoidance criteria for the GRCH (Revised February 1999).

Seasonal Sensitivity	Occupancy Sub-Criteria	Closure Sub-Criteria
High Sensitivity		
Calving (15-30 June) Post-calving (1 July-10 August) Rut (10 October-15 November)	Area based on 20 (15-30 June) telemetry collar sample; or sighting a group of 500 animals	Circular closure radius of 36.1 km centred on collar or group
Moderate Sensitivity		
Summer dispersal(11-30 August) Pre-Rut (1 September-10 October) Late Winter (1 March-15 May)	As above	Circular closure with radius of 27.8 km centred on collar or group
Low Sensitivity		
Early winter/winter (16 November-28 February)	As above	Circular closure with radius of 18.5 km centred on collar or group

to five days following signal emission from Provincial wildlife agencies in Labrador and Québec respectively. New locations for the delineation of successive closures were obtained less than three days apart. Individual satellite collared caribou closures often overlapped so caribou rarely moved outside a closure prior to the reception of new data. Only locations with class >0 (Service Argos, Landover, MD, U.S.) are used to determine closures. Avoidance criteria for closures of the GRCH vary according to seasonal sensitivity, speed and direction of the collared animals, and consider activity observed in previous years of monitoring.

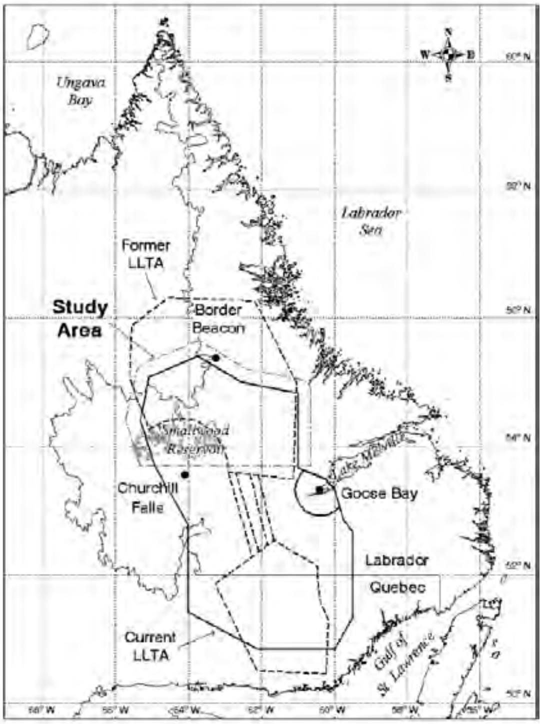

Fig. 1. Location of the former and current LLTA in relation to the study area.

The objective of this study was to compare aerial transect survey information on the distribution and abundance of caribou with the closures around the >20 satellite collars to evaluate the effectiveness of the current mitigation program.

Methods

Aerial surveys were conducted to examine caribou densities within the northern portion of the current LLTA and an adjacent 18.5 km (10 nautical mile) area (approximately 53 220 km^2) (Fig. 1). Surveys were conducted during post-calving (10-16 July 2000, 25-27 July 2001 and 5-6 August 2001), summer dispersal (14-17 August 2000 and 26-29 August 2000), pre-rut (13-18 September 2000) and late winter (11-15 April 2001). Approximately 30% of the study area is forested. Large water bodies and wetlands are common with the remainder of the study area generally open habitat. Detailed descriptions of habitat preferences of the GRCH in general can be found in Crête et al. (1990) and Camps & Linders, (1989).

The study area was divided into two areas of predominant habitat type: open barrens and mature black spruce forest. Survey crews comprised of the pilot plus three observers searched an area approximately 400 m and 500 m wide (on each side of the aircraft) in forested and barren habitats, respectively.

The size of search area varied because it was assumed that caribou sightability would be greater in open areas versus forested habitat types.

Surveys were completed using a Partenavia P68C High Wing twin engine aircraft at a speed of 100 knots and an altitude of approximately 120 m above ground level. The surveys followed north south transects spaced 10 km apart, starting in the east and working westward. Approximately six transects were completed each day. Occasionally, transect spacing was modified (greater spacing in the eastern half, closer spacing in the west) to provide more intensive coverage of that portion of the study area where caribou were more often encountered. Flight tracks and observations were recorded using a Global Positioning System, 1:250 000 National Topographic System maps, and data sheets.

Caribou observations included group size, general sex and age composition and direction of movement. Surveys were completed only during weather conditions that allowed for >500 m visibility from the aircraft. Locations of satellite-collared animals were used to define search areas but not used to locate caribou groups. The approach was not designed to compare animal density or distribution between successive years but to obtain information on the GRCH during the annual cycle when they migrated through the LLTA. Timing and migration patterns of the GRCH may fluctuate annually (Crête et al., 1996; Morneau & Payette, 2000).

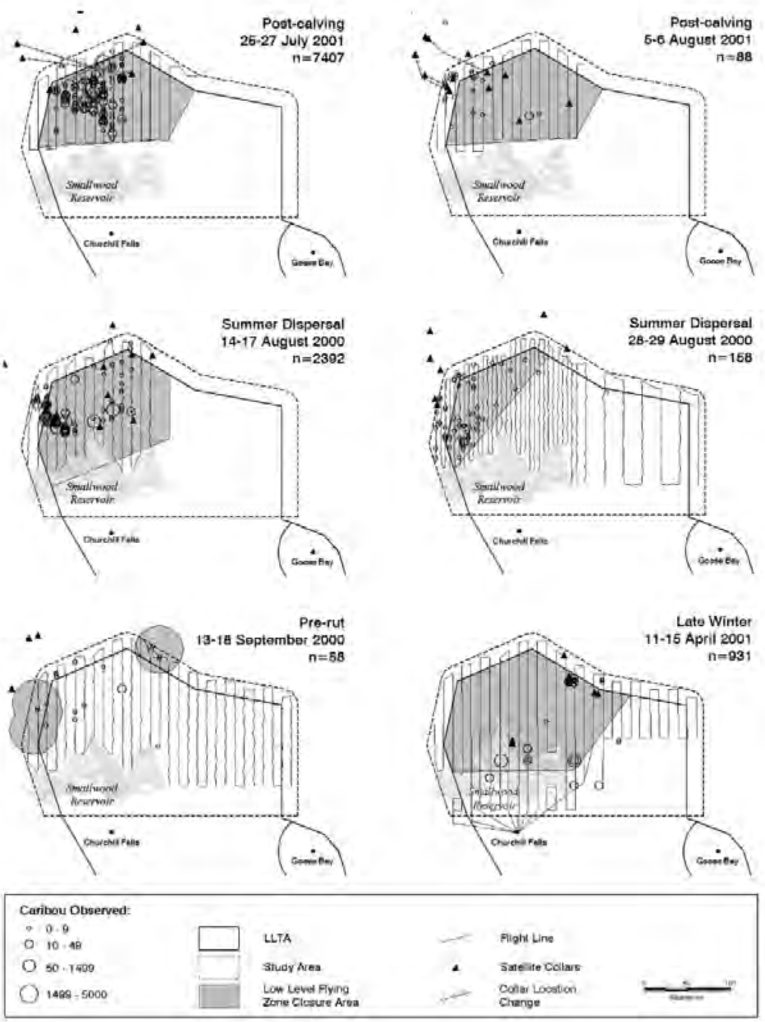

Fig. 2. Caribou observations during aerial surveys in the study area and LLTA during 2000 and 2001.

Results

We conducted seven aerial surveys: four in 2000, three in 2001 (Fig. 2). The results are presented for distribution and abundance and for group size during post-calving, summer dispersal, pre-rut, and late winter periods in the LLTA and entire study area (Table 2).

Distribution and Abundance

A total of 11 037 caribou were observed during all surveys (2611 in 2000 and 8426 in 2001) (Table 2). In 2001, 8295 animals were observed concentrated north of Smallwood Reservoir during the two post-calving surveys. During the summer dispersal surveys in both years all caribou were observed north and north west of Smallwood Reservoir. A similar pattern was observed during the pre-rut survey in 2000. During the late winter survey in April 2001, 931 observed animals were concentrated in the Smallwood Reservoir area and to the east of the Reservoir. The number of satellite collared animals within the study area (i.e., 8) was greatest during the 14-17 August 2000, and 5-6 August 2001, surveys.

Table 2. Number, group size and density of caribou observed during aerial surveys in 2000 and 2001 and number of satellite-collared animals in the study area.

Survey Dates	# Caribou (# groups)	Average Group Size (range)	# of individual caribou[1] (% overall)	Area Searched km² (%)	Density (Caribou /km²)	Collars in Study Area
10-16 Jul 2000	3 (2)	1.5 (1-2)	1 (33.3%)	1124 (9.4)	0.005	0
25-27 Jul 2001	7407 (194)	38.2 (1-4 000)	21 (0.3%)			3
5-6 Aug 2001	88 (22)	4.0 (1-15)	4 (4.5%)			82
14-17 Aug 2000	2392 (91)	26.3 (1-1 200)	18 (0.8%)	1162 (9.7)	2.06	8
26-29 Aug 2000	158 (65)	2.4 (1-10)	27 (17.1%)	2201 (18.4)	0.07	22
13-18 Sep 2000	58 (18)	3.2 (1-14)	7 (12.1%)	1124 (9.4)	0.05	0
11-15 Apr 2001	931 (47)	19.8 (1-500)	3 (0.3%)			0
Totals 2000	2611	8.7 (1-1 200)	58 (2.2%)	-	-	-
Totals 2001	8426	20.6 (1-4 000)	28 (0.3%)	-	-	-

[1] number of sightings of lone caribou.

[2] one additional collar was within 5 km of study area.

Post-calving Surveys

Only three caribou were observed during the 10-16 July 2000 survey. No collared animals were identified within the study area during this survey and therefore no closure areas to military training were established.

During the 25-27 July 2001 post-calving survey, the largest group of caribou observed (4000 animals) was located approximately 60 km north of Smallwood Reservoir. Other concentrations of 800 to 1200 animals were sighted to the north and west of the larger group with numerous smaller groups (<50 animals) scattered in the area between Smallwood Reservoir and the northern boundary of the study area (Fig. 2). The closure area placed around the three collared animals within the LLTA encompassed the main concentration of caribou with a conservative buffer from training activity.

The post-calving survey in August 2001 found 88 animals in study area with the distribution pattern similar to that observed during the July 2001 survey (Fig. 2). Although a relatively low number of animals was observed during this survey and the aggregations were small, eight satellite-collared animals were present in the survey area albeit moving rapidly in a north west direction. At least three of these animals had probably moved outside the LLTA boundary (based on subsequent satellite information) by the time that area was surveyed (Fig. 2). The closure area established the previous month remained in effect, although numerous fresh tracks and trails indicated most caribou had departed the LLTA.

Summer Dispersal Surveys

The summer dispersal survey on 14-17 August 2000 recorded 2392 animals, the largest number of caribou observed during surveys that year. The distribution and movement of caribou was remarkably similar to the activity observed in 2001. All animals were north and north west of Smallwood Reservoir. The largest aggregation was north west of Smallwood Reservoir where 2100 caribou were observed (Fig. 2). It was learned later that eight satellite-collared animals were present in the north west portion of the study area during this survey. At least three additional collared caribou were within 50 km of the study area. Again the closure area encompassed the caribou migration through the LLTA.

Although the distribution of animals was similar to the first summer dispersal survey in 2000, groups of caribou were smaller and more dispersed on the second survey 26-29 August. Most groups (totalling 158 animals) were west and north west of Smallwood Reservoir (Fig. 2). Remaining caribou were west of Border Beacon. Two collared animals were at the northern and western boundary of the study area with four others immediately outside LLTA. The closure area had been revised to reflect the rapid movement of animals towards the northwest. A survey of the entire study area indicated that less than 10 caribou were outside the closure area.

Pre-rut Survey

During the pre-rut survey 13-18 September 2000, small groups of caribou were widely dispersed over the area between Smallwood Reservoir and the northern boundary of the study area (Fig. 2). No collared animals were located within the study area at the time of the survey although three were recorded 35 km north west of the study area. The survey of the entire study area indicated that closure areas at the periphery of the LLTA, encompassed all but approximately 30 animals in the LLTA.

Late Winter Survey

During the late winter survey 11-12 and 15 April 2001, the largest concentration of animals occurred in the area of Smallwood Reservoir and directly east of the Reservoir (Fig. 2). Several groups of <50 animals were also observed approximately 90 km north east of the Reservoir, near the study area boundary. Four collared animals were located within the study area at the time of the survey resulting in a large closure area prior to the start of the flying season.

Group Size, Composition and Density

A total of 438 groups were recorded during the seven surveys, with group size ranging from 1 to 4000 animals (Table 2), average group size was 25.1 animals. Limited data were collected on sex and age of observed caribou. However, groups observed tended to be dispersing females with calves and no large groups of males were observed, including the pre-rut period. Based on observations of animals and fresh tracks, caribou tended to use an area comprising approximately 11 940 km^2 in the north west of the study area during the seven surveys. Extrapolating the results of the area searched (based on 400 and 500 m search patterns on either side of the aircraft), estimates indicated that a density of 2.06 caribou/km^2 or as many as 24 584 caribou may have been present in this portion of the study area during Survey 2 (Table 2). These values are extrapolated without consideration of correction factors (for observer error) or adjustments for water bodies and other potentially unused sections of this area.

Movement

Caribou trails and their general orientation were recorded during the surveys. Trails were more numerous and better defined in the western half of the LLTA than in the eastern portion. During late July and early August of both years, caribou entered the LLTA from the north in the vicinity of Border Beacon, and departed to the northwest. The most common orientation of trails were west to east in the central-western portion, and north to south in the northwestern part of the LLTA. Older trails were noted as well, in a similar orientation.

Discussion

The results of this study to date are compared with earlier studies reporting on GRCH distribution, abundance, and group size and composition, during post-calving, summer dispersal, pre-rut, and late winter periods in the study area and LLTA. General habitat use and movement trends are also discussed.

Distribution and Abundance

Post-calving

Satellite telemetry data have confirmed that the calving range for the GRCH is outside of the current (since 1996) LLTA (Schaefer et al., 2000). However, post-calving animals begin moving in a northeasterly, southwesterly or northwesterly direction as they disperse from the calving range. Those animals moving southwest could be present in, or pass through, the northwest portion of the LLTA. Composite mapping of the seasonal distribution of 68 adult female caribou between 1987 and 1996 indicates the presence of collared animals inside the current LLTA during the post-calving period (DFRA, 1997). A review of RRCS (1992) indicates that out of the large number of caribou present in the former LLTA in July 1991, approximately 10 000 to 12 000 animals would have been inside the western boundary of the current LLTA.

Only three caribou were observed during the 2000 post-calving survey. As no collared caribou were located within the LLTA or adjacent area at that time, it was believed the post-calving movement had not yet reached the LLTA. The observed animals may have been part of the Red Wine Mountains Caribou Herd (Schaefer et al., 1999). In the first 2001 post-calving survey, conducted approximately two weeks later than the 2000 survey, over 7000 animals were observed in the north western portion of the LLTA. During the second 2001 post-calving survey 10 days later, the number of animals observed in the north western portion of the LLTA had declined to 88, possibly indicating a 2-3 week window in late July when aggregations of caribou move through this area.

Three collared caribou were in the LLTA at the time of the July 2001 survey when the largest aggregations (i.e., 4000, 1200, or 800 caribou) were observed. However, because of the buffer zone placed around each collared animal, closure zones encompassed the majority of animals in the study area. As noted earlier, several collared animals in the north western portion of the LLTA during the 5-6 August 2001 survey period, moved directly out of the LLTA in a north westerly direction, possibly indicating the onset of summer dispersal.

Summer Dispersal

Consistent with the findings of earlier studies (DFRA, 1997; Messier, 1992) caribou were common in the north west portion of the LLTA during late August. Ten collared animals were present in the area during the 14-17 Aug 2000 survey while all collared animals were either on the boundary of the LLTA or beyond, during the 26-29 August survey.

Pre-Rut

The results of the September 2000 survey were consistent with the results of earlier studies in that small groups of caribou were present in the north west portion of the LLTA, and collared animals were present outside the boundary.

Late Winter

Descriptions of range use by female GRCH over a 12-year period (1986-1998), indicate that during Mar and Apr the probability of female caribou occurring in the study area is generally low (Bergman, 1998). VHF-radio tracking from 1982 through 1991 indicates a similar pattern with most collar locations during Mar and Apr located north or north east of the study area (Messier, 1992). The results of the 2001 survey support these trends in that less than 1000 caribou were observed in the study area, suggesting that while some caribou of the GRCH winter in this area, the main herd appears to winter outside. No collared animals were located in the LLTA during the late winter survey period, a further indication that caribou numbers in the study area were not high at this time.

Group Size and Composition

RRCS (1993) observed that collared caribou were associated with larger aggregations during late calving, post-calving, and during the rut. A post-calving photo-census in 1993 indicated caribou were the most aggregated at that time (Russell et al., 1996). The smallest groups occurred during pre-calving, August dispersal, and during pre-rut.

Post-calving

After leaving the calving grounds, females and calves rejoin yearlings, barren females and males to form post-calving aggregations as they disperse toward summer range. These groups may be large. In the 1990s, the largest group reported for the current LLTA was 2000 animals in the northwestern portion of the area (RRCS, 1992). The largest group observed during the two years of post-calving surveys, was an aggregation of 4000 caribou during 25-27 July 2001.

Summer Dispersal

The second (26-29 August) summer dispersal survey in 2000 recorded small group sizes and a larger percentage of individual animals (Table 2) compared to earlier summer dispersal studies of the GRCH. The first survey (14-17 August) results were more typical.

Pre-Rut

During this period, caribou that had been part of the post-calving aggregations (both sexes and all age classes) began to come together in preparation for the move toward the rutting range (Skoog, 1968). Although larger groups may form, the number of single animals may remain relatively high. The survey of 13-18 September 2000, indicated that group size was larger than recorded on the second summer dispersal survey, and the percentage of individual animals had decreased.

Habitat

Relief from insect harassment is a primary determinant for summer range as animals spend less time feeding and more time avoiding this parasitism (Roby, 1978). Windswept, upland plateaus (Walsh et al., 1992) and locations where snow patches remain into summer (Ion & Kershaw, 1989), offer such relief. Several researchers have recently raised the issue of overgrazing and/or climate effects on habitat, particularly on summer range, as an explanation for greater energy expenditure and effects on productivity (Jacobs et al., 1996; Couturier et al., 1994; 1996; Crête et al., 1996).

Movement

It is clear from the review of earlier studies that the greatest caribou presence in the current LLTA occurs in the northwestern portion of the area, and movement in and out of this area is from the north and west. The location and orientation of the trails recorded on the surveys support this contention. During spring and fall migration, caribou from the GRCH travel approximately 20 km per day (Schaefer, 1995). Values for July have been reported as daily ranging from 1 to 40 km (Harrington & Luttich, 1991). With improved software for sorting inaccurate locations (Rettie & Messier 1998), Bergman et al. (2000) noted average caribou movements of 1.25 km per day in winter, versus 9.5 km per day during the post-calving period and 14.5 km per day during summer.

During surveys, higher numbers of caribou were observed when more collars were present in the study area. The distribution of caribou observed during the 2000 and 2001 surveys appear to confirm that the northwestern portion of the current LLTA remains within the GRCH core range only for a short period of time.

The main difference between the 2000 surveys and those during the 1990s was in the density of animals observed. However, the current LLTA is configured further south than the former LLTA, thus there is less overlap with the GRCH migration and lower densities of caribou would be expected.

Conclusions

Based on surveys in 2000 and 2001, the 1996 reconfiguration of the LLTA, i.e. moving the training area south of the main GRCH migration route, was an effective means of mitigating spatial overlap (potential disturbance). During the course of the current training season in recent years (i.e., April – October), caribou appear to only migrate through the current LLTA in late July and early August. Caribou densities within the LLTA, were lower than observed prior to reconfiguration in 1996.

The use of satellite collared caribou as a tool to implement avoidance restrictions is an effective form of temporal mitigation. Conservative closure areas based on >20 collared animals contained the majority of caribou present in the LLTA. No large groups and few caribou were observed outside of closures. Satellite collars were effective in monitoring movements and distribution of migrating caribou.

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Caribou, military jets and noise: The interplay of behavioural ecology and evolutionary psychology

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Abstract: Whether a human activity is likely to have a negative impact on a species depends largely on how stimuli from that activity are interpreted and acted upon by individuals, within the context of their behavioural ecology. The interpretations and decisions made by individuals in response to these stimuli are largely governed by neural systems evolved by the species as adaptations to common and recurrent selective pressures. In this paper I will review previous findings concerning the responses of caribou to overflights by military jet aircraft in Labrador/Québec and Alaska, casting them in an evolutionary psychological framework. One prediction from such an exercise is that identical stimuli (noise from jet overflights) that elicit similar responses (short-distance avoidance) can have quite different population consequences for sedentary (woodland) and migratory (barren-ground) ecotypes. For a female woodland caribou, which shares her calving range with a resident predator population, an increase in movements following disturbance may significantly increase her calf's exposure to predators. Similar movements by a female barren-ground caribou, which has fewer predators to contend with, may have only a negligible impact on her calf's predation risk. Thus woodland caribou may be more vulnerable to negative impacts of military jet noise during calving periods, dependent on predator density.

Key words: activity budgets, calf survival, disturbance, jet aircraft, movements, population dynamics, predation, predation risk, *Rangifer tarandus*.

Rangifer, Special Issue No. 14: 73-80

Introduction

The potential negative impacts of human-generated noise on caribou have been of concern for a considerable time (*e.g.*, Calef *et al.*, 1976; Miller & Gunn, 1979). Studies on noise impacts have focused on a wide variety of sound sources, but one important source of noise for some caribou populations has been military training activity. For example, in both Alaska and Labrador, jet fighter aircraft are flown at altitudes as low as 30 m above ground level (agl), generating peak sound levels often well above the 90 dBA level generally considered to be the threshold above which potential negative effects are expected (Manci *et al.*, 1988). Several research programs focused on low-level flying have found short-term effects on behaviour and, in one case, possible negative impacts on calf survival (Harrington & Veitch, 1991; 1992; Maier *et al.* 1998), but at present we have no consensus about long-term impacts that might be useful in assessing new or established activities or planning mitigation programs. For example, Davis *et al.* (1985) indicate there seems to be no obvious negative impacts on population dynamics despite decades of exposure to a variety of low-level training activities on the calving grounds of the Delta Herd in Alaska, whereas Harrington & Veitch (1992) suggest there may be strong negative impacts on calf survival for Red Wine Mountains caribou in Labrador. In an attempt to reconcile these apparent differences, this paper will review previous research on the impacts of jet fighter training on caribou within a framework informed by full consideration of the context within which potential noise disturbances are occurring. This context includes the consideration of the noise stimulus itself as well as both the animals' behavioural ecology and their evolutionary psychology. It will be shown that such a framework not only reconciles the disparate results of previous research but also provides a profitable guide to our thinking about the spatial and temporal impacts of noise and other potentially disturbing stimuli.

When considering the potential impacts of noise, a clear distinction between short-term and long-term impacts should be kept in mind (Bowles *et al.*, 1993; Larkin, 1994). Short-term effects are those that occur coincident with the noise stimulus (*i.e.*, the behavioural and physiological reactions). These reactions are typically the focus of most of our studies of noise impacts, as short-term reactions provide us with quantifiable, objective data that can be directly related to various parameters of the stimulus. Thus, for example, a caribou may startle, or run, or cease feeding when a jet flies overhead, and then resume its previous activities 5 or 10 or 15 minutes later. However, from a population perspective, it may not matter that some or most caribou startle, or run or cease feeding when a jet flies over. What matters is whether these short-term responses translate into long-term effects: are caribou effected at the population level? If individual animals, in general, suffer no long-term negative impacts on their reproduction or survival, then the short-term impacts of a noise, no matter how dramatic, are ultimately inconsequential. After all, caribou react dramatically to their natural predators yet, on average, survive to reproduce.

The ultimate goal in disturbance research is to characterize the long-term impacts of the noise, and this is precisely where our studies of noise effects often fall far short. When we collect data on noise impacts, we naturally focus on the most salient, reliably recorded reactions. These reactions are both explicit (*i.e.*, highly observable) and of short-duration. Typically, we measure responses over durations of seconds to minutes. Intervals any longer than a few minutes begin to obscure the relationship between cause and effect, as now other stimuli have occurred that may potentially influence the subject's behaviour. It becomes impossible to determine whether an overflight today may still have a lingering effect on the animal's behaviour a week or two down the road. Thus we are left to infer long-term impacts solely from the short-term reactions we observe, under the assumption that long-term impacts are merely the sum of the individual short-term responses we note (see caution by Bowles *et al.*, 1993). However, it is possible that the most important reactions to noise are too subtle for us to observe, as they are occurring within the animal's central nervous system with no immediate outside indication.

Evolutionary psychology

In order to understand the subtle, implicit reactions that might provide the link between short-term reactions and long-term effects, we have to "get inside the animal" psychologically. After all, the initial link between the noise stimulus and the animal's short-term response has long been the focus of experimental psychology. Psychology focused on the relationship between stimulus and response (S-R Psychology) in the first half of the last century, but since the 1960s, psychologists have broadened their consideration by focusing on the role that the organism itself plays in modulating the relationship between stimulus and response (S-O-R Psychology) (see Shultz & Schultz, 2000, for a review). Within the past 20 years, this consideration has been further developed by the subdiscipline of evolutionary psychology.

Evolutionary psychology posits that all species are endowed with a set of 'evolved psychological mechanisms' that guide an animal's responses to the stimuli it encounters (Buss, 1999). These mechanisms consist of nervous system modules that are sensitive to a particular subset of stimuli (*i.e.*, 'sign stimuli' or cues) and respond in specific ways when these stimuli are detected. An evolved psychological mechanism is proposed to consist of three components: 1) a recognition component, 2) an activation component, and 3) a decision component. The recognition component ignores the vast majority of incoming stimuli, responding only to a specific limited set of features. Once these features are recognized, an activation component triggers activity in a variety of other areas of the brain (*i.e.*, motor areas, association areas, memory areas, emotional/motivational areas), which have an evolved relationship to the recognized object or event. Neural activity in these areas is integrated with other information concerning both the individual and its environs and an appropriate course of action is selected (see Frid, 1997, for a related behavioural model).

This process can operate rapidly and the quicker a motor response is selected the more likely the process occurs unconsciously. Thus a 'predator detection mechanism' might evolve that is particularly sensitive to a subset of key stimuli that reliably have signaled the presence of a predator over evolutionary time. For example, a sudden, loud noise, over evolutionary time, has likely been associated with predators often enough for caribou to evolve a neural mechanism to categorize such sounds with other cues concerning predators (*i.e.*, sights or smells). Those caribou that possess such a mechanism are more likely to detect a predator, detect it earlier, and make the most appropriate behavioural response.

Thus two key characteristics of evolved psychological mechanisms are 1) their reliance of a limited set of indicators or cues and 2) their adaptation to past, not present, environments. This latter point is important when considering the potential impacts of human-generated noise, as the majority of potentially disturbing sounds are of recent origin, and thus we would not expect wildlife to have evolved mechanisms that would allow them to specifically cope with them. Rather, these evolutionarily-novel stimuli likely activate existing evolved psychological mechanisms and are therefore likely perceived as a member of an existing 'innate' category. Knowing how an animal categorizes the stimulus, and its typical responses to that category of stimuli, will suggest the form and degree of possible impact.

Jet fighter training and caribou

To put our analysis into action, I will briefly review the findings of two research programs, recasting the findings of these studies in an evolutionary psychological framework.

Alaska

The United States Air Force funded a study on the behavioural effects of low-level military jet training conducted at Eielson Air Force Base, Alaska, on barrenground caribou (*Rangifer tarandus granti*) of the Delta Herd (Murphy *et al.*, 1993; Maier *et al.*, 1998). The training at Eielson Air Force Base involved low-level flights of A-10, F-15 and F-16 military jet aircraft. Sound level exposures were highest with the F-series jets. Although bombing, strafing and artillery fire have been part of the military training, they were not assessed in this study. Instrumented caribou (VHF collars with activity and noise monitors) were assigned to control and exposure groups, and exposure animals were targeted for low-level passes as low as 33 m agl and full power. Observers noted the caribou's distance to aircraft and monitored its activity budgets and instantaneous responses to the overflights. Observations were carried out in late-winter, post-calving and insect seasons.

The research program focused on three potential indicators of short-term impact: instantaneous reactions, changes in activity budgets, and changes in movement rates. About half the caribou overflown showed no overt behavioural responses to the overflights, with the remainder either becoming alert, standing up or moving (Murphy *et al.*, 1993). Differences between control and exposure animals were noted in the post-calving and insect periods, when exposed animals fed more, rested less and stood more often. Activity counts (mercury tip switches) from collared animals indicated that exposed caribou spent more time active and less time resting during the post-calving and insect periods (Maier *et al.*, 1998). During the post-calving period, distance traveled during the 24-hour period following exposure (overflight) sessions was significantly greater (by about 50%) for females overflown than for females in the control group. Control animals moved somewhat farther on average during the winter and insect periods, although these differences were not significant (Murphy *et al.*, 1993; Maier *et al.*, 1998). The principal conclusions of this program were:

1) "Females with young calves may be less tolerant…and [their] reactions…suggest that caribou moved away from disturbed areas" (Murphy *et al.*, 1993: 485); and
2) "Overall, …reactions to overflights were mild, but modifications of activity cycles and daily movements were evident" and "… responses were strongest when young calves were present… Therefore, we infer that females with young were more sensitive to aircraft disturbance" (Maier *et al.*, 1998).

Labrador

The Newfoundland Wildlife Division, with partial support from the Department of National Defense (Canada), funded a three-year study on the impacts of low-level jet fighter training conducted from Canadian Forces Base Goose Bay (Harrington & Veitch, 1991; 1992). Caribou (*Rangifer tarandus caribou*) belonging to two herds, the small (approx. 700) Red Wine Mountains herd of woodland ecotype and the larger (400 000+) George River herd of barrenground ecotype. Short-term effects were measured through direct observations of caribou reactions to overflights during late-winter and through remotely gathered data on daily movements and daily activity levels (counts) collected via satellite radiotelemetry during the training season (April to October) (Harrington & Veitch, 1991). Long-term impacts were assessed by monitoring the survival of calves of selected, collared females whose daily level of exposure to low-level training activity was either manipulated or monitored throughout the low-level training period (Harrington & Veitch, 1992). As with the Alaska research program, the 10 collared females each season were split between control and exposure groups.

Visual observations indicated that caribou reacted with a strong startle response to the loudest overflights (*i.e.*, 30 m agl), with the severity of the startle response decreasing with greater distance from the jet's flight path or higher altitudes, and thus lesser noise levels (Harrington & Veitch, 1991). In general, behavioural changes occurring during overflights followed an 'up one notch' pattern: resting caribou scrambled to the feet and sometimes lunged forward a few meters; standing caribou usually surged forward a number of meters but began to slow almost immediately; and caribou already walking broke into a run which lasted longer that the former two situation, but again the animals generally slowed and soon stopped as the jet receded in the distance. Except for the rare occasions where caribou spotted the jet during its approach, caribou did not react to the jet until it passed overhead. It is likely therefore that caribou usually did not detect the presence of the jet visually prior to the arrival of the sound of the jet. From our own experience of overflights in the field, unless the air was nearly calm, there was usually no forewarning of an overpass. It was only after the overpass that animals visually followed the receding jet as they slowed to a stop. Within the next minute or two, animals typically resumed their pre-flight behaviour.

Remotely collected data on movements and activity found few significant correlates of overflights (Harrington & Veitch, 1991). The 24-hour activity index was significantly related to a number of variables, including daily distance traveled and ambient temperature, and it also varied seasonally and individually. Daily distance traveled explained between 11-22% of variance in the daily activity index, suggesting that the activity index was a good indicator of movement by the caribou. However, the activity index was only correlated with level of exposure during one of three years, when it indicated a significant but marginal increase in activity level for some, but not all, of the most exposed animals. The measure of daily distance traveled was not particularly useful, as the error inherent in the Argos locations (± 1 km) represented about one third of the average distance moved during much of the study period. Thus exposure to low-level jet overflights, on a short-term basis, did not appear to cause a significant impact on overall activity level or distance traveled.

To determine calf survival and its relation to low-level jet overflights, the presence of a calf at heel was determined once a month during the training season (from June – September/October), and again in December when satellite radiocollars were removed, from females of the Red Wine Mountains woodland herd (Harrington & Veitch, 1992). Calf survival was negatively correlated with a female's average level of exposure to overflights during the calving and immediate postcalving period. The fact that, despite the small and decreasing sample size (females were removed from the sample once their calves was lost), survival was significantly related to level of exposure to low-level training suggests that the impact of overflights may have been quite large. These are the first data that suggest a long-term, population impact from low-level flight training.

Reconciliation

Davis *et al.* (1985) summarized data on the population demographics of the Delta Herd from 1950 through the early 1980s. Although military activity, including low-level flying by a variety of aircraft, has occurred throughout this period, Davis *et al.* could detect no sign that calving success or other measures of productivity were adversely affected. The population in the early 1950s probably numbered less than 1000 but by 1982, was estimated to be between 6500 and 7500. These findings, combined with those of Murphy *et al.* (1993) and Maier *et al.* (1998), suggest that despite the short-term impacts on activity or movements noted above, especially those seen during the post-calving period, no long-term negative impacts on population were evident. These findings can then be compared to those of Harrington and Veitch (1991; 1992), who found similar mild short-term impacts, yet did find a potential long-term impact on population through the decrease in survival of calves which, along with their mothers, were exposed to higher levels of overflight activity during the calving, immediate post-calving period (*i.e.*, the first 3-4 weeks after birth). Indeed, the Red Wine Mountains population has decreased from approximately 700 animals during the years of the study (1986-1988) to about 150 animals recently (1997) (Schaefer *et al.*, 1999), although no direct link to low-level training can be drawn.

When we first obtained our results on calf survival (Harrington & Veitch, 1992), we were quite surprised, as the short-term effects all seemed to indicate that, at worst, low-level overflights might temporarily alter behaviour and elevate overall activity, but not to such a degree that we would expect a negative impact on female or calf condition, let alone survival. When published in 1992, we did not have an explanation for this unexpected result. However, when our results are combined with those from Alaska, and we focus on the psychology of the animal, the following scenario emerges.

The 'evolved psychological mechanism' behind the various reactions of caribou to low-level jet overflight is that of predator detection and avoidance. This is hardly a surprising conclusion. Frid (1997; 1998) has recently developed an interactive model, based on predation risk, to describe the behavioural decisions made by Dall's sheep (*Ovis dalli dalli*) in response to helicopter disturbance. For caribou, whether it is the noise of the jet that caribou first perceive, as is most likely in a forested setting, or its visual image during its approach, in either case the animal experiences a sound that rises in intensity from ambient levels to as high as 130 dB in under a second (Harrington & Veitch, 1991). On quiet days this increase could span 90 dB, and under average conditions probably exceeds 50 db. Most animals startle in response to a sudden loud noise, and this startle is associated with the body's 'fight or flight' system (Moller, 1978). All the various reactions observed during overflights suggest that the caribou are preparing to take rapid evasive action to a perceived threat. In some sense, this explanation seems quite obvious, as any animal that is vulnerable to predation must make an immediate response to any sudden-onset stimulus, whether auditory or visual. It must react in a reflexive manner first; a more 'leisurely' assessment can then follow.

However, it is important to keep in mind the three components of an evolved psychological mechanism. The first, recognition, occurs in this example in the split second that the animal is 'hit' with the sound. Recognition (of a sudden noise) triggers the activation stage, which involves, among others, the behavioural startle as well as the physiological changes in the autonomic system. There are likely other areas of the animal's nervous system that are also activated at this time, related to various antipredator tactics, but which may not show their effects until later. These may play an important role in the third stage, that of decision. In this case, among other options, the caribou may reassess its predation risk and decide to stay or leave over the next 24 hours.

During most of the year, caribou likely respond to predators only for the duration of the imminent threat. Once the threat is removed (*e.g.*, the wolf moves on, another caribou falls victim, etc.), caribou should return to pre-disturbance activity. This follows as it is not advantageous for an animal to forego other important activity (*e.g.*, feeding, rutting) for a weak or former threat (see also Frid, 1997; 1998). In addition, it is likely not advantageous for the caribou to abandon its current habitat for another potentially safer one, as on average a caribou may not be able to reliably assess the level of predator risk in a local area as the distribution of predators is patchy and unpredictable.

Thus caribou quickly cease reacting and return to previous activity once they 'decide' the receding jet is no longer a threat. Responses to other aircraft (light aircraft or helicopters) tend to last longer than those to jets (Harrington & Veitch, 1991), if only because it takes longer for these other aircraft to overtake the caribou. As long as the aircraft continues to approach, suggesting the approach of a predator, the animals continue to flee. In our observations, caribou always darted quickly sideways as the helicopter passed over, as if avoiding the chase of a predator that has closed on them. As they did, they slowed dramatically and often stopped moving within a few seconds, though they continued to watch the aircraft as long as it was still in sight.

There is one period, however, when caribou are much more concerned with the presence of predators. During the calving period, female caribou are most sensitive to stimuli associated with threats, because their calves are particularly vulnerable during the first several weeks after birth (Bergerud, 1971; Adams *et al.*, 1995). Females with calves do not have an effective direct predator defense (Miller *et al.*, 1984), and thus must rely on indirect means to minimize predation risk. The most effective indirect defense appears to be avoidance of areas inhabited by predators: thus spacing away in barren-ground caribou and spacing out in woodland caribou (Bergerud, 1974; Miller *et al.*, 1984; Bergerud & Page, 1987; Bergerud *et al.*, 1990).

Our study of calf survival was conducted on a woodland caribou population. The 'space out' antipredation strategy was very apparent in this population. During March and April it was quite common to find a significant portion of the population on the Red Wine Mountains, where strong winter winds kept the alpine tundra vegetation assessable at a time when snow in the surrounding forested plateau reached 2-3 meters in depth (Brown & Theberge, 1990; Veitch, 1990). Groups of up to several dozen caribou were typical during the late-winter period on the mountains. During May, however, these groups broke up as females quickly dispersed onto the plateau. Although females sometimes left the mountains together, by the time they reached their calving sites a few days later they were usually alone. Their movements then became particularly restricted during the calving period, which likely represents both a concession to the lower mobility of the calf as well as a passive strategy to minimize contact with predators.

During the period of our study, populations of both wolves and black bears were relatively high (Veitch, 1990; Schaefer *et al.*, 1999). Even though caribou space out from one another, they remain in a habitat rich in predators. Thus the antipredator strategy does not reduce the average risk that a female or calf face from predators, but the restriction of movement at calving may reduce the likelihood of encounters during this critical period. In essence, caribou attempt to disappear within predator habitat long enough to see the calf through to a less vulnerable age. Given a random search model, a predator has an increasing lower probability to encountering a cow/calf pair's sign (olfactory, visual or auditory) the more restricted the pair's movements become.

It is likely that females are predisposed to sit tight in a suitable area unless disturbed by a predator. Given the constrained movements of predators within territories or home range, it is likely that predators will return to areas where they have encountered prey or prey sign in the past. Thus a female that detects predator sign, or a predator itself, may be better off, on average, by moving to a new area, where she can attempt to 'disappear' once again. Stimuli that might be sufficient to generate such a home range shift could include visual, auditory or olfactory sign of predators. The loud noise of an overflight, as it triggers a startle response, may be classed in the same 'predator' category and thus, as Meier *et al.* (1998) found in Alaska, females experiencing a loud overflight may shift their home range.

Shifting a home range in response to predator sign is like any signal/noise problem (Table 1). A female that remains in her original range faces a low risk of losing her calf if she has not been detected by a predator. Once a predator has detected her, her risk to losing her calf increases. For females in the latter situation, movement to another area may reduce that risk, likely to a level intermediate between the two classes of risk faced on her original range. This intermediate level of risk is based on the simple idea that predator risk is a function, firstly, of a predator's ability to detect a prey. As wolves and bears likely use olfactory sign left by caribou, any extra movement by a female increases the area within which a predator may encounter her sign. This sign may be detectable for days to several weeks. In addition, visual and auditory sign occurring during the move also add, briefly, to her level of risk. Assuming a simple linear model, if a female increases the distance moved during one day by 50% (Maier *et al.*, 1998), she may increase the risk of predation by the same degree.

If a female has perfect knowledge of predator distribution, she can make appropriate decisions to keep her risk as low as possible. However, given less than perfect knowledge, a female may fail to detect a local predator, or a female may mistake a benign stimulus (*i.e.*, jet overflight noise) for a predator. Thus noise becomes a signal to the female and her avoidance movements increase. This increase in movements increases her calf's risk.

The scenario developed above holds for any female caribou, whether woodland or barrenground. What differs between the two is the relative level of risk for the same absolute distance moved. The 'space away' strategy of a barren-ground female has already taken her to a region of low predator density. Within this region, any increase in her movements will increase the risk of encountering a predator. However, if the risk is low to begin with, increased movements may still fail to bring a female/calf pair in contact with a predator. Thus the short-term increase in movements found by Maier *et al.* (1998) for migratory Delta caribou may not result in a long-term demographic impact on the herd, given a low density of predators on the calving range. For sedentary caribou, on the other hand, increased movements may turn a moderate risk into a high risk, resulting in a significant long-term population impact.

However, not all sedentary populations may suffer the same long-term consequences, as predator density and hence predation risk is the deciding factor. For populations like the Red Wine Mountains caribou that face relatively high numbers of predators, unnecessary anti-predator movements triggered by false alarms to jet overflights may significantly elevate calf mortality. On the other hand, if local

Table 1. Signal/noise decision matrix for a female caribou exposed to stimuli during the calving season that may or may not represent a predator or other real threat. It is assumed that the female is minimizing predation risk for her calf by restricting her movements as much as possible. When detecting a potential predator, she avoids the area, shifting her activity to an adjacent area. The movement to the new area exposes her to unknown predation risk there, as well as temporarily enlarging the area within which a predator might detect her and her calf. These factors increase predation risk for a false alarm (*i.e.*, treating an aircraft disturbance as a threat) but decrease it for a hit (*i.e.*, avoiding an actual predator).

	FEMALE'S CLASSIFICATION OF STIMULUS	
Actual stimulus	Predator	Not predator
Predator	HIT – female avoids area and increases calf's survival	MISS – female ignores stimulus and decreases calf's survival
Not predator	FALSE ALARM – female avoids area and decreases calf's survival	CORRECT REJECTION – calf's survival unchanged

predator densities are low, then false alarms resulting in excessive movements likely would have no long-term consequences.

Summary

This paper has developed a scenario to understand the behavioural dynamics behind the potential for long-term impacts caused by human-generated noise. By first trying to understand how an animal likely perceives and categorizes the noise stimulus, we can then determine how an animal is likely to respond to that particular type of stimulus. Next, we can place the animal's likely response within the context of its behavioural ecology. Thus by combining the internal 'evolutionary psychology' of the animal with its external 'behavioural ecology,' we can begin to build predictive behavioural models that will allow us to make predictions about the long-term demographic consequences of noise disturbance. As the specific model developed here indicates, the same behavioural responses in two different populations may have quite different long-term consequences. Indeed, the same divergence of consequence can occur within the same population if, in this case, there is a significant change in predator density over time.

Thus the most important impacts of noise on caribou should not be expected to be direct and immediate. Rather, they are likely to involve indirect and secondary consequences stemming from innate behavioural responses to the noise that happen to put some portion of the population at greater risk to other factors. It is these other factors that directly affect the long-term demography of the population. These factors may operate well after the initiating noise stimuli are past and forgotten, at least by human researchers, making it difficult to make the link between noise and demographic response.

Finally, it must be emphasized that, although field data may be consistent with the scenario developed in this paper, the link between low-level jet fighter training and caribou population dynamics remains to be demonstrated. This paper provides only an hypothesis that can, and should, be tested in the field.

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Use of satellite telemetry to evaluate movements of caribou within subsistence hunting areas in northern Alaska

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Abstract: Caribou from the Teshekpuk Herd (TH) are an important subsistence resource for residents of Iñupiaq villages in northern Alaska. In recent years the use of satellite telemetry has increased the understanding of the herd's annual movements and interactions with other herds. Most caribou of the TH are within the National Petroleum Reserve–Alaska (NPRA) throughout the year. The northeastern portion of NPRA has undergone two lease sales for oil and gas exploration, and lease sales are tentatively scheduled for the central/northwest portion of the NPRA in 2004. During 1990–1999, the movements of 27 caribou from the TH were tracked using satellite collars. We evaluated the proportion of time caribou were available to Iñupiaq hunters by incorporating maps depicting subsistence-use areas for each of seven Iñupiaq villages, and then examining seasonal and annual movements of caribou relative to those areas. By combining caribou locations with subsistence hunting areas, we were able to explore spatial and temporal patterns in caribou availability to subsistence hunters. This information is useful for managers to set appropriate hunting regulations and for devising sensible alternatives and mitigation of likely petroleum development in NPRA.

Key words: Alaska, GIS, Rangifer tarandus, Teshekpuk Herd.

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Introduction

Barren-ground caribou (Rangifer tarandus granti) of the Teshekpuk Herd (TH) typically calve in the vicinity of Teshekpuk Lake in the north-central part of the North Slope of Alaska (Philo et al., 1993; Kelleyhouse, 2001; Prichard et al., 2001; Fig. 1). Most TH caribou stay north of the Brooks Range throughout the year, but a portion of the herd winters south of the Brooks Range in some years (Philo et al., 1993; Prichard et al., 2001). The range of the TH overlaps with the range of the Central Arctic Herd (CAH) to the east and the Western Arctic Herd (WAH) to the west. The population of the TH has been increasing since it was first recognized as a herd in the early 1970s (Davis & Valkenburg, 1978). A photocensus in 1999 enumerated 28 627 caribou in the herd (Carroll, 2001).

The TH is an important subsistence resource for local residents (BLM, 1998). A number of Alaskan villages are within the peripheral range of the TH (Fig. 1), but seven villages comprise the majority of the harvest in most years. The population in these villages is predominantly Iñupiat (Table 1), although non-native rural residents also hunt caribou under the same state and federal regulations. In Alaska, the Alaska Board of Game issues caribou hunting regulations that cover all people and all lands in the state, but simultaneously the Federal Subsistence Board issues caribou hunting regulations that cover only rural Alaskan residents on federal public lands. Throughout the western portion of the North Slope,

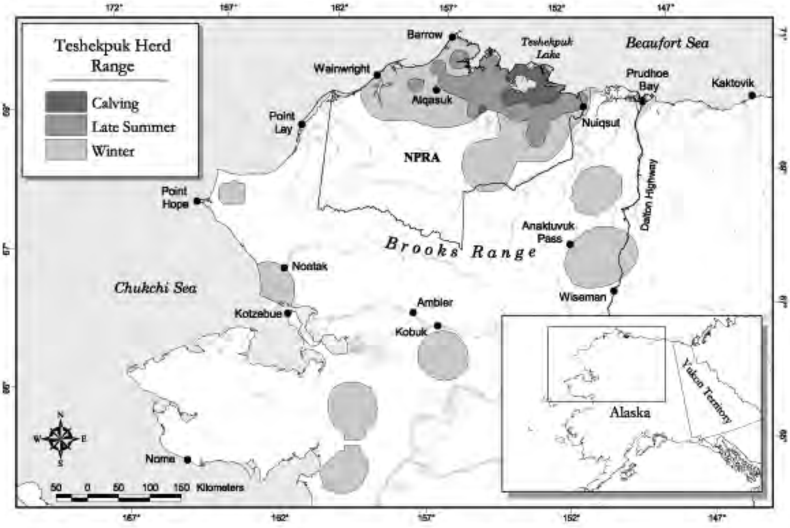

Fig. 1. Seasonal range of Teshekpuk Herd caribou based on satellite collar locations 1990–1999. Ranges represent 95% utilization distributions based on fixed-kernel analysis of one location per transmitting day (Calving=1-15 Jun; Late Summer=8 Aug-15 Sep; Winter=1 Dec-30 Apr; after Prichard et al., 2001).

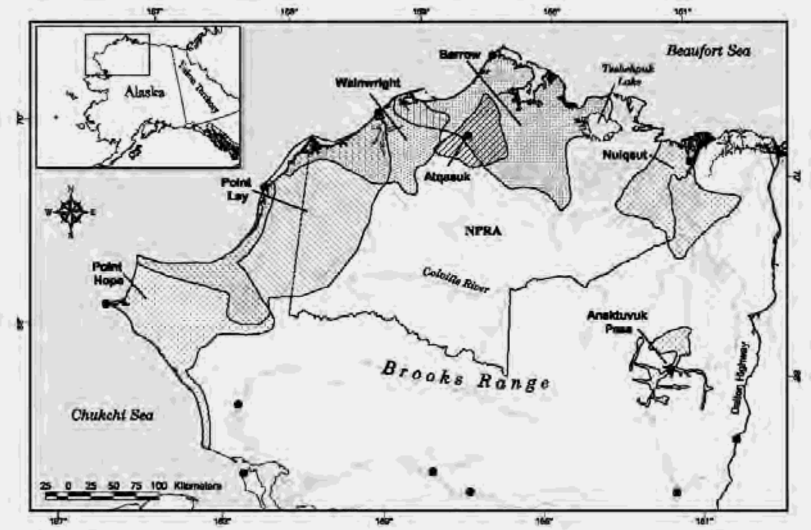

Fig. 2. Approximate subsistence hunting areas for seven villages within the range of Teshekpuk Herd caribou.

caribou of both sexes may be harvested during most times of the year (the season for cows is closed during calving, 16 May–30 June), but the majority of the harvest generally occurs in summer and fall (Fuller & George, 1997; BLM, 1998). Due to the remote location of the TH, sport harvest of the herd is minimal (Carroll, 2001).

It is currently difficult to accurately estimate TH harvest because residents of each of the North Slope villages harvest caribou from more than one herd. In addition, fall movements and winter locations of the herd are quite variable among years, and harvest levels are influenced by the proximity of caribou to villages. Based on subsistence surveys and approximate herd locations, the subsistence harvest of TH caribou in three North Slope villages was estimated at 808–1084 during 1989–1990 (Carroll, 1992) and 2500 per year in all North Slope Villages in 1994–1996 (Carroll, 1997).

Other than several villages, there currently is little development in the core of the TH range (Fig. 1). However, most of the herd's annual range is within the National Petroleum Reserve–Alaska (NPRA). The northeastern portion of NPRA has undergone two lease sales for oil and gas exploration in 1999 and 2002. These areas currently are under exploration and one development has already been proposed. Additional lease sales are tentatively scheduled for the central/northwest portion of the NPRA in 2004. Comments from local residents during the Environmental Impact Statement process indicated that local residents were concerned that oil and gas development would lead to a decrease in subsistence species, decreased access to subsistence areas, and changing movement patterns of subsistence species (BLM, 1998). Such a conflict already is perceived by villagers of Nuiqsut with current oil developments to the east and north of the village (Lawhead et al., 2002; NRC 2003), and residents of Nuiqsut generally avoid the oilfields while hunting (Brower & Hepa, 1997; NRC, 2003).

In this paper, we attempt to integrate the distribution of TH caribou based on the year-round location of satellite-collared caribou with results of sub-

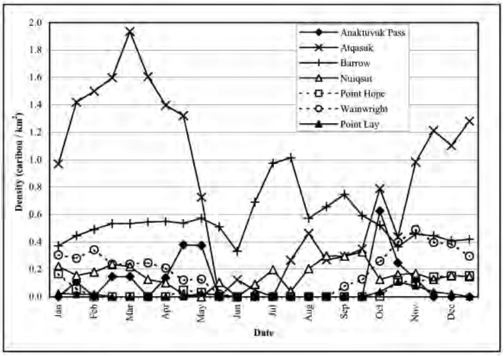

Fig. 3. Estimated density (animals/km^2) of Teshekpuk Herd caribou (proportion × 28 000/area) within the village subsistence hunting areas during 24 time periods, based on locations of 27 caribou outfitted with satellite collars, 1990–1999.

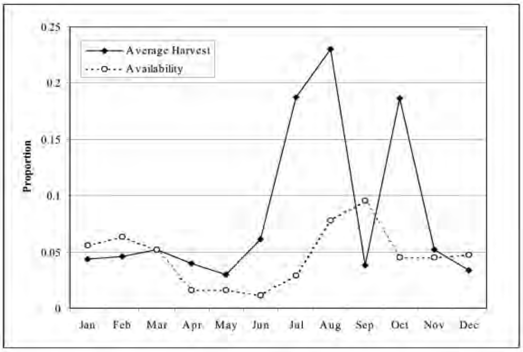

Fig. 4. Comparison of proportion of annual caribou harvest in each month in Nuiqsut (1992 and 1994–1995; Brower & Opie, 1997, Fuller & George, 1997) with availability of Teshekpuk Herd caribou as estimated by the proportion of locations of caribou outfitted with satellite collars within the area used for subsistence hunting, 1990–1999.

sistence surveys in seven villages to explore temporal and spatial patterns of caribou availability to local hunters. This information may be useful in planning development projects as well as assessing impacts of future development on subsistence hunting opportunities.

Methods

In 1990, a cooperative satellite radio-collar caribou-tracking project was initiated by the North Slope Borough Department of Wildlife Management, the Alaska Department of Fish and Game, and the U.S. Bureau of Land Management. From 1990 through 1999, 28 female and one male caribou were captured and outfitted with satellite collars near Teshekpuk Lake in June and July. Two female caribou displayed movements more typical of the WAH and did not return to Teshekpuk Lake during subsequent calving periods. For this paper, we analyzed the distribution of the 27 remaining caribou thought to be from the TH.

Satellite Telemetry

In 1990 and 1991, caribou were captured using a dart containing carfentanil and xylazine fired from a tranquilizer gun from a helicopter. After 1991, in response to concerns of subsistence users, caribou were captured using a helicopter and a skid-mounted net gun (Philo et al., 1993; Carroll, 1999). All caribou were fitted with a satellite transmitter and a conventional VHF radio-transmitter attached to a collar produced by Telonics, Inc. (Mesa, AZ). Data were retrieved using Service Argos (Landover, Maryland). The collars were programmed to transmit location data for 6 hours every 2 days in most cases and 6 hours every day for one caribou. Collars transmitted locations for an average length of 427 days (min=94, max=789). Location data included a location quality score (NQ) of 0 to 3 calculated by Service Argos based on six criteria corresponding to estimated spatial accuracy (Service Argos, 1988; Keating et al., 1991).

Data Screening

Data were screened to remove duplicate records, locations acquired prior to collaring, locations acquired after mortality, and locations that were obviously wrong (e.g., far offshore). In addition, we analyzed each combination of two successive vectors of movement to identify suspect locations based on rate of travel and the angle of change between three successive locations. Locations were removed if three successive locations formed an angle of less than 20 degrees and both vectors of the angle had speeds of greater than 10 km/h (indicating rapid movement and an abrupt change of direction). After screening data, one location of the best NQ score was selected for each transmitting day. This screened set of point locations was used to create a linear route track for each caribou using ArcView GIS 3.2a software (ESRI Inc., Redlands, CA).

Subsistence Areas

Village subsistence areas were identified for seven villages based on previous studies. Information on caribou hunting locations for North Slope villages was used for Barrow and Wainwright (Braund, 1993a; Braund, 1993b). For the other villages, cari-

Table 1. Human population data (2000 census) and the approximate size of subsistence hunting areas, as well as the estimated annual caribou density and average distance of Teshekpuk Herd caribou within the subsistence hunting areas for the seven villages that regularly harvest caribou from the Teshekpuk Herd. Density and distance were calculated based on 27 satellite-collared caribou 1990–1999.

	Population (2000)	Alaskan Native (%)	Subsistence Hunting Area (km^2)	Estimated Caribou Density (Caribou/km^2)	Average Distance (km)
Anaktuvuk Pass	282	88.3	2026	0.07	36.7
Atqasuk	228	94.3	3520	0.62	21.2
Barrow	4581	64.0	18013	0.61	90.8
Nuiqsut	433	89.1	8714	0.18	47.3
Point Hope	757	90.6	15589	0.05	98.1
Point Lay	247	88.3	24272	0.02	100.1
Wainwright	546	93.0	8728	0.16	43.7
Total	7074	73.4			

bou hunting areas were estimated based on data from North Slope Borough surveys for all terrestrial mammals, including furbearers. In most cases, these areas probably overestimate caribou hunting areas, but, because caribou are harvested throughout the year as part of other hunting activities, they are probably a reasonably accurate representation of potential harvest locations.

For Barrow and Wainwright, areas used for caribou hunting were available for the years 1987–1989 and 1988–1989, respectively (Braund, 1993a; Braund, 1993b). The subsistence hunting area was determined as a minimum convex polygon encompassing all harvest locations. This area then was "clipped" at the coast to exclude offshore areas (Fig. 2).

The Atqasuk caribou hunting area was estimated using the total harvest area for all species for the years 1994–1995 (Brower & Hepa, 1997). The hunting area was relatively small despite the fact that it probably overestimates the area used solely for caribou hunting.

No recent data were available for Point Hope or Point Lay caribou hunting areas, so we based the Point Hope and Point Lay caribou hunting area on data gathered for the North Slope Borough Coastal Management Program (North Slope Borough, 2000). Interviews were conducted with approximately 10 senior hunters in each village by staff from the North Slope Borough Planning Department and the Department of Wildlife Management. The perimeters of the subsistence hunting areas reflected hunting regions used over the previous decade and included both terrestrial and marine species. We used the total hunting area (marine areas excluded). This technique appears to have resulted in overestimates of the areas where caribou are actually harvested, particularly for Point Lay.

The caribou hunting area for Anaktuvuk Pass was determined from hunting areas reported in Brower & Opie (1996). Specific harvest locations for caribou were not reported, so the village harvest area was determined as the sum of all traditional hunting areas where successful harvests were made in 1994–1995. The hunting area excludes high mountain peaks and generally follows river and creek drainages. The Nuiqsut caribou hunting area was determined as a minimum convex polygon encompassing the terrestrial harvest area for the period July 1994 to June 1995 (Brower & Opie, 1997).

Spatial Analysis

By entering subsistence hunting areas and caribou routes as layers in ArcView GIS 3.2a, we were able to record each time a caribou was in a subsistence area. We calculated the proportion of locations within a subsistence area for each caribou for each of 24 time periods throughout the year (1–15 January, 16–31 January, 1–15 February, etc.). We then calculated the average of the proportions for all collared caribou during each time period. If a caribou was collared for more than a year, it could be counted more than once in a given time period. The average proportion of time satellite-collared caribou were within a subsistence hunting area was used as an estimate of the proportion of the herd within each hunting area per day for each of the 24 time periods. This assumes that collared caribou were randomly distributed throughout the herd. Proportions were converted to approximate caribou densities within a subsistence area by multiplying by 28 000 (approximate size of the herd in 1999; Carroll, 2001) and dividing by the area of the subsistence hunting area. In addition, we used collar locations to calculate the average distance from villages for all points within the subsistence area for the same 24 time periods.

Published accounts of caribou harvest exist at

Table 2. Average, minimum, and maximum percentage of time caribou spent in the Barrow subsistence hunting area each year based on satellite collar locations 1990–1999. Only months with 5 or more active collars were included in the analysis.

	Percent of time			
Month	Average	Minimum	Maximum	Number of years
Jan	23.2	0.0	42.9	4
Feb	39.0	33.3	44.8	2
Mar	43.6	38.6	48.6	2
Apr	41.1	25.0	57.1	2
May	40.4	37.3	43.5	2
Jun	48.0	48.0	48.0	1
Jul	63.7	29.9	96.9	5
Aug	35.7	6.8	53.3	4
Sep	40.4	3.8	64.4	4
Oct	25.3	6.4	46.5	4
Nov	23.6	0.0	49.0	4
Dec	20.0	0.0	42.9	4

varying levels of detail for all seven villages, enabling comparison of harvest levels with herd availability estimates. We compared harvest levels from Nuiqsut in 1994–1995 (Brower & Opie, 1997) and in 1992 (Fuller & George, 1997) to caribou locations. We compared the average proportion of caribou harvested monthly in Nuiqsut in the two studies to the estimated proportion available, based on satellite telemetry data

Results

The size of the seven village subsistence areas (Fig. 1; Table 1) varied greatly. Because the telemetry data set consists almost entirely of female caribou, our results may not accurately represent the probability of males being close to villages at times when males and females are spatially segregated, such as during calving.

The proportion of caribou encountering village subsistence hunting areas varied greatly from village to village. The Barrow hunting area had the highest overall proportion of satellite-collared caribou (65% in late July; 36% average of all time periods), however, the Barrow area also is the second largest hunting area. The approximate density of caribou (proportion of collared caribou × 28 000/area) was highest for Atqasuk, second highest for Barrow, and lowest for Point Lay (Table 1). There were large seasonal differences in densities of satellite-collared caribou present among villages (Fig. 3). Atqasuk, Wainwright, and Point Hope had their largest densities in the winter months, Barrow and Nuiqsut had higher proportions available in the summer than winter, and Anaktuvuk Pass had the highest densities available during spring and fall migration. Wainwright, Anaktuvuk Pass, Point Hope, and Point Lay had no satellite-collared caribou within the subsistence hunting areas during June, July, or August.

There were also large differences among villages in the average distance from the village of caribou that were within a subsistence hunting area (Table 1). These distances were, of course strongly affected by the size of the defined hunting areas, as well as the traditional range use of the TH. Average distances of caribou within a subsistence area did not fluctuate greatly throughout the year.

An estimate of the amount of time an individual caribou spent within any of the seven village hunting areas on the North Slope was generated for each two-week period in the annual cycle. The overall average percent of time an individual caribou spent in any of these seven hunting areas was 51.5% (SE=7.0%, n=51). The percentage was lowest in early June (21.9%, SE=8.4%, n=24) and highest in early July (68.9%, SE=8.1%, n=33). The percentage was fairly constant from November through April (min=45.7%, max=50.2%).

The proportion of time caribou were within subsistence hunting areas can also be used for determining the annual variation in caribou distribution within the village subsistence areas. The annual variability in time caribou spent in the Barrow hunting area each month varied (only months with at least 5 collared caribou were included) (Table 2). Some caribou, for example, were within the Barrow hunting area in all years and in all months except November, December, and January.

The caribou harvest in Nuiqsut was estimated at 249 caribou in 1994–1995 (Brower & Opie, 1997) and 278 in 1992 (Fuller & George, 1997). Both studies reported monthly harvest numbers. Caribou harvest was highest in July, August, and October, but was low in September. Caribou availability based on satellite collar locations, however was highest in August and September (Fig. 4).

Discussion

Determining baseline levels of herd availability and harvest provides a basis for quantifying the effects of oil and gas development on herd movements and subsistence hunting. Because caribou movements are highly variable, seasonally and annually, long-term knowledge of movements is needed to determine if changes in herd distribution after development are unusual. Because of the large amount of overlap in herd ranges in this area, traditional ecological knowledge cannot always supply herd-specific information on past range use. The use of subsistence hunting areas and satellite telemetry may provide a framework for more accurately estimating subsistence harvest by herd. Accurate estimates of harvest of the TH would allow herd managers to make more effective hunting regulations in times of low herd productivity or abundance.

The pattern of average monthly harvest in Nuiqsut (1992 and 1994–1995) was fairly similar to the pattern of TH availability estimated using satellite collar locations (1990-1999; Fig. 4), except in September when the harvest level was low despite the highest proportion of TH animals available. This discrepancy may be because many hunters concentrate on whaling during that time of year (Brower & Opie, 1997) or because travel is difficult in years of early freeze-up. Nuiqsut hunters also have access to CAH caribou as well as TH caribou, and further study is needed to determine what percentage of the harvest comes from each herd.

In future studies, we hope to compare herd availability data for different North Slope herds with village monthly harvest numbers to estimate herd-specific harvest levels. If we assume that monthly harvest of each herd is proportional to the relative availability of each herd, harvest of TH caribou could be approximated by the number of TH caribou within the subsistence area divided by the total number of caribou of all herds within the subsistence area, multiplied by the number of caribou harvested in each month. Analysis of harvest of TH, CAH and WAH caribou is continuing.

Two current limitations of this approach are that sample sizes are generally small and, in this study, only one male was collared. In 2001, 10 satellite collars were attached to CAH caribou and 10 additional collars were attached to TH caribou. Six of the TH collars were attached to mature males. In addition, satellite collars can be used in conjunction with the VHF collars to provide a larger sample size. There are numerous VHF collars on all 3 herds, and radio-tracking surveys can be conducted to determine the relative proportion of caribou from the three herds that are in the hunting areas during times when caribou are being harvested.

Another limitation is the inconsistency of harvest data and hunting areas. The amount of information available varied greatly among villages. In addition, some hunting areas were delineated based on harvest locations, whereas others were based on areas used for hunting. In order to make accurate estimates of harvest among herds, current and accurate harvest data are needed for as many villages as possible. In order to be most useful, harvest data should include the time and place of harvest as well as a delineation of areas used for caribou hunting. Ideally, hunting patterns should be considered over multiple years to integrate the annual variability in caribou abundance and harvest locations. By integrating seasonal changes in hunting locations and some measure of hunting intensity into hunting area boundaries, a more accurate assessment of harvest potential can be conducted. For instance, the Barrow hunting area is so large that it encompasses much of the TH during most of the year. By differentiating high and low use areas, as well as winter and summer areas for Barrow, we could get a more detailed depiction of actual availability of TH caribou and harvest of the North Slope caribou herds.

Despite a number of limitations of this analysis, the approach seems quite sound. The combination of subsistence hunting areas, GIS, and satellite collar locations can provide managers with another tool to estimate and predict impacts of future development on subsistence users and set appropriate hunting regulations.

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Caribou response to human activity: research and management

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Abstract: This paper describes the need by researchers and managers of caribou (Rangifer tarandus) to carefully assess the impact of their study methods on animals and results. An error made during a study of barren-ground caribou is described. Assumptions made during preparation of study methods need to be tested during collection of data. Study plans should include communication with, and respect for, residents who depend on the caribou resource. During field observations of caribou behavior, feeding habits, rutting activity or sex and age composition, closer is not better. During capture, handling and marking activities, shorter processing time is better. During aerial surveys, photography, sex and age determinations, higher is better. When interpreting data collected from marked caribou, and generally applying to the unmarked population, caution is advised. The merits and drawbacks of helicopter use to capture and mark caribou for research and management need to be discussed.

Key words: behaviour, capture, helicopter use, mark monitor, population dynamics, Rangifer tarandus, survival, trauma.

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Introduction

Caribou response to research and management investigations is a difficult and perhaps unpopular topic for caribou biologists. I feel well qualified, however, to present this topic after 43 years conducting caribou research and management projects at Provincial and Federal levels, and after having been introduced to caribou in 1957 by the "Father of the George River Herd" - Dr. A. Tom Bergerud. I have assisted Dr. Bergerud on caribou studies in Newfoundland, Labrador, Quebec, Ontario and in the British Columbia Provincial Parks, especially Spatzizi. I have also conducted studies on mountain caribou in Idaho and British Columbia (Selkirk Mountains), woodland caribou in Manitoba and Quebec (Parc de la Gaspesie) and Barren-ground caribou in Manitoba, Saskatchewan and the Northwest Territories. During 14 of the past 15 years (1985 to 2000) I have studied caribou during the rut on Mont Albert, Quebec.

In designing any research or management program, caribou biologists make assumptions regarding techniques to collect information. The errors we make, and I'm as guilty as anyone, are that once methods of study are selected, we tend to accept them without further examination. In fact, we need to constantly re-examine our assumptions to test their validity. Invalid assumptions can produce erroneous conclusions no matter how great the statistical confidence limits. I will show how I fell into this trap and only recently realized my error.

In 1963 - 1965, as the Northern Wildlife Biologist of the Manitoba Wildlife Branch, I was in charge of the Duck Lake barren-ground caribou tagging project. We used numbered cattle eartags with an attached 6 x 1.5 inch yellow herculite streamer. In late summer, usually August, when the insect season ended, the Kaminuriak (Qamanirjuaq) caribou population would migrate south from tundra summer range through the Duck Lake area in northern Manitoba. Migrating caribou could be captured and tagged while swimming across Duck Lake. This tagging operation was initiated in 1959, along with a similar operation in the adjacent Beverly barren-ground caribou population on the Thelon River in the Northwest Territories. Red streamers were used on the Beverly population. The objective of these operations was to determine if an interchange of caribou occured between the two populations (Kelsall, 1968). The basic assumptions of these two tagging operations was that there was very little trauma experienced by the tagged caribou and that they would be representative of the entire population. I thought the assumption was valid because each captured animal was processed and released in one to two minutes. However, in 1965, there was evidence to the contrary after we tagged over 500 caribou at Duck Lake (about 1% of the population). I didn't recognize it immediately but I should have. After most caribou had migrated through the Duck Lake area we observed single caribou on two separate islands in the lake. I chased each caribou into the water where they were intercepted by a tagging crew. Both caribou, which appeared to have no physical problem had been tagged earlier that year. I think these two caribou had been so traumatized by their tagging experience that they were afraid to enter the water to join their band as they normally would have done. How this particular observation affected the conclusions in our publication (Miller & Robertson, 1967) on the Duck Lake caribou tag returns is uncertain, but the basic assumption was certainly not valid for these two tagged caribou.

One aspect of caribou research and management that too often is not part of the study plan is to communicate with and respect the human residents within the study area. Our study plans, as well as the resulting management decisions need to be carefully explained to residents, especially those who are dependent on the caribou resource. We need to confer with them early on in the study plan stage to incorporate their knowledge and concerns into the final study. I found that the best way to communicate with these residents is to hire them as assistants and make them part of the study (Miller, 1974; 1976). We learn from them, they learn what we are doing and why, and they share this information in their communities. We are visitors in their environment and need to act and work accordingly - with respect.

When choosing the methods of data collection in our caribou studies, we need to review Friend et al. (1996) to be sure we are considering the impacts our study may have on individual animals, members of the associated band and on the herd. These guidelines, in the Wildlife Society's Research and management techniques for wildlife and habitats manual, state (p. 96) that "professional scientists must consider the effects of their activities on the organisms under study, on the validity of study, results, and on the use of these organisms by other segments of society." We need to be aware of and minimize impacts of our data collection methods.

Closer is not better

It took me a very long time to learn to observe caribou from as far away as possible during rut. Even when down wind, in excellent cover and using binoculars an observer risks being observed by caribou traveling between rutting groups. I use 15 - 60X spotting scopes to observe rutting caribou 0.45 to 0.8 km or more on Mont Albert, Par de la Gaspesie. Even when caribou move near me and become alarmed they are so far from the rutting group that they rarely disturb the harem. As anyone knows who has observed caribou, even subtle behavior can alert other caribou in the vicinity. There appears to be an instinctive fear by most ungulates of unfamiliar objects up slope. A silhouette or reflection from equipment, let alone movement, above caribou will elicit immediate concern and quite likely a movement response. Often caribou aware of danger up slope, if not too disturbing, will gradually move around and above the perceived threat. Caribou respond less strongly to potential threats that are below them than to those from above. Danger from below or even on the same contour may elicit an initial response of movement closer, apparently more out of curiosity than fear. Yearling caribou seem to be most curious, while females, especially those with calves, are often first to detect danger and first to flee. If an observer is detected by a female, it is essential to freeze until she relaxes and lies down or begins to graze. Especially in rutting groups, caribou seem to be aware of the body language of each other although immature males seem less aware than others.

Shorter time is better

When capturing, handling and fitting caribou with marking devices, less trauma will generally be imposed on those individuals released most rapidly. The collection of additional data from the captive animal will obviously require more time than simply marking it. In any event, the captured caribou is not the same as it was prior to the capture and will likely respond with more fear to noises and people. More information may negatively impact the validity of a scientific study by causing trauma through additional processing time. In a study of greater Snow geese Menu et al. (2000, p. 550) suspected that "Because neck - banded birds were handled longer and received a larger marker, they could have experienced more stress than those marked with leg bands only, provoking a higher rate of emigration from the banding areas (trap shyness)." Paton et al. (1991) on spotted owls and Burger Jr. et al. (1991) on greater prairie-chickens also report on the influence of radio transmitters, and caution researchers who use them.

Higher is better

When surveying caribou from a fixed-wing aircraft or helicopter it is important not to disturb the caribou observed. Accurate counts or sex and age determinations are much easier to get with undisturbed caribou than with running, terrified animals. Caribou tend to bunch up and run when threatened by low flying aircraft, especially helicopters. Some biologists use helicopters and even fixed-wing airplanes to collect data on the productivity of adult females and the survival of calves by flying low enough to identify enlarged mammary glands. The terrain these caribou are frantically racing over is anything but a level field. If those kinds of data are required it would be less traumatic and dangerous for the caribou if the biologists conducted surveys on foot or, at least, landed the helicopter out of sight and walked to a viewing point where binoculars or a spotting scope could be used. Flying higher to reduce or eliminate caribou response below usually results in more accurate data.

Use of helicopters in caribou research and management

Very early in my experiences with caribou I learned that helicopters terrify caribou. In the fall of 1959, as Central District Biologist in Newfoundland I was given the task by my Director to use a helicopter to locate a prime male caribou for a visiting dignitary. I found a prime specimen southeast of Grand Falls and directed the helicopter pilot to hover low over the male caribou so I could count the points on its antlers. The male caribou seemed to become disoriented as I counted the points on its antlers and seemed to rear up and almost fall over backwards so I told the pilot to go up and leave. This experience revealed absolute fear by caribou for helicopters, hovering low overhead. Low flying helicopters and fixed-wing aircraft too, usually cause caribou to run.

Caution is advised Interpretation of data collected from marked caribou needs to be carefully assessed to avoid the potential pitfalls of abnormal movements caused by the method used to capture and mark the caribou and the time interval held in captivity. Since the late 1970s, when VHF radio collars were first used in caribou research, more and more caribou have been fitted with radio collars (including the satellite type, in the 1990s). In the sixth, seventh, and eighth North American Caribou Workshops (NACW), satellite radio collar results have been increasingly reported in workshop presentations. Not only have radio collars been used on caribou in every state and province that supports Rangifer populations, but most populations within each has radio collared individuals. These collared caribou are being used to determine movements, range, mortality and most every aspect of the population. I propose extreme caution in the use of data from these collared caribou to represent different aspects of the population, and especially where calves are collared and used to determine calf mortality in the population (Fuller & Keith, 1981). Wildlife biologists need to share the problems experienced in their study and how they solved these problems in their talks, reports and publications to eliminate duplication in future studies (Boertje & Gardner, 2000). What part of the study plan didn't work as expected and how was the plan changed to make it better?

I've never tried to tranquilize or use the net gun method of capturing caribou from a helicopter, techniques commonly used to capture caribou for attaching radio collars today. My first exposure to the net gun method was at the 6th NACW in Prince George, British Columbia in 1994. The wildlife biologists in British Columbia had been using this method and had a video of the technique in use available for Workshop participants in the hotel lobby. My impression was that the technique worked to capture caribou, but how severe was the trauma to the captured caribou? Some netted caribou don't survive, one went over a cliff (I was told). No mention was made of injuries. The unknown was how the technique, when successful, influenced subsequent behavior and mortality. According to reports at the seventh and eighth NACWs, these radio-collared caribou in British Columbia (Heard & Vagt, 1998) as well as Alberta (Smith et al., 2000) and Yukon (Farnell et al., 1998) have provided them with the data needed to determine the location and range of their many separate caribou populations. This is very important for management decisions. We must use common sense, however, in the use of any caribou capture method that potentially causes injury or mortality and should rarely be employed with small, isolated populations.

Radio collars are providing valuable information on caribou populations across Canada and Alaska. However, there is little or no mention of injuries or fatalities during the capture process. In many cases the capture method is not described or a citation of a separate study is given. Shouldn't costs as well as benefits be presented so that other biologists can assess the suitability of the techniques for their needs? Even the distribution of radio-fixes from radio-collared caribou may be misleading if the traumatized, collared caribou avoids certain habitat features (alpine, for example) where they had been captured. It is possible that traumatized, radio-collared caribou (or marked by any method) may move to less optimal habitat to avoid the habitat type where helicopter disturbance occurred. The biologists using the radio-fixes to collect data, need to determine the representation of the information on a population scale. There is a need to test findings from radio-marked caribou in the field with unmarked caribou to varify conclusions.

Finally, I would refer the reader to "Panel Discussion: Human Developments and their effects on Caribou" summarized by Farnell (2000). If one specifically inserts the subject of "Research and Management" into this summary, especially into the topic covered by Stephen Murphy (pp. 116 - 117), the reader will become aware of a more elegant use of words to communicate the emphasis of this paper. Farnell includes Murphy's conclusion as "caribou are capable of habituating to many types of disturbances, however there are apparent intensity and frequency thresholds beyond which caribou can become energetically stressed or which will cause the animals to abandon the effected area." Helicopter use is especially pertinent here, but fixed-wing aircraft can also cause caribou stress along with snow machines and overland vehicles. Timing of these mechanized disturbances is crucial and wildlife biologists need to use common sense when caribou are vulnerable (physically stressed). As Farnell (2000, p. 121) stated, "the caribou research and management studies we carry out is in itself a human activity that can greatly effect caribou."

Conclusions

1. We as wildlife biologists need to respect the animals and their environment we are researching and managing.
2. In our research and management projects we need to use methods that minimize trauma to caribou.
3. When conducting research and management projects on caribou we need to be especially considerate of the people who reside in the caribou range and especially those who depend on caribou.
4. Caribou captured by any method, handled and marked may not provide information representative of the entire herd.
5. It is very important that we periodically test our basic assumptions, made during the planning stages of our caribou research and management projects, for their validity.
6. When observing caribou behavior and natural movements from the ground it is more productive to remain far away than to move closer.
7. When capturing, handling and marking caribou, the individuals released in the shortest amount of time will produce the most dependable data.
8. When conducting aerial surveys of caribou populations, classifying to sex and age or photographing from the air higher is better to collect data on animals that are stationary or moving naturally.
9. In the use of helicopters in caribou work be considerate of the caribou's fear, and its subsequent reaction to all helicopter exposure.
10. Published results of caribou investigations need to include the methods used and the problems experienced. It is not adequate to simply cite other studies or publications for methods used or problems incurred. A good discussion of problems experienced allows biologists who use the same methods to avoid similar pitfalls. We hope to seek truths not perpetuate errors.

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Estimation of arboreal lichen biomass available to woodland caribou in Hudson Bay lowland black spruce sites

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Abstract: An arboreal lichen index to be utilized in assessing woodland caribou habitat throughout northeastern Ontario was developed. The "index" was comprised of 5 classes, which differentiated arboreal lichen biomass on black spruce trees, ranging from maximal quantities of arboreal lichen (class 5) to minimal amounts of arboreal lichen (class 1). This arboreal lichen index was subsequently used to estimate the biomass of arboreal lichen available to woodland caribou on lowland black spruce sites ranging in age from 1 year to 150 years post-harvest. A total of 39 sites were assessed and significant differences in arboreal lichen biomass were found, with a positive linear relationship between arboreal lichen biomass and forest age. It is proposed that the index be utilized by government and industry as a means of assessing the suitability of lowland black spruce habitat for woodland caribou in this region.

Key words: woodland caribou, *Rangifer tarandus caribou*, black spruce, arboreal lichen index, logging.

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Introduction

Arboreal lichens represent a significant portion of woodland caribou (*Rangifer tarandus caribou*) forage throughout the winter season (Edwards et al., 1960; Edwards & Ritcey, 1960; Bloomfield, 1980; Van Daele & Johnson, 1983; Darby & Pruitt, 1984; Morash & Racey, 1990; Ouellet et al., 1996; Warren et al., 1996; Wilson, 2000). In Wells Gray Park, British Columbia, arboreal lichens consisting of foliose (*Cetraria* spp., *Parmelia* spp., *Hypogymnia physodes*) and fruticose species (*Bryoria* spp., *Usnea* spp., *Evernia* spp.) have been found to be the primary forage available to caribou during winter (Edwards et al., 1960). Winter survival of woodland caribou in the black spruce peatlands of northeastern Ontario also appears to be dependent on the availability of ground and arboreal lichen and arboreal lichen biomass has been shown to be an important parameter identifying late winter habitat selected by this species (Van Daele & Johnson, 1983; Wilson, 2000).

Arboreal lichens have been shown to be sensitive to disturbance and habitat destruction (Gilbert, 1977; Seaward, 1982; Esseen et al., 1996); however, there has been little quantitative analysis of the effects of forestry on lichen biomass (Esseen et al., 1996). Studies have indicated that logging eliminates most arboreal lichen species from harvested areas and that older forests with lower tree densities and canopy cover are associated with increased arboreal lichen biomass (Esseen et al., 1996). As logging is an important factor influencing lichen availability, the impact of logging on lichen ecology and biomass is an important issue for maintaining sustainable woodland caribou populations (Stevenson, 1979; Van Daele & Johnson, 1983; Hansen et al., 1991; Kouki, 1994; Esseen et al., 1996; Webb, 1996).

Van Daele & Johnson (1983) identified the need (1) to assess the impact of logging on arboreal lichen biomass and (2) to evaluate arboreal lichen biomass availability to woodland caribou. Stevenson et al.

Table 1. Arboreal Lichen Abundance Classes with number of trees sampled (n), mean arboreal lichen biomass (gm/tree between 0 and 4 m from ground), standard deviations of means (S.D.M.), standard errors of means (S.E.M.), and significant levels of ANOVA.

Class	n	Mean	S.D.M.	S.E.M.	F	P-value
1	6	0.73	0.30	0.12	94.545	0.001
2	6	1.35	0.11	4.51		
3	6	1.67	7.24	2.96		
4	6	1.91	9.81	4.01		
5	6	2.42	0.10	4.22		

(1998) developed a method for scoring arboreal lichen biomass on Engelmann spruce (*Picea engelmanni*) in British Columbia; however, a similar index has not been developed for conifer species in the Boreal Forest Biome.

For these reasons, the primary objective of this study was to develop a arboreal lichen index that could be used to visually estimate the arboreal lichen biomass available to woodland caribou in the boreal lowland black spruce communities of northeastern Ontario.

Material and methods

During the summer of 1999, black spruce trees north of Cochrane, Ontario were sampled from two sites identified from aerial photographs, as lowland black spruce habitat commonly utilized by woodland caribou in northeastern Ontario and northwestern Quebec (Wilson, 2000). Thirty randomly chosen black spruce trees were selected and each tree was visually classified and placed into one of five arboreal lichen abundance classes, ranging from minimal lichen to abundant lichen. The first 4.0 m of each tree was photographed and presumed to represent the height accessible to woodland caribou during winter (Van Daele & Johnson, 1983). Arboreal lichens were sampled using methods outlined by Van Daele & Johnson (1983). An estimate of lichen biomass available to woodland caribou on each tree was calculated by multiplying the number of branches within the first 4.0 m by the sum of the dry weights of the foliose and fruticose arboreal lichens removed from the same branches. Data were tested for normality and were considered to have a normal distribution, if skewness was less than ± 2.0. Log_{10} transformations were used if normality was not found. A one-way analyses of variance (ANOVA) was used to evaluate whether significant differences in arboreal lichen biomass occurred among the five arboreal lichen classes and a Pearson's correlation was used to determine whether a linear relationship existed. Photographs were used to assign trees to each class within each class.

To assess whether the arboreal lichen index could be used to estimate arboreal lichen biomass available to woodland caribou, thirty-nine plots (10 m by 10 m) from stands aged 1, 8, 30, 70, and 150 years were sampled. The 150 year-old black spruce sites were considered control sites and had not been previously logged. The 1 and 8 year old sites had been careful-logged using machines, while the 30 and 70 year-old sites had been careful-logged using horses. The careful-logged machine method was designed to simulate the careful-logged method using horses and minimized disturbance of the ground and shrub layer regeneration in the logged area. In each plot, live trees with a DBH (diameter at breast height) greater than 10 cm and heights greater than 6 m were counted to provide a measure of tree density and each tree was assigned to an arboreal lichen class. Arboreal lichen biomass was estimated for each tree and plot using the formula:

$$M = (4B)\,(Br)\,(N),$$

where, M = lichen biomass, 4 = number of segments per tree, B = mean lichen biomass per branch, Br = mean number of branches per segment, and $N = 1$ (number of trees) (Van Daele & Johnson, 1983). The four segments per tree (0.0 – 1.0 m; 1.0 – 2.0 m; 2.0 – 3.0 m; 3.0 – 4.0 m) were assumed to be accessible to woodland caribou during winter (Van Daele & Johnson, 1983). Biomass values were analyzed to test for normalcy and an ANOVA was used to determine significant differences in arboreal lichen biomass among stands (kg/ha) of different ages. A post hoc analysis (Tukey) was employed to identify where differences in mean arboreal lichen biomass per hectare occurred among the black spruce stands of different ages. A Pearson's correlation test was also used to calculate whether biomass was positively correlated with stand age. Statistical analyses were performed using SPSS 9.0 for Windows.

Results

Arboreal Lichen Index

The arboreal lichen biomass data had skewness at levels greater than ± 2.0 and required log10 transformations to produce values with a normal distribution. Class 1 represented minimum arboreal lichen abundance within the arboreal lichen index, while class 5 represented maximum lichen abun-

Table 2. Stand characteristics and arboreal lichen biomass (kg/ha) available to woodland caribou in lowland black spruce sites from northeastern Ontario (DBH=diameter at breast height).

Site Age (yrs)	Trees Sampled (n)	Mean DBH (cm)	Mean Number Branches/Segment	Mean Biomass/ Segment (g)	Lichen Biomass (kg/ha)
1	15	11.47	11.42	1.17	7.28
8	16	11.80	7.04	3.00	10.41
30	89	13.13	11.54	4.26	60.35
70	92	19.41	7.50	4.27	40.65
150	63	16.64	11.13	3.55	99.53

dance. The mean arboreal lichen biomass per tree for each of the five arboreal lichen classes was calculated and found to range from 0.73 g ± 0.12 (mean +/- SE) in class 1 to 2.42 g ± 4.22 (mean +/- SE) in class 5 (Table 1). Arboreal lichen biomass per tree varied and significant differences were found among the arboreal lichen classes ($F = 94.55$; $P < 0.001$). A general positive correlation was also found ($r = 0.82$; $P < 0.01$) between mean arboreal lichen biomass per tree and the five arboreal lichen classes.

Arboreal Lichen Biomass

Using the arboreal lichen index, the mean arboreal lichen biomass per hectare was calculated for each black spruce site and analyzed for changes with forest age. Arboreal lichen biomass per hectare ranged from 7.28 kg/ha on sites 1 year post-harvest to 99.53 kg/ha in 150 year-old sites. These data indicated that between 1 and 150 years post-disturbance, there was approximately a 92.69% increase in arboreal lichen biomass in lowland black spruce forest sites in northeastern Ontario and northwestern Quebec. The results indicated a general increase in arboreal lichen biomass (kg/ha) as the forest aged and stand age and arboreal lichen biomass were significantly and positively correlated using a Pearson's correlation ($r = 0.90$; $P < 0.05$). However, there was a significant decline in arboreal lichen biomass per hectare on 70 year-old sites (40.65 kg/ha) compared to 30 year-old (60.35 kg/ha) and 150 year-old sites (99.53 kg/ha). Table 2 outlines the characteristics of the trees and arboreal lichen biomass from sampled areas. The number of trees sampled was used to calculate tree density and the biomass of arboreal lichens (kg/ha). After biomass was calculated, significant differences between arboreal lichen biomass in the differently aged stands were found to exist using an ANOVA ($F = 12.24$; $P < 0.05$). Post hoc (Tukey) analysis indicated that the mean ($\log_{10}$) arboreal lichen biomasses per hectare for stands aged 1, 8 and 70 years post-harvest were not significantly difference from each other, but were significantly lower than that for stands 30 and 150 years of age. In contrast, the mean ($\log_{10}$) arboreal lichen biomass per hectare was significantly greater in stands 150 years of age than 30 years of age (Table 2).

Discussion

The results of this study support the conclusion that arboreal lichen biomass available to woodland caribou in lowland black spruce sites of northeastern Ontario and northwestern Quebec could be estimated using an arboreal lichen index developed specifically for this region. As significant differences existed among arboreal lichen classes, they were used to assess arboreal lichen production in multi-aged stands and calculate abundance, expressed as biomass per hectare. This expression integrates arboreal lichen abundance and tree density into a single measure, which can be used to assess differences in arboreal lichen biomass available to woodland caribou among sites. In addition, analysis of arboreal lichen dynamics and ecology can also be studied using this technique.

Information on arboreal lichen biomass would facilitate decisions regarding "cut and leave management" by forest and government managers in caribou habitat (Stevenson et al., 1998). Wilson (2000) concluded that biomasses of arboreal lichen ranging between 15 kg/ha and 81 kg/ha were characteristic of late winter habitat selected by woodland caribou in northeastern Ontario and were essential for sustaining woodland caribou populations in this region. In this study, stands aged 1 to 8 years post-harvest were found to have arboreal lichen biomass values that were less than those required to support woodland caribou as found by Wilson (2000). In contrast, stands of 150 years of age had excessive amounts of arboreal lichen compared to data presented by Wilson (2000).

Studies have indicated that clearcut logging eliminates most arboreal lichens from harvested areas and lengthens lichen rotation cycles by changing the microclimate and substrate (tree species) that supports the lichen community (Stevenson, 1979; Esseen et al., 1996). Because of their sensitivity to disturbances, lichens represent good indicators of forest integrity and health in the boreal ecosystem (Tibell, 1992; Selva, 1994; Esseen et al., 1996). Young managed stands have reduced lichen biomass compared to older undisturbed stands. Careful logging in this region shortens the rotation period of forests to approximately 60 to 80 years in black spruce dominated habitat. Studies of the long-term impacts of logging on forest understory have recorded a general increase in lichen abundance with time post-harvest; however, data were limited (Lesica et al., 1991; Hyvarinen et al., 1992; Tibell, 1992; McCune, 1993; Goward, 1994; Esseen et al., 1996; Brakenhielm & Liu, 1998; Esseen & Renhorn, 1998). The 30 and 150 year-old sites sampled in this study had more arboreal lichen biomass per hectare and more branches per tree segment between 0.0 and 4.0 m than the 70 year-old sites. In contrast, trees in the 70 year-old sites had the largest mean DBH suggesting that the mean age of trees on the 70 year-old site was greater than those of the 30 and 150 year-old sites. These results support the conclusion that trees on 70 year-old sites had reached their prime and the relatively closed upper canopy had caused natural pruning of lower branches and limited arboreal lichen development. In contrast, sites at 30 years and 150 years post-harvest had more open canopies due to younger age and blow-down, respectively, and light penetration to the forest floor may have facilitated lower branch growth and lichen development. In conclusion, the study indicated that mature black spruce sites not exposed to logging have increased biomasses of arboreal lichen and that sites with mature trees and a more open canopy may provide optimal conditions for lichen growth and woodland caribou.

As logging clearly impacts lichen biomass in lowland black spruce forests in northeastern Ontario and northwestern Quebec and lichen is the primary late winter forage for woodland caribou in this region, it is important to develop sustainable forest management practices that will sustain this species. It has been suggested that management techniques could be developed which would ensure adequate lichen abundance for woodland caribou and still sustain commercial forestry (Lesica et al., 1991; Esseen et al., 1996). In this regard, where site conditions are suitable for winter ranges, lichen biomass assessment methods developed in this study could be used to rank stands and identify potential woodland caribou wintering areas (Stevenson et al., 1998).

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Brief communication

Use of satellite telemetry data, GIS, and HTML to create an interactive display of caribou movements

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Key words: Alaska, animation, ArcView, Rangifer tarandus, Teshekpuk Herd.

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Introduction

Caribou from the Teshekpuk Herd in northern Alaska are an important subsistence resource for a number of native villages, and much of the herd range is within the National Petroleum Reserve–Alaska (NPRA). Because interest in oil and gas development within NPRA has recently increased, a cooperative study was undertaken to gain a greater understanding of herd distribution and movements.

It is often difficult to get an intuitive feel for the temporal aspect of caribou movements using maps depicting a series of caribou locations. In an effort to make caribou movement data more accessible to the general public, we used satellite telemetry data collected over a 10-year period from female caribou of the Teshekpuk Herd to create interactive animations of caribou movements. Here we present a method to create an interactive display using only basic knowledge of Geographic Information Systems (GIS) software and web page production.

Methods

Satellite data were collected from 27 different caribou of the Teshekpuk Herd for varying lengths of time during the period 1990–1999 as part of a cooperative study by the North Slope Borough, Alaska Department of Fish and Game, and U.S. Bureau of Land Management. Data were screened and one location of the highest quality rating score (provided by Argos, Landover, MD) was selected per duty cycle (generally one location per 48 hours).

Geographic Information Systems (GIS) are used to compile spatial data as a series of computer "layers" that allow the user to make detailed maps and explore spatial relationships among layers. We used this technology to create a series of maps that could be combined to form animations of caribou movements. Using ArcView GIS 3.2a (ESRI Inc., Redlands, CA), we developed a series of animations depicting caribou movements over this 10-year period. These animations were created with GIS and compiled in Hyper Text Markup Language (HTML) with text and figures to create an interactive computer display that could be used by anyone with basic knowledge of web browsers. Different animations were created for the entire 10-year period, annual movements, seasonal movements (winter, spring migration, calving and post-calving, insect season, late summer, and fall migration and rut), a sample of individual animals, and for movements near subsistence hunting areas. A total of 16 animations were included in the final display.

Software

We created image files (JPEG format) in ArcView GIS 3.2a using ArcView Tracking Analyst Extension. Image files were then converted to Windows Media™ Format files (extension .WMV) files using ImageN (http://www.pixoid.com) and Windows Media Encoder v.8 software. Windows Media™ Format files, text, and image files were combined in an HTML framework using Netscape Composer to create a graphical user interface viewable on computers with up-to-date web browsers and Windows Media Player or other software capable of playing WMV files.

The ArcView Tracking Analyst Extension allows the user to change symbols based on the location or the value of a data field, specify the speed of movements, the length of time symbols remain on the screen, and colors of symbols and arrows. Users create the background using standard GIS layers.

Conclusions

The use of animation clearly reveals the large annual variation in wintering areas and large differences in daily movement rates for this herd. This interactive display can be adapted for school groups, subsistence hunters, the general public, or scientists. Animations are effective for quickly portraying a large quantity of data to any audience, and they should be useful for educating the public and user groups about herd range, seasonal movements, and annual variation in distribution. Caribou movement animations also provide biologists with another tool to understand range use and identify important habitat and range areas. This method is easy to use and presentations with single or multiple animals can be made with basic skills in GIS and HTML.

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Session four

Population Dynamics and Behaviour

Naskapi Elder's Story:

Minnie Uniam, Kawawachikamach, Québec

Minnie Uniam was born in Fort Chimo on June 15, 1931 and grew up there. As a young bride, she raised her children in a tent and followed her husband, who was a migrant hunter and trapper. She came to Schefferville in 1956 and raised 10 children. Over the years, she has become a skilled craftswoman, and her work has frequently been exhibited at the Guilde des Métiers d'Art in Montréal and in a German museum.

For centuries, caribou provided food, clothing, shelter, and medicine for the Naskapis. Using only traditional tools and natural tanning ingredients, Ms. Uniam will demonstrate how caribou hides are prepared for their various uses.

The Ninth North American Caribou Workshop,
Kuujjuaq, Québec, Canada,
23–27 April, 2001.

Voles, lemmings and caribou - population cycles revisited?

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Abstract: Although we may be confident that many caribou populations fluctuate, we have not made much progress in linking patterns of fluctuations with their underlying processes. Caribou abundance is relatively synchronized across continents and over decades which points to climatic variation as a causative factor. Progress on describing intrinsic and extrinsic factors for smaller-bodied and larger-bodied mammalian herbivore population dynamics also reveals the role of climatic variation and specifically decadal variations. Based on experience elsewhere, we can expect complex relationships between caribou, climatic variation and their forage rather than simple correlations. Caribou responses to decadal trends in climate likely accumulate through successive cohorts as changes in body mass which, in turn, leads to changes in lifetime reproductive success.

Key words: *Rangifer tarandus*, abundance, decadal climatic variation, cohort memory.

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Introduction

If there is one thing that those knowledgeable about caribou *Rangifer tarandus* would agree on, it is that caribou abundance fluctuates over decades. However, agreement is less when it comes to describing the mechanisms underlying those fluctuations. Past North American caribou workshops have featured papers relaying or querying our progress in linking fluctuating abundance with the underlying processes. For example, Bergerud (1996) reviewed caribou population dynamics and Crête & Payette (1990), Valkenburg et al. (1994), and Whitten (1996) offered single herd case histories. Those papers largely relied on retroactively correlating abundance and vital rates (births, recruitment or mortality) with harvest, predation and weather events such as severe winters. This paper takes an alternative approach which is to summarize information on caribou abundance across North America and Greenland over centuries to see if that reveals hints about mechanisms underlying fluctuations in abundance.

This paper also approaches changes in caribou abundance through what can be learnt from other mammalian herbivores. Progress in understanding the mechanisms underlying the cyclic abundance of smaller-bodied arctic and sub–arctic herbivores (voles, lemmings and snowshoe hares (*Lepus americanus*) may be applicable to understanding caribou fluctuations. This is likely given the universality of scaling laws (fixed mathematical rules about the relationships within and between living organisms). Although there has been debate about the relationship between body size and mechanisms for population regulation, it ignored timescale. As Yoccoz et al. (1998) suggested that if for voles, months are considered equivalent to years, then their population dynamics are similar to larger bodied herbivores. Forage intake scales to body size and body size relates to age at maturity and fecundity. Lemmings and caribou have similar gut turnover times when corrected for metabolic weight (Batzli et al., 1980) and the average lemming cycle periodicity of 4 years scales to 71 years for a caribou of body mass 100 kg when scaled to power of $^1/_4$ (longevity scales as $^1/_4$).

This paper, then, asks four questions and discusses some possible answers: firstly what can be learnt from the fluctuations in caribou abundance at a larger geographic and longer timescale. Secondly and thirdly, what is to be learnt from the population dynamics of smaller and larger-bodied herbivores, respectively. And fourthly, where does the information take us? Before going further, it is worth quoting what Krebs (1996) wrote when reviewing population cycles: "Population ecology is not a baseball game in which one team wins and another loses. All our ideas will be revised and improved in the long run". In any body of knowledge, the current context is established by the efforts of those who preceded and this paper is no exception. The paper's title is a play on the title of Charles Elton's (1942) classic text 'Voles, mice and lemmings' as an acknowledgement of his pioneering work on cycles in the abundance of northern small mammals.

Terminology

Terminology describing the relationship between abundance and rate of increase is from Caughley (1987). Intrinsic regulation is when population density has an instantaneous effect on rate of increase (animals are doing something to each other for example, territoriality or dispersal). Extrinsic regulation is when the effect of increasing density on the rate of increase is indirect (mediated, for example, through forage supply, predation or parasitism/disease). If the rate of increase is predictable from density, the population trend is density-dependent or density-independent if the rate of increase does not correlate with density. Density-dependence is a correlation between abundance and rate of population change but one which reveals little of the underlying mechanisms. A common trap from the correlation is assuming herbivore abundance is exceeding available forage rather than testing to determine if the decline in forage is caused by the herbivores themselves, an environmental factor or both effects interacting. Intrinsic regulation is sometimes referred to as direct density-dependence and extrinsic regulation as delayed density dependence - the connotation of the delay is that population density acts on the rate of increase of the forage or through the numerical increase of a predator.

Population cycles have three phases (increase, decrease and low numbers) with measurable phase-related changes in reproductive rates and survival (Krebs, 1996). Phase-related changes are known for caribou in the increase and decline phase, but available data for the third phase is insufficient to determine if fluctuations in caribou abundance strictly meet this definition of cyclic.

Another term used in this paper is environmental stochasticity which is random and therefore unpredictable variability. Describing how environmental variability (usually climatic) translates as ecological effects is not necessarily simple (Laakso et al., 2001). Complexity also follows when the responses to environmental variability have a time lag.

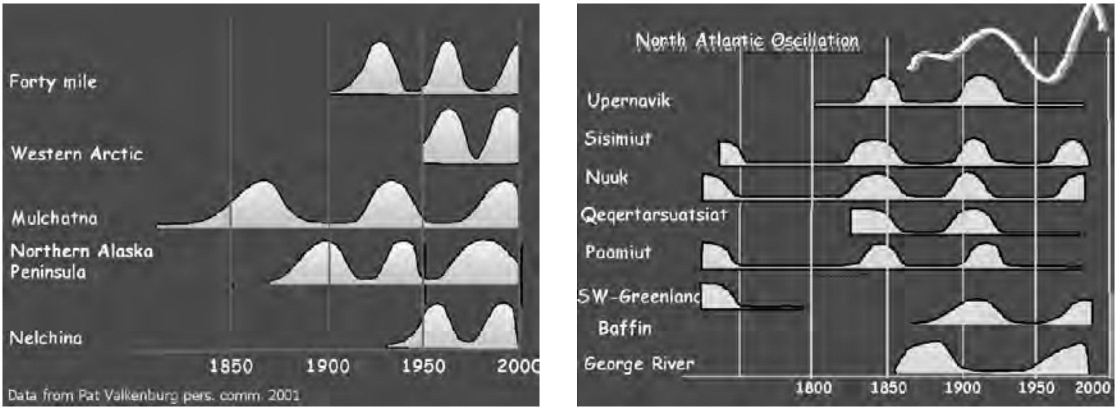
Fluctuating caribou abundance

The first question is whether considering caribou abundance at a larger geographic scale and longer time scale reveals anything about possible underlying mechanisms? Fluctuations in caribou abundance are known from survey data and can be extended back in time using archeological, historic, traditional aboriginal and dendroecological information (for example, Meldgaard, 1986; Ferguson et al., 1998; Morneau & Payette, 2000). The precise timing of the phases of increase, decrease and low numbers is dependent on sampling frequency, which contributes to variation between herds (Gunn & Valkenburg, in prep.). The mean doubling rate for Alaskan (P. Valkenburg unpubl. data) and Canadian barren-ground caribou herds is 10 ± 2.3 SE years and the mean halving rate 7.2 ± 2.6 years (the time taken for population to halve in size calculated from the exponential rate of increase: Caughley, 1977). Herds that increase slowly also are the herds that decrease slowly. The phase of low numbers is the most variable in duration (similar to smaller herbivores) and the ratio between maximum estimated and minimum size (amplitude) is 11 ± 2.2 years (3-24 range). The spread in amplitude suggests that a few herds such as the Porcupine herd fluctuate in size through a narrow range, which might suggest that they are 'trapped' in the phase of low numbers.

Reducing herds to a standard amplitude smoothes out noise and reveals some synchrony between phases of increase and decrease in western North America herds with most information suggests periodicity of between 40 and 70 years. Western North America (Fig. 1a) and Greenland and eastern North America (Fig. 1b) also have regular fluctuations that operate with a measure of synchrony on a sub-continental scale. The relative spatial synchrony on sub-continental scale suggests an external factor is spatially synchronizing the fluctuations and the most likely candidate is climate. Koenig (2002), for example, reported spatial synchrony in mean annual temperatures and rainfall over large distances which argues for environmental variation rather than dispersal in spatial synchrony.

Smaller herbivore cycles

Turning to the second question, which is what can be learnt from vole, lemming and snowshoe hare cycles?



Data from Pat Valkenburg pers. comm. 2001

(a) (b)

Fig. 1. Standardized fluctuations in caribou abundance in (a) Alaska and (b) Greenland and eastern North America .

Voles and lemming abundance cycles over 3-5 years with a low phase of 1-3 years and amplitudes can reach 200:1 (Krebs, 1996). Snowshoe hare abundance in boreal forest cycles at 8-13 years with a mean of 9-10 years. The amplitude is 50-180 depending on latitude. The variability in the cycle length is largely the duration of the low numbers phase. An additional characteristic is that spatial synchrony of peak abundance is regional (voles) or continental (snowshoe hares) (Krebs et al., 2002).

The generalized conclusion is that cycling in voles and lemmings is the consequence of extrinsic factors of predation interacting with food as well as intrinsic factors (Krebs, 1996). Earlier hypotheses and research concentrated on factors intrinsic to the animals themselves which were observable as phase-dependent qualitative changes. And although some ideas such as stress caused by crowding and the hereditability of spacing behavior did not stand the test of field data, other ideas were valid. For example, Lambin & Yoccoz (1998) determined that pup survival was higher in related family groups.

Predation appears to be more important in snowshoe hare cycles and snowshoe hares also differ from voles and lemmings if nothing else because they do not have spacing behavior or socially related survival. However, other forms of intrinsic mechanism are possible such as maternal effects that are the carry-over from early life (Krebs, 1996).

Environmental (climate) variability is also being advanced as a factor in population cycles and to explain their spatial synchrony (Sinclair et al., 1993; Yoccoz & Ims, 1999; Krebs et al., 2002). Population modeling is suggesting a case for stochasticity as a driving force in cycles as log-linear models mimic many of attributes of wild populations although without specifying the mechanisms (Stenseth et al., 1998). This is, in a sense, a reversion to earlier investigation which emphasized how winter and spring snow conditions modified predation levels. For example in Alaska, brown lemming *Lemmus trimucronatus* cycled 1949-1965 but then the populations fluctuated at low levels for 7 years partly due to unpredictable weather interacting with predation (Pitelka, 1973).

Larger herbivore population dynamics

Turning to the paper's third question which is what can we learn from the population dynamics of larger-bodied herbivores. The role of climatic variation is being increasingly acknowledged (Gaillard et al., 2000). Weather interacts with density dependence through directly and indirectly affecting forage availability and subsequently both fecundity and mortality (Saether, 1997) especially at higher herbivore densities. Grenfell et al. (1998) modeled the interaction between environmental noise and sheep *Ovis aries* density. The best-fit-model was non-linear with a density-dependent threshold below which population increased exponentially and noisily and above which environmental conditions determined whether numbers increased, stabilized or declined. Experimental evidence for the interaction of density-dependence and independence is, however, scarce. An exception is Portier et al. (1998) who experimentally tripled ewe density to examine interactions between density dependent and density independent factors for bighorn sheep *Ovis canadensis*.

Further evidence for the role of climatic variability is apparent from examining the relationships between decadal fluctuations in climatic variability and body mass and growth early in life. Climate variability occurs as repeatable patterns caused by teleconnections which are recurring and persistent, large-scale pressure and circulation anomalies on a sub-continental scale and over oceans (Hurrell, 1995; Brown & Braaten, 1998). The Pacific North American (PNA) teleconnection influences western North America and the Arctic Oscillation/North Atlantic Oscillation (NAO) influences eastern North America, Greenland and east to Europe. Characteristically, those teleconnections oscillate over decades switching from one mode to another.

In eastern North America, western Greenland and Europe, the North Atlantic Oscillation is the dominating feature as variation between Atlantic high and low pressure centers flips between two states. The positive NAO index is when Iceland low is enhanced which strengthens flow of northerly colder and drier airflow toward western Greenland reducing precipitation. When NAO is negative, more snow falls (NOA explains 59% of the annual variation in snowfall). The snow accumulation for 350 years has been indexed from ice cores which reveal that there are also trends imposed on the decadal oscillations. Since 1980, the index has tended to be positive and more variable but in the 1960s, it was frequently negative (Appenzeller et al., 1998).

The signals of the climatic oscillations are far-reaching: for example, their signature is detectable in plant growth (Post & Stenseth, 1999; Aanes et al., 2002), tree-growth and the timing of freeze-up and break-up (Robertson et al., 2000). The oscillations also coincide with changes in caribou abundance. The NAO index, when positive, coincided in the early 1900s and late 1900s with peak caribou abundance in western Greenland (Post & Forchammer 2002), Baffin Island and northeast Canadian mainland (Fig. 1b). Describing the effects of the decadal trends in climate variation is complex as for example, elevation can confound generalities (Loison et al., 1999). Elevation differences are greater among the ranges of the caribou herds in Alaska which may be why the Pacific North American teleconnection does not correlate closely with fluctuations in abundance.

The relationships between climate variability, forage and body mass are characterized by non-linear and reversed relationships (Mysterud et al., 2001). Body mass subsequently influences survival, age for reproductive maturity, adult body size and lifetime reproductive success. Complexity is increased by time lags: the effects of climate variability on intra-uterine growth may be compensated and if not, persist into adulthood leading to inter-cohort variation in body size and reproductive success (Post et al., 1997a). In Norwegian red deer, the effect of the North Atlantic Oscillation partially lagged at least 1 year. The effect of winter weather on fetal growth and birth mass was not fully compensated during calf's summer feeding and weather during gestation explained 13% variability in winter calf body mass (Loison et al., 1999). Subsequently, in the Norwegian red deer, the cohort differences persisted only for 2 and 3-year olds after which they were able to compensate and calve every year. In contrast, cohort effects persisted and reproduction paused in alternate years on the Island of Rum where deer abundance affects forage availability (Albon et al., 1987).

To summarize progress in population dynamics, in smaller-bodied herbivores, the interaction between forage and predation is relatively well described and there is evidence for intrinsic processes. The mechanisms for the role of environmental variation is less secure which is in contrast to larger-bodied mammalian herbivores, where the relationships are better understood. However, in the latter, relatively little has been studied about intrinsic factors or how predation interacts with foraging. In voles and snowshoe hares, it is the interaction between predation and forage rather than either alone or intrinsic factors (spacing and dispersal) also have a role. In both the smaller and larger bodied herbivores including caribou, the cycles or fluctuating abundance are spatially synchronized on a regional to sub-continental scale that suggests a pervasive factor and the most likely is climatic variation (the geographic scale and genetic distinctness of herds (K. Zittlau, unpubl. data) argues against dispersal as the main process for temporal and spatial synchrony in caribou fluctuations). The climatic variation is patterned into decadal trends and the ecological consequences of those decadal trends is beginning to be understood in large–bodied herbivore population dynamics.

Conceptual model for caribou fluctuations

We can propose a conceptual model for how caribou abundance responds to decadal patterns of climatic variation. Simple relationships between caribou abundance and weather are only likely during particularly severe events (shocks) and on the edge of the range. Elsewhere, relationships will be complex given for example, the functional and numerical relationship of caribou to forage plants which in their turn are dancing to the environmental variability (for example, Aanes et al., 2002).

Mechanisms for the relationship between climate and caribou abundance will operate through how variability in weather affects fecundity, mortality and dispersal. A key component is the tightly coupled relationships between forage intake, body mass, pregnancy and calf survival (Cameron, 1994; Russell et al., 1996; Griffith et al., 2002). The role of climatic variation does not preclude but adds complexity to the roles of predation and probably as well, parasitism. For example, Post et al. (1997b) detected the signature of the North Atlantic Oscillation in predator prey relationships and Stenseth et al. (1999) correlated regional synchrony in lynx (*Lynx canadensis*) with regional climates including NAO.

Trends in weather likely accumulate as cohort effects on body mass (cohort memory). Within the decadal timescale and at a regional scale, when weather trends are favorable, the caribou are in the increasing phase of abundance and are resilient with abundant forage readily available (high indices of condition and fecundity; high calf and adult survival). Calves during summer will be able to compensate any reductions in intra-uterine growth caused by variations in winter weather and buffer the annual variation in weather. Predator numerical response is also lagging.

Near peak abundance, fecundity and juvenile survival decline as the caribou are starting to affect their forage and are consequently less resilient to environmental variation. The decadal oscillation changes to a run of less favorable years with greater forage unavailability during winter and lag effects on summer plant growth as summers are cooler and cloudy (Aanes et al., 2002). Population increase slows and halts although exactly why the system switches so abruptly at the peak is unclear. However, the shape and duration of the peak is uncertain as it depends on the frequency of population estimates. The abruptness argues against predation but more that a threshold in resilience is exceeded. Predation increases due to the predator's numerical response but also the increasing vulnerability of prey in poorer body condition and their vulnerability in winters with more snow (cf. Post et al., 1997b). Predation likely accelerates the decline and then possibly maintains the low numbers phase.

One of the few data sets available to examine for cohort variability is from the Beverly caribou herd. March fetal weights annually varied (1980-87) presumably as the cows were facing different foraging conditions (D. C. Thomas, pers. comm. 2001). The variability between years within cohorts changes with age possibly due to growth compensation or 'weeding out' of individuals. Juveniles compensating for intra-uterine conditions are trading off between growth and accumulating body fat which raises interesting speculation about fitness, as body size is a factor in social status. In small social birds, for example, Gosler (1996) determined that social status and predictability of food determined fat reserves. Rate of fattening increased when food was less predictable. Those findings and social interactions of caribou during foraging hint at intrinsic regulation mechanisms.

Because the trends in climate variation are subcontinental they could serve to entrain the noisy dynamics of the caribou abundance and impose a sub-continental spatial and temporal synchrony. The variation between herds and each 'cycle' reflects differing strengths of interactions between factors and for example, dispersal opportunities, hunting levels and alternate prey to mention three levels of detail. The idea that weather, forage and predation are interacting to affect caribou abundance has also been suggested before (Valkenburg et al., 1994; Whitten 1996) but without possible mechanisms. The suggested role for cohort memory could be how more subtle changes accumulate even when the effects of variation in weather are not enough to cause conspicuous effects such as die-offs.

Climatic variation is unpredictable between years and accentuates seasonality but over decades, climatic variation is patterned and at longer time intervals is likely entrained by solar fluctuations. For example, the NAO correlates with sunspot peaks as indicated by strong oxygen isotope lows (proxy for winter temperature from ice core records) during the sunspot highs in the 1930s to 1950s. An example of how oscillating systems may be coupled is Sinclair et al.'s (1993) phase analyses for snowshoe hares cycles. Peak hare numbers correlate with browsing marks on white spruce tree-rings and the white spruce growth correlates with the annual snow accumulation measured from ice cores which has a 10.5 year cycle and 42-46 year cycle. Snow accumulation, tree marks and hare fur records cross correlate with sunspot activity (solar variability influences climate through effects in upper atmosphere). The solar cycles do not cause the hare cycles directly but entrain the different trophic levels including tree–growth and predation.

The likely role of the decadal fluctuations in climatic variability contrasts with Caughley & Gunn's (1993) explanation that the fluctuations were simply a consequence of a randomly variable climate. Even a weak negative feedback between an herbivore and its forage can interact within a randomly variable environment and cause apparently periodic fluctuations in abundance (Caughley & Gunn 1993). The model did not include the decadal fluctuations in climatic variation which may serve to strengthen the fluctuations through the cohort effect. Although the caribou-forage likely is a non-equilibrium grazing system (*sensu* Behnke, 2000), over the longer-term, the climate variability may be entrained by solar cycles similar to the arguments developed by Sinclair et al. (1993) for snowshoe hares.

The paper's fourth question was where do we go now? Given the status of many herds are at high abundance, we can focus on what happens at the peak - what halts the increase and what starts the decrease? Then, the question becomes what maintains the phase of low numbers which is when management (meaning regulation of hunting) becomes important. The answers include in measuring cohort differences and their relationship to trends in climatic variability. Monitoring fall calf body mass and survival may be adequate to track 'cohort memory' especially as juveniles likely contribute highly to annual variation in population growth (Gaillard et al., 2000). Measuring trends in climatic variation could include looking at the relationships between plant phenology and biomass data and forage intake which can then be modeled to predict effects on body mass. Consideration has to be given to describing which processes at which scale – from individual forage selection to the sub-continental scale where the coupling effects of stochastic entrainment operate. Hypotheses will have to be devised to start to determine how intrinsic factors including spacing (forage or mating opportunities) and spacing/dispersal strategies (reduce risk predation or parasites vs. forage) will interact with the extrinsic factors.

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Winter range drift in the George River Caribou Herd: a response to summer forage limitation?

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Abstract: Space use by the George River caribou herd (GRCH) changes in correspondence with migration patterns. The traditional range of this herd encompasses an area of approximately 900 000 km^2. Range use is seasonal and includes travel to traditional calving grounds. Winter range use however, is more variable. The GRCH has grown rapidly from 5000 animals in 1954 to approximately 775 000 in 1993. Beginning in the mid 1980s, the calving and summer range habitats of the GRCH have deteriorated, resulting in a decline in physical condition and subsequent poor calf survival and low pregnancy rates. We assessed the importance of the winter range as a food source compensating for poor summer range quality through an evaluation of winter range drift and use intensity. We hypothesized that if winter ranges provide a compensatory source of forage, then George River caribou should avoid sites heavily used during the previous winter at a population level. Winter ranges for the GRCH were calculated using 4300 caribou locations obtained 1986-2000. We found that in spite of a doubling in net range area, the size of annual winter ranges did not increase, indicating the occurrence of range drift. Further, George River caribou exhibited avoidance of wintering areas at several spatial scales. Avoidance occurred across a use threshold, where the degree of use (or density) during the previous winter determined the level of avoidance during the subsequent winter. As the spatial scale decreased, the degree of avoidance increased. Caribou significantly avoided areas used the previous winter at spatial scales below and including 245 km^2 (corresponding to a 75% use distribution). Results suggest winter foraging allows caribou suspend the effects of density-dependent summer forage limitation on herd productivity. As such, analysis of GRCH population trends should be considered in light of both summer and winter range resources.

Key words: habitat, Labrador, Nunavik, population ecology, range fidelity, Rangifer tarandus, spatial, telemetry.

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Introduction

The migratory George River caribou (Rangifer tarandus) herd (GRCH) is a vital wildlife species of the taiga of Labrador and Northern Québec, and has been an integral component of the way of life for aboriginal peoples for many centuries. In modern times, caribou meat remains an important food resource for many residents, particularly those residing in isolated northern communities. Currently, the GRCH provides the basis for a lucrative sports-hunting industry and developing commercial hunt.

A combination of traditional knowledge, historical records, and scientific censes suggest that this herd has undergone at least 2 population cycles, and that these have incorporated both periods of rapid increase and great abundance and precipitous declines (Couturier et al., 1990; Messier et al., 1988; Russell et al., 1994). Historical records suggest that caribou were abundant in the mid and late 1800s (Elton, 1942), but became rare beginning early in the 19th century. This lasted for a period of approximately 40 years, an event that resulted in widespread starvation of native peoples (Messier et al., 1988; Bergman, 1998). In 1958, a systematic aerial census indicated a population size of around 15 000 caribou

(Bergerud, 1967). For the next 30 years, the herd increased rapidly (annual rate of increase of 0.11 estimated from census data; Messier et al., 1988), eventually peaking at 775 891 (plus or minus 13.4%) caribou, including calves, in 1993 (Couturier et al., 1996; Russell et al., 1996). At that level of abundance, the herd was considered to be the largest in the world (Williams & Heard, 1986; Couturier et al., 1996).

During the late 1980s, several demographic indices including low pregnancy rates, poor adult survival, and declining physical condition, indicated that herd size had stabilized or begun to decline by the time of the 1993 census (Messier et al., 1988; Huot, 1989; Hearn et al., 1990). In 1985, Huot and Goudreault documented an unusual phenomenon for a northern ungulate: female caribou appeared to increase their fat reserves over the winter. However, they believed that the surprisingly poor fall condition of females was related to a sampling bias. Couturier et al. (1988) also presented data confirming that the fat reserves of female caribou were better in the spring than in the fall in during the 1980s. Their explanation for this unique phenomenon among caribou was based on the deterioration of the calving grounds of the GRCH. Generally, caribou increase their protein and fat reserves during summer, when forage is plentiful, and lose fat and protein during the long winters. Documented erosion of the quality of summer calving grounds (Couturier et al. 1990; Manseau et al., 1996) was a likely cause of the poor summer physical condition observed in the latter studies. The fact that caribou were nutritively stressed during summer led Messier et al. (1988) to suggest that forage limitation on the summer range may be an important component of population regulation in the large GRC herd. Expanding on that theory, Couturier et al. (1990) proposed that caribou might be using the winter range to compensate for the poor quality of the summer range.

The goal of this study was to test the importance of the winter range as a component of forage-dependent population regulation in the GRCH. If winter ranges provide a compensatory source of forage, then George River caribou should avoid sites heavily used during the previous winter. Our hypothesis was based on the assumption that the removal of terricolous lichens, the main winter food of caribou (Thomas & Hervieux, 1986), exceeds annual production on any given winter range (Arsenault et al., 1997; Couturier et al., 1990). We evaluated avoidance as a function of range drift, a spatial behaviour in which expansion occurs on one front while contraction occurs on another, and animal density. Specific objectives in our assessment of interannual winter range use in the GRCH included 1) determining changes in total (or cumulative) winter range size 1986 to 2000, 2) assessing long-term changes in annual winter range size, and 3) evaluating winter range fidelity (or avoidance) at the population level as a function of use intensity during the previous winter.

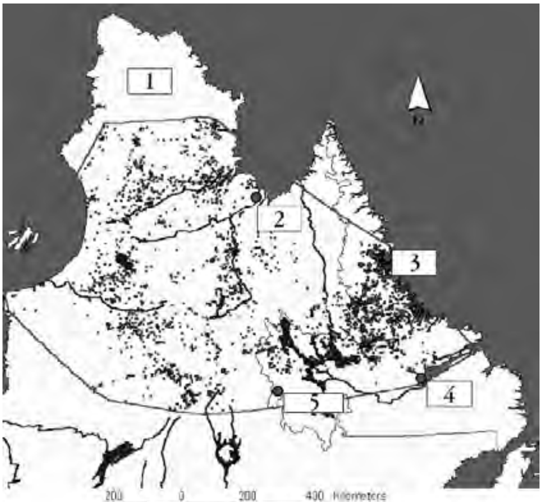


Fig. 1. Map of Labrador and Northern Québec showing the total winter range (Dec.-Mar. inclusive) of the George River Caribou Herd. Range boundaries are delineated based on 4306 locations (NQ 1-3) of 61 radio-collared animals, tracked from 1986-2000. 1: Ungava Peninsula, 2: Kuujjuaq, 3: Nain, 4: Goose Bay and 5: Labrador City.

Methods

Study Area

The George River caribou herd occupies much of the Ungava peninsula of Northern Québec and Labrador encompassed between the latitudes 54° and 61°N, an area extending from Hudson Bay to the Labrador Sea, approximately 900 000 km^2 (Fig. 1). The southern latitudes of this range are characterized by open lichen woodland composed of black (Picea mariana) and white spruce (P. glauca) and larch (Larix laricina) with a continuous lichen carpet (mostly fruticose species such as Cladina) or peatlands. Moving north, the taiga gives way to forest tundra that consists of stands of ericaceous plants (Ledum groenlandicum, Vaccinium spp.), dwarf birch (Betula glandulosa) and willow (Salix spp.). Most of the area north of 58° in Québec and 56° in Labrador consists of arctic tundra, a treeless area dominated by mosses, graminoids, lichens and water, although forest tundra persists in many river valleys. Elevation rises to approximately

1600 m a.s.l. on the height of land east of the George River and toward the Torngat Mountains in the east. Snow cover lasts from mid October to early May in the taiga, and approximately half of the annual precipitation falls as snow. Goose Bay receives an average annual snowfall of 440 cm (Goose Bay, 1951-1980 average), while forest and Arctic tundra receive about 224 cm of snow per year (30 year average ending 1980). The daily mean temperature during January for the villages of Kuujjuaq, Schefferville and Goose Bay, respectively, are -23.4, -22.7 and -13.4 °C, respectively.

Data Collection and Preparation

The study was conducted over a 14-year period for winters beginning 1 December 1986 and ending 1 March 2000. GR caribou belong to the migratory Rangifer ecotype (Bergerud, 1996), and their space use and movement changes in correspondence with sub-annual time periods. Bergman (1998) and Bergman et al. (2000) identified 6 such periods on the basis of mean daily travel rates and direction of travel. The winter period was characterized by low daily travel rates and hence reduced space use for the period December through April. As GR caribou tend to move north toward the calving grounds beginning in April (Bergman et al., 2000; NFWD unpubl. data), we restricted use of locations to the period January through March for each winter. We captured adult (≥ 1-year-old females) using chemical restraint agents, administered by dart fired from helicopter (1986-1997), or by using nets also fired from a helicopter (1998-2001). Captured caribou were fitted with satellite-tracked (Service Argos, Landover, Maryland, USA) ultra high frequency Platform Terminal Transmitters (PTTs; Telonics, Mesa, Arizona, USA). PTTs were set to 3 or 4-day transmissions cycles, and were replaced or removed prior to battery exhaustion. We tracked the movements of a total of 61 different animals over the study period. Service Argos Inc. provides 6 location quality classes based on the number of signals received by the satellite. These classes range from -2 (poorest) to 3 (highest, about 150 meters), and provide users with an estimate of location precision (Keating et al., 1991; Rodgers 2001). PTT locations belonging to location quality (NQ) classes 1 to 3 were selected on a basis of one location per transmission day for one particular collar. We discarded locations with NQ ≤ 0 due to their inherent imprecision (Keating et al., 1991; Rodgers 2001). In addition, data were plotted using a GIS and visually screened within each winter season and among individual animals per season, and any outliers were removed unless another nearby location of NQ 1-3 (equivalent to an accuracy of £ 1 km; Rodger 2001: 100) within the same transmission period could confirm them. Otherwise, the location was discarded. The resulting dataset contained a total of 4306 individual locations over 14 winter seasons. Table 1 summarizes the number of individual caribou, and the number of locations by quality class, for each of the 14 winters of the study.

Table 1. A summary of George River caribou winter location data, showing the number of individual caribou, and the number of locations by quality class (NQ), for each of the 14 winters of the study.

Winter	Number of locations			
season	NQ = 3	NQ = 2	NQ = 1	n
1986-1987	135	12	43	4
1987-1988	28	170	55	8
1988-1989	4	59	44	4
1989-1990	6	55	35	5
1990-1991	12	186	133	13
1991-1992	18	188	150	16
1992-1993	20	138	128	12
1993-1994	30	169	153	14
1994-1995	85	171	129	13
1995-1996	127	182	102	15
1996-1997	187	272	143	13
1997-1998	238	248	110	15
1998-1999	114	106	59	11
1999-2000	76	114	62	13

Data Analyses

Range Expansion and Drift

Changes in total GRCH winter range size 1986-2000 were calculated using a minimum convex polygon (MCP) home range estimator. MCPs are one of the oldest and most common methods used to estimate home range size (Mohr, 1947). The area polygon is constructed by connecting the outer locations to form a convex polygon, and home range size is then calculated as the area of that polygon (White & Garrott, 1990: 148). MCP home ranges were calculated using Arcview™ GIS and the 'Animal Movement' program (Hooge & Eichenlaub, 1998). By dividing the 14-year period into 5 segments of 2 or 3 years each, changes in winter range size over time were calculated by constructing the cumulative MCP (an outer boundary encompassing all radio-collared animal locations for a given time period), and calculating the area for each time segment. Changes in area over time were plotted. Because the size of minimum area polygons increases with number of animal locations, and because they do not reflect intensity of use within the polygon, they often overestimate home ranges (Jennrich & Turner, 1969; White & Garrott, 1990). However, their simplicity, data inclusivity, and the ease with which they may be calculated make MCPs a popular method for home range estimation. Additionally, further precision obtained by the use of a more sophisticated technique is unnecessary given the coarse time and spatial scale of pooled changes in winter range size.

To evaluate long-term changes in winter range size occurring as a function of range expansion/contraction, or range drift, annual winter ranges for several intensities of use were calculated and mapped for each of the 14 years of the study using a nonparametric kernel density estimator (Worton, 1995). Kernel estimators allow one to assess use distribution (UD) by creating a probability density estimate based on location data (Seaman & Powell, 1996). Proportional usage of different portions of the home range can therefore be estimated. The core area of a given probability is the area enclosed by a contour within which locations are closer together than would be expected under the assumption of uniform use of the home range area (Worton, 1987). Calculation of a kernel-based home range estimate requires that a grid be superimposed on the location data. The probability that each cell lies within the home range can then be calculated (UD), and a smoothing parameter 'H' (Worton, 1989) estimated. Using least squares cross-validation (LSCV), the smoothing parameter that minimizes discrepancies between the estimated and true densities is selected (Worton, 1995). The bivariate normal density kernel with least squares cross-validation of the smoothing parameter has been shown through simulations to produce the most accurate home range estimates among several available nonparametric methods (Seaman & Powell 1996).

We calculated and plotted 50, 75, and 90 percent probability polygons using Arcview™ GIS and the 'Animal Movement' program (Hooge & Eichenlaub, 1998), which uses the Worton (1989) algorithm. Least squares cross validation was used to calculate an optimal smoothing parameter for each year. Grid size was set at 5 km^2 for all analyses. However, area values increase at higher levels of 'H', and, given that optimal 'H' values differed between years, the smoothing parameter was fixed in order that area estimates between years be comparable. The value of the fixed parameter was determined by taking the median value based on all LSCV calculated winters. Probability polygons for each winter season were then recalculated using the fixed smoothing parameter. Table 2 lists the values of the LSCV calculated 'H' and the fixed value used for the final area calculations.

Table 2. A comparison of cross-validated and model-forced smoothing parameters calculated for GRCH winter ranges 1986-2000, showing discrepancies between estimated and true densities. Parameters calculated using least squares cross validation (LSCV) are shown relative to the median value that was forced into all final models. For years with an LSCV-based smoothing parameter lower than the median value, probability polygons will overestimate true areas. Conversely, if LSCV values are larger than the (forced) median values, probability polygons will underestimate actual areas. Note that no pattern of consistent over/under estimation occurs. Accordingly, study results are not an artefact of the algorithms used to estimate winter range size in the George River caribou herd.

Winter season	LSCV based H	Forced H (Median value)	Estimate?
1986-1987	36.3	46.7	Over
1987-1988	57.6	46.7	Under
1988-1989	46.6	46.7	Good Fit
1989-1990	64.9	46.7	Under
1990-1991	80.7	46.7	Under
1991-1992	46.9	46.7	Good Fit
1992-1993	47.4	46.7	Good Fit
1993-1994	45.9	46.7	Good Fit
1994-1995	65.3	46.7	Under
1995-1996	25.3	46.7	Over
1996-1997	32.5	46.7	Over
1997-1998	40.9	46.7	Good Fit
1998-1999	42.9	46.7	Good Fit
1999-2000	87.7	46.7	Under

Over the course of the study period, the number of radio-collared caribou (and thus the number of locations) ranged from 4 to 19 (96-569 locations). To evaluate the possible influence of variation in sample size on the area calculations, we plotted the number of radio-collared caribou and the number of locations, respectively, with area estimates for each probability polygon, and visually assessed each for any linear trends.

Winter Range Fidelity

To evaluate inter-year fidelity in GR caribou to win-

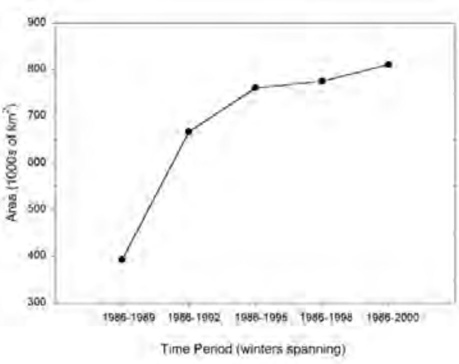


Fig. 2. Cumulative winter range size in the George River caribou herd 1986-2000, based on 100% MCP for each time period indicated (n = 4306).

tering areas, avoidance of sites used in subsequent winters was assessed at several spatial scales and degrees of use intensity. If winter forage is an important determinant of winter range use and site selection, then the probability of caribou occurring in an area one year should be negatively related to the probability of occurring in the same area the following year, particularly at higher use intensities. Based on this principle, we assessed avoidance to wintering areas used in preceding years at 5 spatial scales. In order to link use intensity to avoidance or fidelity behaviors, scales associated with mean values for 50, 75 and 90 per cent contours were chosen. These corresponded to a grid size of 320 km^2 (15 grid cells), 245 km^2 (24 grid cells) and 150 km^2 (60 grid cells), respectively. Additional scales were added at the landscape level, set at 500 km^2 (6 grid cells), and at the individual level, set at 100 km^2 (135 grid cells). A smaller scale was not selected to reduce the possibility that animals occur in multiple cells within the same year. In order to keep cell locations consistent among years, the same grid extent was used for all analyses, and pooling winter locations for the entire 14-year period set its boundaries. Radio-collared animal density was estimated using two methods: first by counting the number of radio-collared animals, and second by counting the number of locations observed by radio transmissions within each cell, for all 5 spatial scales. Spearman rank correla-

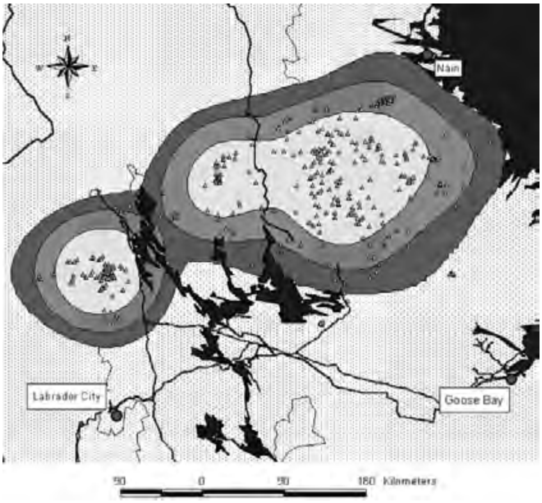


Fig. 3. An example of a kernel home range estimate for winter 1995-6, showing probability contours for 50, 75, 90 per cent use distributions. Observed animal locations are superimposed on the kernels.

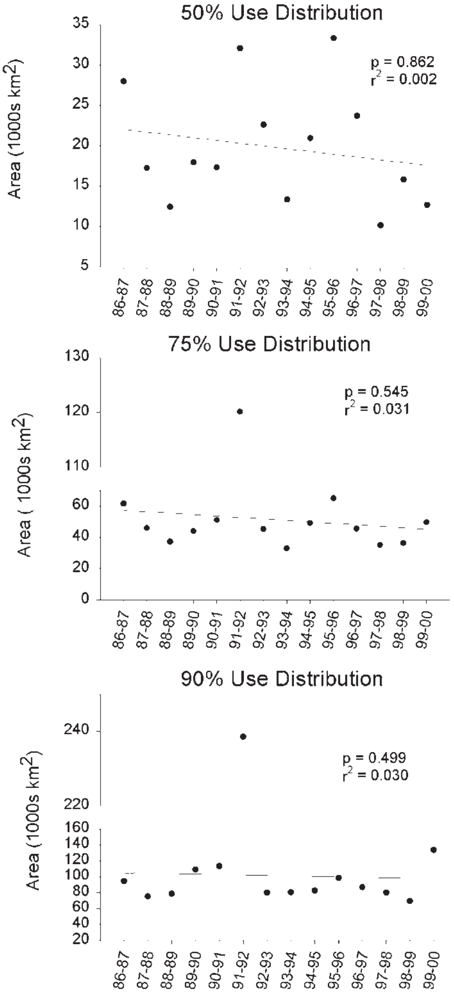


Fig. 4. The relationship between winter range size and year for George River caribou for three different use distributions for the period 1986-2000. No significant trends in winter range size over time exist.

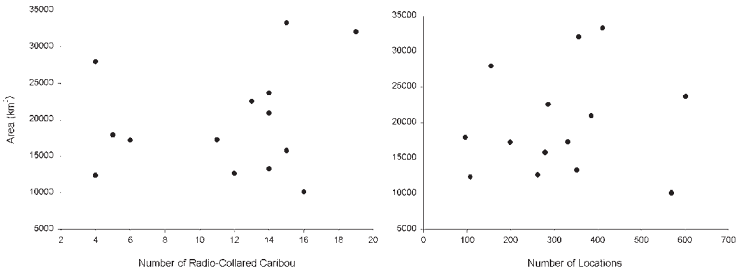
tions were used to compare cell densities (animals and locations) at time t versus time t-1, and a significant negative relationship among years was interpreted to indicate avoidance. Double 0's were disregarded. This analysis was repeated for each spatial scale.

Results

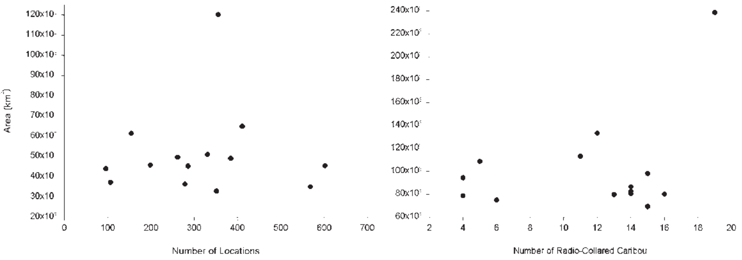
Range Expansion and Drift

The cumulative winter range of the George River caribou herd doubled in size during the period 1986-2000, from 392 796 km^2 (1986-1989) to 811, 138 km^2 (1998-2000) (Fig. 2). Much of this increase occurred prior to 1995; areas calculated based on the 100% MCPs show a marked expansion of winter range size of about 90% from 1986 to1995, and a gradual increase thereafter (Fig. 2). However, while the total (or cumulative) winter range of the GRCH increased, this expansion did not occur as a result of an increase in winter range size over time, but rather as a consequence of range drift. Fig. 3 shows an example of annual winter range size calculated using a kernel home range estimator for 50, 75 and 90 percent-use distributions. No significant relationship in annual winter range size over time was observed at any of the latter use intensities ($P = 0.862$, $P = 0.545$, $P = 0.499$, respectively) (Fig. 4). This result is unlikely to be the product of use of a fixed smoothing parameter, as the forced median value provided a good approximation of LSCV calculated values, and no pattern of consistent underestimation was observed (Table 2). In most cases, the forced median value was a good approximation of LSCV calculated values, and succeeded in minimizing discrepancies between estimated and true densities. Exceptions include the winters of 1990-1991 and 1999-2000, in which winter range size were underestimated, and the year 1995-1996, in which areas were overestimated through use of the fixed smoothing parameter (Table 2). Further, area estimates for all probability polygons did not vary with either the number of radio-collared caribou or the number of locations per year (Fig. 5), a feature indicating that changes in winter range size over time are not an artefact of variable sample size between years.

a) 50 % Use Distribution



b) 75% Use Distribution



c) 90% Use Distribution

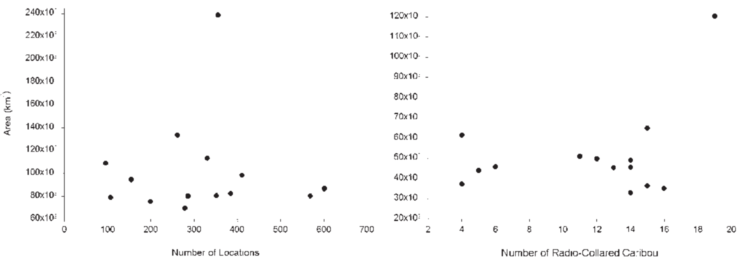


Fig. 5. Area estimates for 50 (a), 75 (b) and 90 (c) Probability Polygons as a function of the number of satellite-derived locations and radio-collared caribou, respectively. The absence of a positive linear relationship indicates that changes in winter range size over time cannot be ascribed to variable sample size between years.

Winter Range Fidelity and Avoidance

George River caribou exhibited avoidance of wintering areas at several spatial scales. Avoidance occurred across a use threshold, where the degree of use (or density) during the previous winter determined the level of avoidance during the subsequent winter (Table 3). At the landscape scale (500 km^2) and for the area associated with the 90% use distribution (320 km^2), caribou exhibited neither avoidance nor

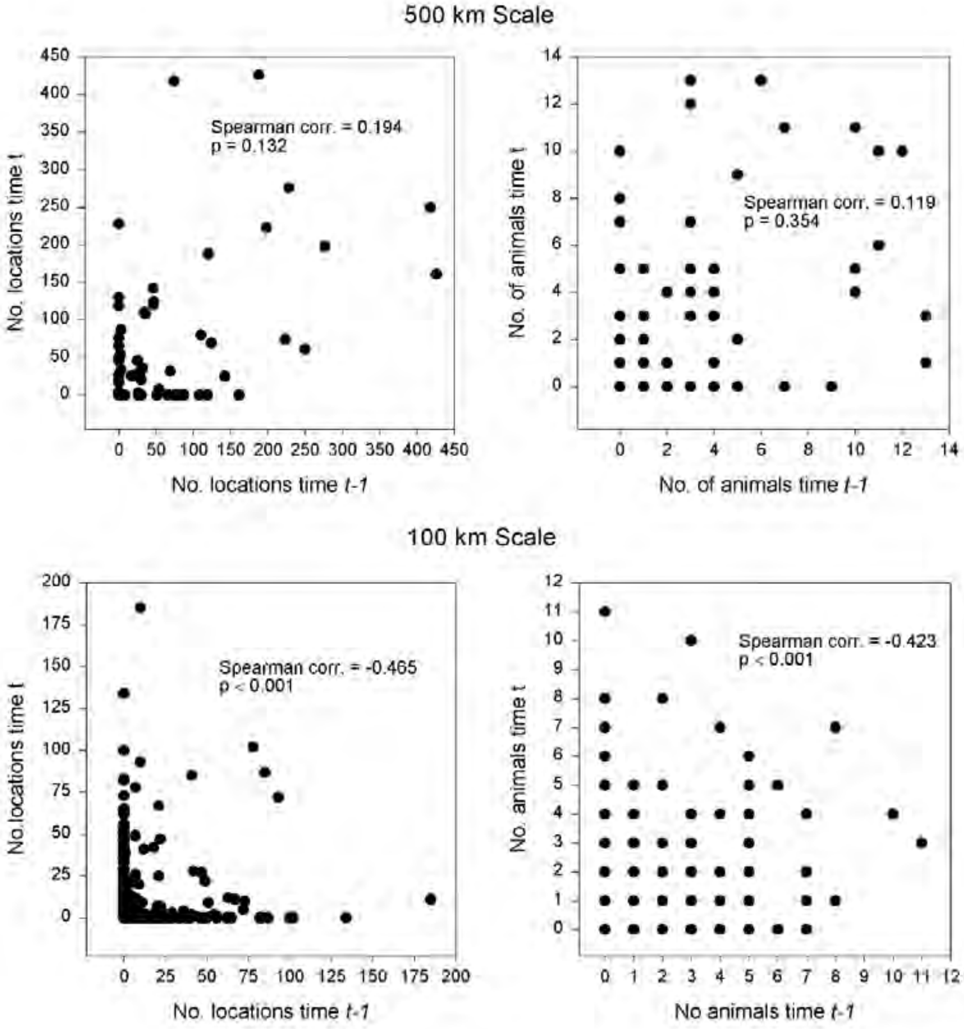


Fig. 6. An example of inter-year winter range use in the George River caribou at two levels of use intensity (500 km and 100 km spatial scales). Caribou density at time t is plotted as function of density at time t-1. At the landscape level, caribou do not avoid areas used during the previous year. At smaller scales (and thus greater levels of use intensity) however, caribou avoid areas used extensively the previous year.

fidelity (Table 3, Fig. 6). However, caribou significantly avoided areas used the previous winter at spatial scales below and including 245 km^2 (corresponding to a 75% use distribution) (Table 3). As the spatial scale decreased, the degree of avoidance increased. For example, at the 100-km^2 scale, location and radio-collared animal density explained 47% and 42% of the variation in the following winter, respectively ($P < 0.0001$). That is, there was an almost 50% probability that there would be little use in presently heavily used cells in the following winter at that spatial scale. The same patterns were observed in both indicators of use intensity, though trends were more pronounced in the location density estimator. The latter could be due to the fact that location density within grid cells incorporates time spent at the location: a high number of locations within an area are a product of both the number of animals in the cell and the duration of time spent within the cell. Given this characteristic, location density is probably a better indicator of use intensity.

The large winter range size observed over 1991-1992 at 75 and 90 per cent use (Fig. 4, outlier) distributions reflects range use by the GRCH during that winter: radio-collared animals were widely dispersed among 3 focal areas, two in close proximity just north of the Smallwood Reservoir, and a 3rd much further NW, near Ungava Bay. At higher use distributions (an hence lower animal densities), larger portions of location data are included within the probability polygon, thus dispersion of location data across the landscape will also result in larger area estimates (but accurate depictions of the distribution of radio-collared animals during that period).

Discussion

Ecotypic designations of Rangifer have been established on the basis of site fidelity, the propensity of animals to remain in or return to a particular place, during parturition (Bergerud, 1996). The George River caribou are migratory, traveling large distances over the Québec-Labrador peninsula, and aggregating on traditional calving grounds each June, thereby displaying one of the most consistent behaviors of migratory caribou (Gunn & Miller, 1986). Winter ranges however, are far less predictable. Schaefer et al. (2000), in a multi-scale study of site fidelity in the GRCH, found that individual caribou displayed no philopatry to wintering areas. They denote a distinct annual rhythm where average distances in inter-year locations during winter for individual animals was 400-450 km (Schaefer et al., 2000). Indeed, it is widely believed that one of the most predictable characteristics of caribou winter ranges is that they are unpredictable. Consequently, shifts in winter ranges are not well known. Ferguson & Messier (2000) documented mass winter emigration of caribou in Canada's high Arctic between 1984 and 1992, and proposed that the range shift occurred as a result of forage depletion caused by long-term overgrazing. Winter range drift allowed caribou to maintain access to adequate forage, and caribou that emigrated to ungrazed winter areas improved their body condition (Ferguson & Messier, 2000).

Range drift was associated with a density-dependent response to forage limitation in the GRCH. Forage depletion occurs rapidly in lichen-dominated subarctic and arctic woodlands given the low productivity of these regions. Further, the standing crop of terricolous lichens is the product of several decades of annual production (Arsenault et al., 1997). Studies on the influence of caribou winter grazing on the landscape have suggested that lichen removal exceeds annual production (Arsenault et al., 1997), and that consequently lichen may become progressively depleted through both consumption and trampling (Klein, 1987; Messier et al., 1988). By shifting winter ranges, George River caribou maximize their intake of winter forage, possibly compensating for the poor quality of their summer range (Manseau et al., 1996). Huot & Groudreault (1985) observed that female caribou shot in April 1984 were fatter than those shot in the fall of 1983. Poor physical condition of George River caribou in fall, an unusual occurrence for herbivores in northern ecosystems, was also documented by Couturier et al. (1990). During the period 1983-1987, winter survival of this herd generally increased or remained stable during the winter, yet declined during the summer (Hearn et al., 1990).

The relative importance of summer versus winter ranges to caribou population productivity and physical condition, however, is controversial. In a study of a southern Alaska Peninsula caribou herd, Post & Klein (1999) found that differences in forage availability and quality on winter ranges were of secondary importance in explaining differences in herd productivity. However, they qualified their interpretation by emphasizing the importance of a good quality summer range for this to be true. Additionally, winter ranges of poor quality were able to reduce the productivity of the herd, though to a lesser degree than summer ranges (Post & Klein 1999). Alternatively, Skoglund (1985; 1986) found that a decline in female body size, and a reduction in recruitment in populations of wild reindeer were attributable to winter food limitation, and that these effects were most apparent at high population densities. With respect to the GRCH, summer nutrition has been linked to poor physical condition and insufficient milk production in female caribou (Crête & Huot, 1993). The demographic consequences of sub-optimal summer foraging were falling pregnancy rates and decreased survival (Crête et al., 1996). Collectively, these traits indicate that summer nutrition is an important component of population regulation in the GRCH (Messier et al., 1988, Hearn et al., 1990; Crête & Huot, 1993; Crête et al., 1996).

Nonetheless, this study shows that George River caribou shift winter range use between years, and that range drift is associated with use intensity (below a use threshold), where more use presumably results in added forage depletion, and leads to subsequent avoidance during the following winter. This study suggests that the relative importance of winter or summer ranges to population trends may be dynamic, and contingent on the quality of the summer range. If, as is the case for the GRCH, the summer grounds are overgrazed, then winter foraging (and hence winter ranges), may be used to compensate for the poor quality of the summer range. Winter foraging thus allows caribou to ameliorate their physical condition and suspend the effects of density-dependent summer forage limitation on herd productivity. In situations were the summer range contains abundant, nutritious forage, winter ranges may be of diminished importance to the productivity of caribou (as in Post & Klein, 1999). Regardless, the available evidence underscores the importance of forage limitation as a mechanism of population regulation in the GRCH, and suggests that caribou population trends should be considered in light of both summer and winter range resources. We propose the following hierarchical model to estimate the potential importance of summer and winter ranges to herd productivity. The model is contingent on the quality of the summer range: if it is good or adequate, winter range use is of secondary importance. If the summer range has deteriorated, winter ranges become increasingly important as a compensatory mechanism. If both summer and winter ranges are in poor condition, or if appropriate winter habitat is located prohibitively distant from the summer range, then the population is in imminent danger of collapse. A declining population trend (Couturier et al., 1990), an overgrazed summer range (Manseau et al., 1996), poor fall physical condition (Couturier et al., 1988; Huot, 1989), and the occurrence of winter range drift all suggest that currently, winter ranges are an important component of the population dynamics of the GRCH.

The population consequences of compensatory winter foraging by the GRCH may be dramatic fluctuations in population size caused by delayed density-dependent effects (Messier et al., 1988; Couturier et al., 1990). In shifting winter ranges once a use threshold is reached, caribou expand their cumulative range and may continually access areas with ample forage (Ferguson & Messier, 2000). In theory, this behavior would be successful in delaying the physical and demographic effects of overgrazing on the summer range as long as there was no shortage of areas with sufficient forage to access, or until the distance traveled to new wintering areas were to exceed the energetic benefits obtained from foraging within them. If the latter criteria were to occur, the population would have nowhere to go but down as the full effect of density-dependent forage limitation is experienced. Messier (1994) and Saether (1997) have suggested that a stable equilibrium between large herbivores and their food supply is unattainable in situations where delayed-density dependence is occurring through compensatory foraging, and in the absence of large numbers of predators. Accordingly, large, possibly cyclic fluctuations in population size have been observed in North American caribou herds, including the GRCH (summarized in Couturier et al., 1990).

In order to clarify the nature of interactions between habitat use in the George River caribou and linkages to population dynamics, further research is necessary. Most importantly, information on space use must be joined with associated demographic parameters such as survival and fecundity, and with seasonal and annual changes in physical condition. Also, behavioral research centered on activity budgets and degree of mobility should be combined with measures of use intensity to assess winter range quality. Finally, a model simulating the energetic costs associated with range drift should be developed. Collectively, the latter research projects would allow for the development of realistic models of the population dynamics of a northern ungulate highly adapted to life in a subarctic environment.

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Modeling the decline of the Porcupine Caribou Herd, 1989–1998: the importance of survival vs. recruitment

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Abstract: The Porcupine caribou (Rangifer tarandus granti) herd increased from approximately 100 000 animals during the 1970s to 178 000 in 1989, then declined to 129 000 by 1998. Our objective was to model the dynamics of this herd and investigate the potential that lower calf recruitment, as was observed during 1991-1993, produced the observed population changes. A deterministic model was prepared using estimates of birth and survival rates that reproduced the pattern of population growth from 1971-1989. Then, parameters were changed to simulate effects of lower calf recruitment and adult survival. Reducing recruitment for 3 years caused an immediate reduction in population size, but the population began to recover in 5-6 years. Even a dramatic temporary reduction in recruitment did not explain the continuing decline after 1995. In contrast, a slight but persistent reduction in adult survival caused a decline that closely followed the observed pattern. This suggests that survival of adults, and perhaps calves, has declined since the late 1980s.

Key words: Alaska, population model, Rangifer tarandus.

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ntroduction

The Porcupine caribou herd (PCH) has been the subject of a variety of research and monitoring efforts that began during the early 1970s, increased greatly during the 1980s, and has continued at a reduced level since 1994 (Griffith et al., 2002). Throughout this period, a series of surveys were conducted to estimate population size by counting caribou on aerial photographs taken during the post-calving period. In addition, research during the 1980s provided estimates of parturition, survival, and sources of mortality of calves and adults (Fancy et al., 1989, 1994; Fancy & Whitten, 1991; Whitten et al., 1992). Since 1994, fieldwork has been focused primarily on estimating parturition rates and survival of calves during June, photographic population estimates at intervals of 2–4 years, and estimating the age and sex composition of the herd during late winter (Stephenson, 1999). Some additional data have been collected regarding body condition and the occurrence of diseases (Farnell et al., 1999).

During this period, the PCH increased from approximately 100 000 caribou in 1970 to 178 000 in 1989. From 1990–1998, the herd declined at a rate of 3–4% per year, and was estimated at 129 000 in 1998 (Stephenson, 1999). No measure of sampling variability is available for these surveys; thus, it is not possible to estimate confidence levels for the presumed changes among years. However, identical methods were used for all surveys, and the decline was consistent across surveys from 1989–1998, contrary to what would be expected if differences were due to random errors. Thus, we assumed that the indicated trend did exist, and that the magnitude of the decline was similar to what the surveys suggested.

From 1990–1993, a series of environmental events occurred that greatly reduced calf recruitment, as

Table 1. Summary of demographic data for the Porcupine Caribou Herd, 1987-2000. Data are from Fancy et al. (1994), Alaska Department of Fish and Game (unpubl.) and Yukon Department of Environment (unpubl.).

Year	Cows Observed[a]	Parturition Rate (%)	June Calf Survival[b]	1 July Calf:100 Cows[c]	Population Estimate[d]
1987	51	78	71	55	165 000
1988	91	84	65	55	
1989	74	78	74	58	178 000
1990	74	82	90	74	
1991	74	74	82	61	
1992	78	86	57	49	160 000
1993	63	81	56	45	
1994	98	91	77	70	152 000
1995	95	69	86	59	
1996	74	89	81	72	
1997	48	75	77	58	
1998	58	83	82	68	129 000
1999	39	84	83	70	
2000	44	73	60	44	
Mean	69	81	74	60	

[a] Number of radiocollared cows for which parturition status was determined. Parturient cows include those seen with calves and those judged to be pregnant or to have recently given birth to a calf that was not seen (Whitten, 1995).

[b] Estimated as July calf:cow ratio divided by parturition rate.

[c] Includes only radiocollared adult cows ≥3 years old.

[d] Total population estimated from photographic counts.

indicated by estimates of parturition and survival during June. Deep snow on the herd's winter range during the winter of 1990–1991 was followed by a reduced parturition rate during 1991. The following winter was relatively mild, but persistent snow cover delayed spring migration. The summer of 1992 was short and cool, influenced by lingering effects of the eruption of the Mt. Pinatubo volcano the previous year. Although parturition was relatively high in 1992, calf survival during June was low. The winter of 1992-1993 was again characterized by deep snow, and parturition rate was low during 1993. The combined effect of this series of events was that the ratio of calves:100 cows during July 1993 was the lowest recorded during the 1990s (Table 1).

Soon after the decline began, two modeling studies were published wherein the authors attempted to evaluate potential causes of the decline. The first of these (Fancy et al., 1994) used a deterministic spreadsheet model based on birth and survival rates that had been estimated from radiocollared caribou. The second study (Walsh et al., 1995) used a stochastic model to evaluate potential effects of changes in birth rate and calf survival on herd size. Both of these models were sensitive to changes in adult survival rates and calf recruitment. Because reported harvest levels had not increased and measures of winter body condition remained relatively high, it was believed that changes in the population were largely influenced by reduced recruitment, although small changes in adult survival might also have contributed to the decline (Fancy et al., 1994). This was thought to be a temporary condition that would be reversed as the larger cohorts produced after 1993 entered the adult population (International Porcupine Caribou Board, 1998). However, despite favorable weather and increased rates of parturition and early calf survival from 1994–1998 (Table 1), the decline continued. Thus, our objective was to model the dynamics of the PCH to evaluate whether 3 years of reduced recruitment could account for the observed decline, or if some other change might have occurred.

Methods

Fancy et al. (1994) estimated parturition rates and survival of radiocollared calves (1983–1985 and 1988) and adults (1982–1991) of the PCH using the staggered entry product-limit method of Pollock et al. (1989). We used similar methods to estimate survival of radiocollared adult females during 1997–2001. However, beginning in 1993, calves were not radiocollared and radiocollared adult caribou were

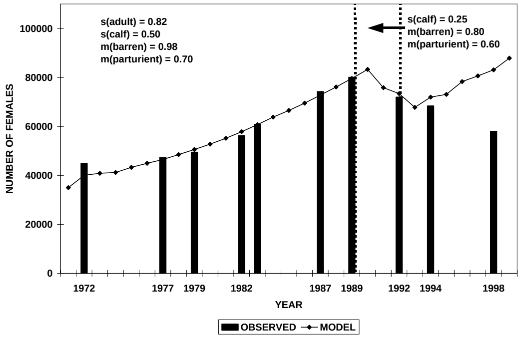

Fig. 1. Observed and predicted changes in population size of female Porcupine caribou, 1971–1999. Observed data are from photographic counts, assuming adult females were 45% of the herd. Predicted data are from a model using the specified parameters for survival (s) and birth rate (m), with a reduction during 1991-1993. Birth rates differ depending on parturition status during the previous year (barren or parturient).

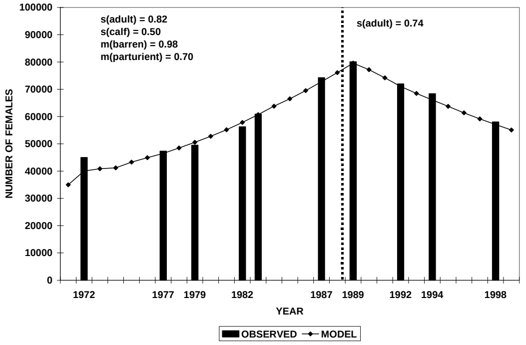

Fig. 2. Observed and predicted changes in population size of female Porcupine caribou. Observed data are from photographic counts, assuming adult females were 45% of the herd. Predicted data are from a model where survival rate (s) of adults was reduced during 1990–2001. Birth rates (m) differ depending on parturition status during the previous year (barren or parturient).

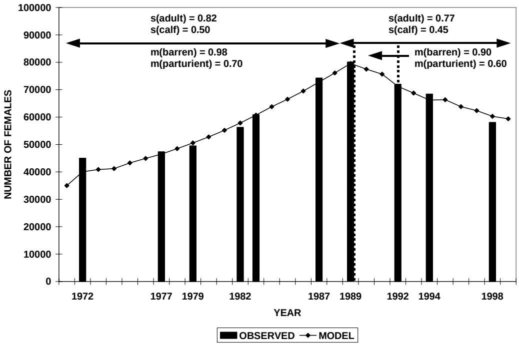

Fig. 3. Observed and predicted changes in population size of female Porcupine caribou. Observed data are from photographic counts, assuming adult females were 45% of the herd. Predicted data are from a model where survival rate (s) of adults was reduced during 1990–2001 and birth rates (m) were reduced during 1991–1993. Birth rates differ depending on parturition status during the previous year (barren or parturient).

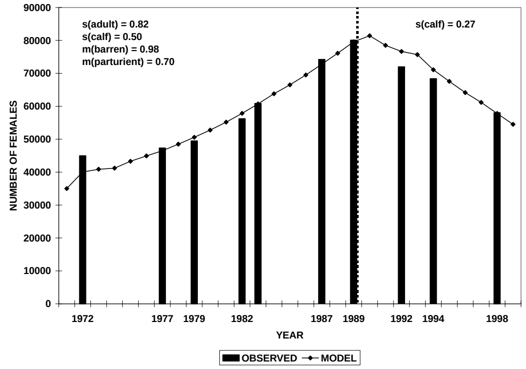

Fig. 4. Observed and predicted changes in population size of female Porcupine caribou. Observed data are from photographic counts, assuming adult females were 45% of the herd. Predicted data are from a model where survival rate (s) of calves was reduced during 1990–2001. Birth rates differ depending on parturition status during the previous year (barren or parturient).

located less frequently, so annual survival rates could not be estimated as precisely as in earlier years. Because of infrequent radio locations, we assigned deaths only to the year in which they occurred (year = 1 June–31 May). Even so, there were relatively large numbers of censored animals during some years. Most of these likely had died (many deaths were confirmed later) but the year in which these deaths occurred could not be determined. To partially accommodate this problem, we determined a maximum estimate of survival by eliminating censored data beginning with the period following an animal's last location (assumes that cause of censoring was not related to survival) and a minimum estimate by assuming that censored animals had died during the year following their last location. Because both of these extremes likely are inaccurate (death was a likely cause of censoring, but not all censored ani-

Table 2. Estimates of annual survival for radiocollared adult female caribou of the Porcupine Herd, 1997–2001. Rates were estimated for 1-year periods ending 1 June of the year indicated using the staggered entry design of Pollock et al. (1989).

	Censored animals eliminated[a]			Censored animals counted as deaths[b]						
Year	At risk	Deaths	Censored[c]	Survival	Upper CL[d]	Lower CL[d]	Survival	Upper CL[d]	Lower CL[d]	Mean[e]
1997	58	0	8	1.00			0.88	0.95	0.80	0.94
1998	51	2	22	0.96	1.00	0.91	0.67	0.76	0.58	0.82
1999	52	10	14	0.81	0.90	0.71	0.64	0.73	0.54	0.73
2000	39	6	16	0.85	0.95	0.74	0.60	0.70	0.50	0.73
2001	48	5	5	0.90	0.98	0.81	0.81	0.91	0.72	0.86
Mean				0.90			0.72			0.81

[a] Assumes that censoring is not related to survival.

[b] Censored animals are added to numbers at risk and numbers of deaths.

[c] Fate or year of death was unknown.

[d] Upper and lower 95% confidence limits on survival estimate.

[e] Mean of survival estimates with and without censored animals.

mals had died), we chose the mean of these estimates as our best estimate of survival.

We then constructed a deterministic spreadsheet model similar to the one used by Fancy et al. (1994). The major differences in the models were that ours considered only the female segment of the population, and we used 2 different rates of parturition, so that females that produced a calf in 1 year had a lower parturition rate during the following year. This modification was suggested by data that indicated an alternate-year fluctuation in parturition rate by the PCH (Table 1). Such a pattern is a consequence of multi-year reproductive cycles (Gilbert & Udevitz, 1997) when periodic reproductive failures synchronize breeding among individuals. A similar effect can be produced in populations that reproduce annually, if probability of parturition differs depending on reproductive success during the previous year (this study). As is the case with multi-year reproductive cycles, the alternate-year fluctuations are most noticeable following years when reproductive success is temporarily reduced, and gradually dampen out when reproductive rates are near the long-term mean. The initial population was established using the stable age distribution calculated by Walsh et al. (1995), assuming that females ≥1 year old were 45% of the population (International Porcupine Caribou Board, 1990). The initial population size was determined so as to approximate the observed changes in population size during 1970–1989 (Fig. 1). The model assumed that no caribou produced a calf until age 3 and that parturition of caribou aged ≥3 was equal to 1 of 2 rates, depending on reproductive success the previous year. Caribou were assumed to live a maximum of 12 years, and separate survival rates were used for calves and for caribou aged 1–11 years. Fancy et al. (1994) reported higher survival for caribou aged 1–2 years compared to those aged ≥3 years. However, these authors believed that survival rates of 1- and 2-year old caribou in their study likely were overestimated, due to small annual samples and the number of censored animals. Thus, we used one survival rate for all caribou aged ≥1 year.

After the initial model was constructed, various input parameters were changed to determine the magnitude of changes that would be necessary to duplicate observed changes in population size. First, we reduced parturition rate and annual calf survival during 1991–1993 to produce a population decline similar to what was observed from 1987–1994. These rates were restored to their initial levels beginning in 1994. Next, we modeled the population using constant rates for parturition and calf survival, but with reduced adult survival beginning in 1990 and persisting for the duration of the model period.

Table 3. Estimates of initial productivity (calves/100 cows during mid–late June) of caribou herds in arctic Alaska, 1987–1998.

Year	Western Arctic[a]	Teshekpuk[b]	Central Arctic[c]	Porcupine[d]
1987	74		74	55
1988	81		66	55
1989	78		48	58
1990	72		75	74
1991		66	45	61
1992	86	80	73	49
1993	54	39		45
1994	72		65	70
1995	59	73	50	59
1996	61			72
1997	57	46	72	57
1998	53	67		68
Mean	68	62	63	62

[a] Data from mid June; counts of calves may be higher due to less calf mortality and the inclusion of some pregnant cows (Dau, 1999).

[b] Data from post-calving (Carroll, 1999).

[c] Data from post-calving (Lenart, 1999).

[d] Data from post-calving (Stephenson, 1999).

For the third model, we altered parturition, calf survival, and adult survival. As in the first modification, parturition and calf survival were reduced only during 1991–1993, but adult survival was reduced in 1990 and then held constant for the duration of the period modeled. Finally, we reduced calf survival during 1990 by an amount sufficient to duplicate the observed population decline, and maintained that rate for the duration of the model period. In all cases, attempts were made to approximate the observed changes in population size by manipulating the specified parameters.

Results

From 1982–1992, mean annual survival rates of adults and calves were 0.84 and 0.51, respectively, and mean parturition rate was 0.80 for cows aged ≥3 years (Fancy et al., 1994). From 1997–2001, mean annual survival of adults was 0.90 if censored animals are removed and 0.72 if censored animals are assumed to have died. Annual means of these extremes ranged from 0.73–0.94, and the mean over all years was 0.81 (Table 2).

For our initial model, we used parturition rates of 0.98 and 0.70 for 3-year-old and older cows that were barren or parturient, respectively, during the previous year. These rates produced a parturition rate of 0.80 for all adult females. This model required survival rates of 0.82 and 0.50 for adults and calves, respectively, to match the observed rate of increase during this period. These rates were within the 95% confidence limits reported by Fancy et al. (1994) and the rate for adults was similar to the mean of our minimum and maximum estimates of adult survival from 1997–2001. The predicted growth of the PCH based on this model closely matched the observed counts from 1972–1989 (Fig. 1). Reducing parturition rates during 1991–1993 to 0.60 and 0.80 for cows that either did or did not produce a calf during the previous year produced annual parturition rates of 0.68–0.70 for all adult females, similar to the lowest parturition rate observed during 1991–1993 (Table 1). This model required a calf survival rate of 0.25 to produce a decline similar to that observed between 1989 and 1993. However, the model population began to increase within 2 years after parturition and calf survival rates were restored to previous levels, and had exceeded 1989 levels by 1998 (Fig. 1). In contrast, reducing adult survival to 0.74 starting in 1990 caused the model population to decline in a pattern that closely matched the observed decline through 1998 (Fig. 2). Similarly, reducing adult survival to 0.77, calf survival to 0.45 (both beginning in 1990) and parturition from 1991-1993 to 0.60 or 0.90 (for cows previously parturient or not parturient, respectively) also caused a decline similar to what was observed (Fig. 3). Reducing calf survival to 0.27 while holding the other parameters constant caused the population to decline but the slope and timing of the decline differed from what was observed (Fig. 4).

Discussion

Our intent was not to estimate true values of model parameters, but to evaluate different scenarios that might have led to the observed population decline. Thus, none of the simple models that we developed can be expected to accurately represent the dynamics of the population. However, our results strongly suggest that, in the absence of any other changes, a reduction in recruitment much greater than what was thought to have occurred during 1991–1993 would have been necessary to produce the initial decline shown by the PCH. Furthermore, the effects of this reduction would have been short-lived. Although changes in parturition and calf survival through June were recorded during the early 1990s, we have no data to suggest that these were accompanied by changes in calf survival through the remainder of the year. If calf survival were reduced substantially (e.g., by 50% as in our model), then the observed reductions in birth rate and initial survival might have been sufficient to cause the decline shown by the PCH during the early 1990s. However, unless calf survival remained low, the herd should have recovered to former levels by 1998.

Conversely, a relatively small but persistent change in adult survival could have produced the observed population decline. When combined with a 3-year reduction in recruitment, only a 6% reduction in adult survival was necessary to duplicate the observed decline, and the survival rate necessary to produce this effect was greater than our minimum estimate of adult survival during 1997–2001. This conclusion is supported by other studies that have demonstrated the sensitivity of ungulate population growth rates to small changes in adult survival (e.g., Nelson & Peek, 1984; Eberhardt, 1985; Hern et al., 1990; Crête et al., 1996; Walsh et al., 1995).

Depending on whether censored animals are excluded or counted as deaths, estimated adult survival during 1997–2001 was either greater or less than survival during 1982–1992. This illustrates some of the difficulty involved in detecting relatively small changes in adult survival in a herd with a range as large as that of the PCH. Even if there were no censored animals, it would be difficult to detect small changes with any statistical precision. For example, Walsh et al. (1995) estimated that for samples of 100 radiocollared caribou, there was only an 80% chance of detecting changes in survival rates of ≥24% at the 95% confidence level. Even if the radio-tracking effort were doubled, changes as small as 5–10% would be difficult to detect.

Potential causes of increased adult mortality include density-dependent nutritional effects, disease, and losses to predation and human harvest. Condition indices of harvested and live-captured caribou did not suggest that PCH caribou were under nutritional stress (Yukon Department of Environment and Alaska Department of Fish and Game, unpubl. data), and the incidence of common disease agents in the PCH was relatively low (Farnell et al., 1999). Although accurate data on predator populations are not available for the PCH range, observations of wolves and lynx increased during the 1990s in much of the area (U.S. Fish and Wildlife Service, unpubl. data). Conversely, during this period populations of moose declined by as much as 75% in the western half of the herd's summer and winter ranges (Stephenson, 1998). Snowshoe hares (*Lepus americanus*) in interior Alaska increased during the 1990s (McIntyre & Adams, 1999; Alaska Department of Fish and Game, unpubl. data). This increase was correlated with increased nesting success by golden eagles (McIntyre & Adams 1999). Radio-tagged immature eagles dispersed from the Alaska Range to the PCH calving grounds on the Arctic coastal plain (C.L. McIntyre, U.S. National Park Service, pers. comm.), where eagle predation was the major cause of calf mortality (Whitten et al., 1992). Thus, predation on caribou likely was high and may have increased during the 1990s. Reported human harvests have fluctuated between 2000 and 3000 caribou, and did not increase during the 1990s (International Porcupine Caribou Board, 1995; Stephenson, 1999; Yukon Department of Environment, unpubl. data). This was only 1.5-3.0% of the estimated population. However, unreported harvest and wounding losses were unknown. Other modeling efforts (Hayes & Russell, 2000; Hanley & Russell, 2000) suggested that, considered separately, neither wolf predation nor human harvest was likely to limit the PCH at current levels. However, these models did not consider potential combined effects of hunting, high predation, and reduced recruitment.

Compared to other caribou herds in arctic Alaska, the maximum observed rate of increase of the PCH is relatively low (4.9% during 1979–1989, vs. 9.5, 13.0, and 10.3 % for the Western Arctic, Teshekpuk Lake, and Central Arctic herds, respectively [Griffith et al., 2002]). Reasons for this difference are unknown, but annual estimates of initial productivity (parturition rates and June calf:cow ratios) for the PCH were generally similar to estimates for the other herds (Table 3), suggesting that mortality was higher for the PCH, even during periods of population growth. We recommend that future management and research concerning the PCH should direct more effort towards estimating survival rates and the relative importance of various mortality factors.

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Population dynamics of caribou herds in southwestern Alaska

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Abstract: The five naturally occurring and one transplanted caribou (*Rangifer tarandus granti*) herd in southwestern Alaska composed about 20% of Alaska's caribou population in 2001. All five of the naturally occurring herds fluctuated considerably in size between the late 1800s and 2001 and for some herds the data provide an indication of long-term periodic (40–50 year) fluctuations. At the present time, the Unimak (UCH) and Southern Alaska Peninsula (SAP) are recovering from population declines, the Northern Alaska Peninsula Herd (NAP) appears to be nearing the end of a protracted decline, and the Mulchatna Herd (MCH) appears to now be declining after 20 years of rapid growth. The remaining naturally occurring herd (Kilbuck) has virtually disappeared. Nutrition had a significant effect on the size of 4-month-old and 10-month-old calves in the NAP and the Nushagak Peninsula Herd (NPCH) and probably also on population growth in at least 4 (SAP, NAP, NPCH, and MCH) of the six caribou herds in southwestern Alaska. Predation does not appear to be sufficient to keep caribou herds in southwestern Alaska from expanding, probably because rabies is endemic in red foxes (*Vulpes vulpes*) and is periodically transferred to wolves (*Canis lupus*) and other canids. However, we found evidence that pneumonia and hoof rot may result in significant mortality of caribou in southwestern Alaska, whereas there is no evidence that disease is important in the dynamics of Interior herds. Cooperative conservation programs, such as the Kilbuck Caribou Management Plan, can be successful in restraining traditional harvest and promoting growth in caribou herds. In southwestern Alaska we also found evidence that small caribou herds can be swamped and assimilated by large herds, and fidelity to traditional calving areas can be lost.

Key words: *Canis latrans*, *Canis lupus*, coyotes, Kilbuck caribou herd, lichens, Mulchatna caribou herd, Northern Alaska Peninsula caribou herd, Nushagak caribou herd, nutrition, predation, rabies, *Rangifer tarandus granti*, Southern Alaska Peninsula caribou herd, Unimak caribou herd, volcanic ash, wolves.

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Introduction

Five naturally occurring caribou herds and one transplanted herd occur in southwestern Alaska (Valkenburg, 1998) (Fig. 1). Together, these herds composed about 20% of Alaska's statewide caribou population in 2001. Two of these herds (Northern Alaska Peninsula [NAP] and Mulchatna [MCH]) have been particularly important to the subsistence economy of southwestern Alaska and also to the guiding industry (Sellers, 1999a; Woolington, 2001). In 1995, however, the NAP began to decline in size, and the MCH also appeared to be on the brink of a major decline. Therefore, to better prepare managers and the public for the potential turmoil that inevitably accompanies the population declines of important game species, the Alaska Department of Fish and Game (in cooperation with federal agencies) intensified work on the caribou herds of south-

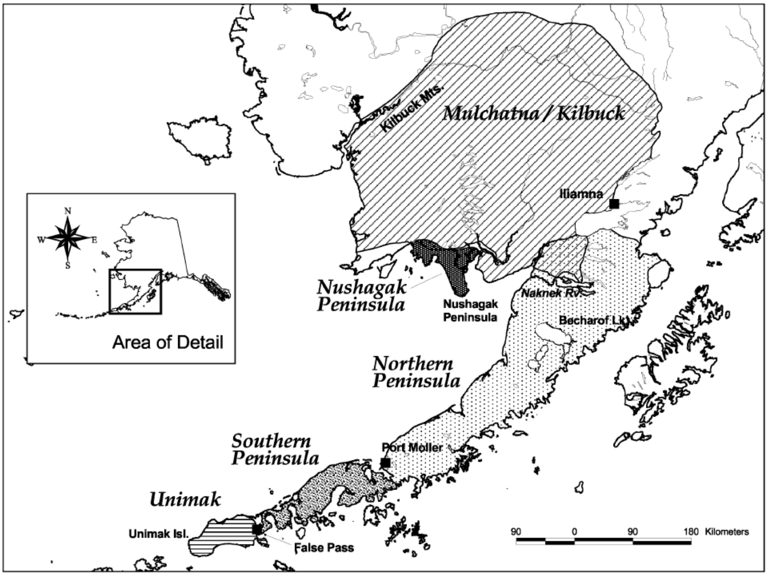

Fig. 1. Location of caribou herds in southwestern Alaska.

western Alaska. We had 2 goals in this work. The first was to review the historical literature (much of it is unpublished) from the late 1800s to the early 1990s to determine if there was a pattern of caribou population fluctuations in southwestern Alaska. We realized that older estimates of population size were undoubtedly less accurate than those done since the 1960s, but it appeared that even the older estimates were sufficient to show major population trends.

Our second goal was to collect basic data on caribou population parameters to determine if limiting and regulating factors were similar to those found in the more thoroughly studied caribou herds of the Alaskan Interior. Because of limited funding, we were not able to collect comprehensive or continuous data from all herds. However, we did begin to collect more frequent data on population size, and annual data on recruitment in 4 of the 5 naturally occurring herds and in the 1 transplanted herd. In addition, we conducted calf mortality studies in the NAP and the Southern Alaska Peninsula (SAP) herds (Sellers et al., 2003, this volume) and also monitored natality and mortality rates of radiocollared females, condition of newborn, 4-month-old, and 10-month-old calves, and began to study nuclear DNA and the prevalence of disease (Valkenburg, 1997; Valkenburg et al., 2000a). In this paper, we present results of our review of the historical literature and also the results of studies of the population dynamics of the caribou herds of southwestern Alaska between 1995 and 2002. We also discuss evidence for density-dependent population regulation, disease, and other possible causes of decline and increase.

Methods

We reviewed the published and unpublished historical literature on the caribou herds in southwestern Alaska. Skoog (1968) reviewed much of the information prior to the early 1960s. Most information collected from the early 1960s through the mid-1990s was previously only reported in agency management reports.

During the mid-1990s we attempted to conduct annual autumn composition counts (in early to mid-October) on all herds except the Kilbuck (KCH). We also increased the numbers of radiocollared caribou in these herds by radiocollaring female calves at 4 and 10 months of age. Because small helicopters were usually not available for charter in southwestern Alaska in spring or autumn, we chartered helicopters from other areas and conducted composition counts, collaring, and collections in as many herds as possible on the same trip. Occasionally, bad weather prevented us from completing fieldwork, especially on the southern Alaska Peninsula and on Unimak Island. During composition counts, caribou were classified as cows, calves, small, medium, or large bulls. In this paper, we report only calf:cow and total bull:cow ratios. We radiocollared only female calves because we were also interested in assessing size and condition of calves relative to calves in other herds, determining age-specific natality, and determining mortality rates of calves, especially during their first winter. For radiocollaring, calves were darted from helicopters with a Palmer Cap-Chur pistol (CO_2) and 1-cc darts with 1 mg of carfentanil citrate (Wildnil®, Wildlife Pharmaceuticals, Fort Collins, Colorado, USA) and 33 mg of xylazine HCl (Anased®, Lloyd Laboratories, Shenandoah, Iowa, USA) (Valkenburg et al., 1999). Caribou calves were weighed and measured and these data were compared with other cohorts of calves from the same herd and from other Alaskan herds (Valkenburg et al., 2002). Caribou that were collected for the assessment of condition and prevalence of pneumonia were shot from a helicopter, and the carcasses were delivered to local villages for consumption.

Estimates of population size of the MCH in 1996 and 1999 were from counts of large format aerial photographs (Zeiss RMK-A 9x9 in. camera) with

Table 1. Estimates of herd size, fall calf:cow ratio, and calf weight in the Mulchatna Caribou Herd, 1981–2002.

Year	Estimate of herd size	Autumn calf:cow	Autumn bull:cow	Estimated harvest[a]	Mean calf weight[b], $s_{\bar{x}}$, n
1981	18 599	45		280	
1982				1330	
1983	25 416			420	
1984	33 214			2060	
1985	42 945			1980	
1986		37		2500	
1987	45 742	60		2250	
1988	60 328	54		2970	
1989				2700	
1990	70 652			2650	
1991				3270	
1992	110 073			3400	
1993		44	42	4800	
1994	168 351			6000	
1995				7250	50.1(A), 1.4, 10
1996	192 818	34	42	4570	
1997				5100	
1998		34	41	9770	48.3(O), 2.6, 10
1999	175 000[c]	15	41	9470	
2000		24	39		46.9(A), 1.2, 11 51.2(O), 1.8, 10
2001		25	25		49.8(A), 0.9, 13
2002		28	26		49.5(A), 0.8, 22 50.4(O), 2.1, 10

[a] Harvest estimates combined the reported harvest from Harvest Ticket Report Cards and an estimate by the Area Biologist of unreported harvest for nonresident, nonlocal resident, and local resident hunters. Harvest was estimated to be about two-thirds males and one-third females.

[b] Weight in kilograms. Letter in parentheses after mean calf weight indicates month of collection: A = April, O = October.

[c] Actual count was 149 012. Estimate was derived by extrapolation for missing radio collars.

extrapolation for missing radio collars (Woolington, 2001). Population estimates for the other herds were from complete visual counts and counts from 35-mm photographs.

Mulchatna Herd (MCH)

Skoog (1968) exhaustively reviewed historical records of caribou in southwestern Alaska and concluded there was a "very large caribou population along the Bering Sea coast from Bristol Bay to Norton Sound." Numbers apparently peaked in the 1860s but by the 1880s the herd was very low (Skoog, 1968). The population increased during the 1930s, but was very low again by the time the first aerial surveys were flown in 1949, and only about 1000 caribou were counted (Taylor, 1981). By 1965 the population had increased to about 5000, and when the Alaska Department of Fish and Game (ADF&G) conducted the first systematic aerial census in 1974, just over 13 000 caribou were found (Taylor, 1981). The herd apparently was stable or declining during the late 1970s, but then it increased steadily from 1981 to about 1994 ($\lambda = 1.19$) (Taylor, 1983; Van Daele, 1995). In 1999 the MCH was the second largest caribou herd in Alaska, with 175 000 caribou, but there were indications (declining bull:cow and calf:cow ratios) that population growth was slowing or that the herd had begun to decline (Valkenburg, 1998; Woolington, 2001) (Table 1).

The MCH expanded its range rapidly during the 1980s, especially to the southeast, north, northwest, and west, although total density remained exceptionally high ($>2/\text{km}^2$). By the early 1990s, besides supplying a significant amount of meat to local residents, the MCH had become a favorite destination for nonresident hunters from the United States, Mexico, and Europe, and harvest increased to over 5000 caribou annually by 1993 (about 5–10% of herd size) (Van Daele, 1995) (Table 1). Mulchatna caribou became noted for their large antler size, and several new world record caribou were taken from the herd during the 1980s and 1990s (Boone and Crockett Club, 2000).

During its rapid expansion from 1980 to the mid-1990s the MCH began to interact with the adjacent KCH and the NAP. In 1986 about 10 000 caribou from the NAP moved north of the Naknek River and began using winter range between the Naknek River and Lake Iliamna (Sellers, 1993). At about the same time, approximately 50 000 caribou from the MCH also began using the same area (Sellers, 1997). This area (approximately 10 000 km^2) was one of the most spectacular lichen ranges in Alaska but by the mid-1990s casual aerial observations indicated that lichen biomass was reduced. Use of the area by the MCH became sporadic, and many MCH caribou began searching to the north and northwest for new winter ranges. During 2001–2002 and 2002–2003, about two-thirds of the MCH continued to winter east and southeast of the Nushagak River as far as the Naknek River.

We began more intensive work on the MCH in 1995 by collecting 10-month-old female caribou calves to assess body condition and by increasing the frequency of recruitment and population estimates. Mean weights of cohorts of 10-month-old calves was low compared to weights of calves in Interior Alaska and calves in the adjacent Nushagak Herd (NPCH) (Valkenburg et al., 2000b). However, the calves were relatively fat and appeared to be in good condition (Valkenburg, 1997). However, after 1995, fall calf:cow and bull:cow ratios in the MCH began to decline and we noticed fewer trophy class bulls while conducting autumn composition counts (Woolington, 2001). The autumn 1999 calf:cow ratio was the lowest on record for the herd (Table 1). In autumn 2000, although mean weight of calves was still relatively heavy for the MCH, individual weights were variable, and 6 of 10 calves we collected had moderate to severe bacterial pneumonia. In summer 1998 there was a major outbreak of hoof rot (*Spherophorous necrophorous*) in the herd, and during autumn composition counts, about 1 caribou out of 20 was limping noticeably. Hunters continued to observe symptoms consistent with hoofrot through December. During 1997–2000 it also appeared that mortality of radiocollared caribou increased (Woolington, 2001). At present it appears the MCH is declining from the combination of lower recruitment and higher mortality because autumn calf:cow ratios have been declining and more radiocollared caribou may be dying. Predation is probably not a major mortality factor because of the relatively low wolf population in much of the herd's range and the migratory nature of MCH caribou. A population census conducted in 2002 confirmed the decline in herd size.

Northern Alaska Peninsula Herd (NAP)

The NAP occupies the Alaska Peninsula from Lake Iliamna south to Port Moller. Previously, all caribou on the Alaska Peninsula south to, and including, Unimak Island were considered 1 herd, but by the early 1960s, Skoog (1968) considered them to be divided into 3 populations. However, ADF&G continued to consider all the caribou on the Alaska Peninsula as 1 herd until about 1980 (Smith, 1981). During the early 1980s, ADF&G began differentiating between the caribou living north of Port Moller and those occupying the Alaska Peninsula and Unimak Island south of Port Moller, and since the mid-1990s, the caribou on Unimak Island have been considered a separate herd because of their geographic isolation and lack of interaction with SAP caribou.

Caribou numbers on the Alaska Peninsula have fluctuated between 2000 and 20 000 since the late 1800s (Skoog, 1968; Sellers, 1999a, 2001a). Population highs were reached in the late 1880s and again in the late 1930s. The NAP declined to a low level during the 1940s but then increased between the 1950s and early 1980s. From 1980 to 1993 there was a sustained population of >16 000 in the NAP, and this may be one of the more protracted population highs for the herd (Table 2). During this period, harvest was substantial and hunters often killed at least 10% of the herd each year (Table 2).

Historically (1880–1990), although there is no direct evidence, occasional volcanic eruptions from Mount Iliamna, Mount Spurr, Mount Vemiaminof, Mount Shishaldin, Mount Saint Augustine, and the Pavlov Sisters may also have played a role in caribou distribution and perhaps in numbers because of the extensive and deep ash falls that have occurred (Skoog, 1968). Icing during winter has also been recorded, particularly during the 1930s when up to 50% of the caribou in some local areas were estimated to have died in some years (Skoog, 1968).

The Alaska Peninsula is known for its dearth of lichens, and caribou apparently have existed for long periods on a diet composed primarily of sedges in winter (Skoog, 1968). The only extensive high-biomass lichen ranges on the Peninsula were found north of Becharof Lake and that area has historically

Table 2. Estimates of herd size, fall calf:cow ratio, and calf weight in the Northern Alaska Peninsula Caribou Herd, 1975–2002.

Year	Estimate of herd size	Autumn calf:cow	Autumn bull:cow	Estimated harvest[a]	Mean calf weight[b], $s_{\bar{x}}$, n
1975	10 340	45	33	1500	
1976	11 368			1000	
1977				2100	
1978		55	48	1600	
1979				1800	
1980		56	53	1900	
1981	16 600	39	34	2000	
1982	18 000	52	43	1500	
1983	19 000	27	39	1795	
1984	20 000	39	39	1940	
1985	19 000			1951	
1986	17 000	34	51	1908	
1987	17 000	51	54	2300	
1988	20 000	48	49	2400	
1989	20 000			2300	
1990	17 000	29	41	2000	
1991	17 000	47	42	2000	
1992	17 500	44	40	2300	
1993	16 000	39	44	2800	
1994	12 500	34	34	1725	
1995	12 000	24	41	1550	51.4(A), 1.3, 19 44.7(O), 1.6, 10
1996	12 000	38	48	1650	46.0(O), 2.4, 10
1997	10 000	27	47	1350	48.4(A), 2.1, 10 48.3(O), 1.4, 14
1998	9 200	30	31	1000	49.4(O), 1.3, 29
1999	8 000	21	40	200	51.9(O), 1.3, 11
2000	7 200	18	38	200	
2001	7 000	28	49	200	54.3(A), 0.9, 21
2002	6 800	24	46		

[a] Harvest estimates combined the reported harvest from Harvest Ticket Report Cards and an estimate by the Area Biologist of unreported harvest for nonresident, nonlocal resident, and local resident hunters. Prior to 1998 the harvest was estimated to be about two-thirds males and one-third females, but from 1998 to 2001 harvest was restricted to bulls only and was estimated to be about 95% males.

[b] Weight in kilograms. Letter in parentheses after mean calf weight indicates month of collection: A = April, O = October.

been the NAP's main winter range (Skoog, 1968; Sellers, 1997). During the mid-1980s, biologists became concerned that the NAP had depleted its winter range between Becharof Lake and the Naknek River (Sellers, 1997). Subsequently, in 1986 the herd began using the abundant lichen forage to the north, between the Naknek River and Lake Iliamna west to the Kvichak River (Sellers, 1989). By the mid-1990s, however, increasing numbers of MCH caribou had also obviously depleted this area of lichens although from aerial observation, it appeared that lichen biomass was still relatively good (Sellers, 1997).

As in the MCH, we began more intensive work on the NAP in 1995. Weights of female calves that we captured for radiocollaring or collected to determine condition were low relative to Interior caribou and to those of the adjacent MCH and NPCH (Tables 1, 2, and 4). In addition, natality of females also appeared to be relatively low and calf:cow ratios in autumn were declining (Sellers, 1999a) (Table 2). The bull:cow ratio also declined and many calves collected for assessment of body condition had lesions on their lungs that were consistent with lungworm infection or pneumonia (Sellers, 1999a). By 2000 the herd had declined to about 7000 or about one-third of its size during the previous high (Table 2).

Southern Alaska Peninsula Herd (SAP)

During the early 1900s, caribou became numerous on the Alaska Peninsula south of Port Moller and Murie (1959) recorded 5000 there in 1925. However, the icing conditions of the 1930s apparently were associated with a major decline with a probable low point in the early 1940s. In 1949 only 500 caribou were in the range of the SAP and in 1960 there were about 1000 (Skoog, 1968). By 1983 the herd had peaked again at about 10 200 (Sellers, 1999b). Population size, recruitment estimates, and harvest records have been regularly kept since then (Sellers, 1999b) (Table 3). The herd declined during the mid to late 1980s. During the decline, natality was low, mortality of radiocollared cows was high (40%), and newborn calves were light (Pitcher, 1991). Post & Klein (1999) concluded that summer and winter range conditions were still limiting herd productivity during the early 1990s. During the late 1990s, natality improved, and calf weights (newborn and 4-month-olds) were comparatively high (Sellers, 1999b, 2001b) (Table 3). Recruitment also improved and we observed many trophy class bulls during the autumn composition counts in 1998. During the decline and the population low, hunters had remarked on the lack of large bulls in the herd (R. Gunlogson, pers. comm.). By the time we began increasing data collection from the SAP, the population had increased significantly, calves were in excellent condition, and many large, magnificent bulls were again present (Table 3).

Unimak Caribou Herd (UCH)

Unimak Island is the only island in the Aleutian chain to have native caribou. It is separated from the Alaska Peninsula by a narrow (1 km) ocean passage (Isanotski Straight) that has strong tidal currents. During 1900–1925 caribou were occasionally observed swimming across Isanotski Straight, but there have been no records of more than a few animals making the movement more recently, except perhaps for 1976 (Skoog, 1968; Sellers, 1999b). Biologists now consider the caribou on Unimak Island a separate herd.

Caribou were numerous on Unimak Island during the early 1900s, and they probably reached a population high of at least 7000 in 1925 (Murie, 1959). By the 1940s, caribou had declined, and during the first aerial survey of Unimak Island in November 1949, no caribou were observed (Skoog, 1968). In a 1953 survey, again no caribou were found on Unimak, but by 1960, almost 1000 were present (Skoog, 1968). In 1975, Irvine (1976) counted 3334 caribou and estimated there were about 5000 on the island. After the mid-1970s the population declined, and during most of the 1980s and early 1990s only about 300 caribou could be found. Recently, the population has expanded again, and in 2000, a hunting guide counted 981 caribou and estimated a population of at least 1100 on the island (Schuh, pers. comm.).

During the last few decades, at least, hunting has been a minor influence on the population size of caribou in the UCH. The island is remote, there are no light commercial aircraft for hire nearby, the weather is notoriously bad, and the interior of the island was closed to aircraft access from the late 1970s until the mid-1990s. Most of the island is also closed to the use of ground vehicles. During the 1970s when the population was high, only about 40 caribou were taken per year.

Unimak Island is so remote, and the weather so consistently poor that we were unable to collect extensive or continuous data there during the late 1990s. However, we were able to weigh and measure 12 female caribou calves there in 1999, and we found them to be relatively heavy ($\bar{x}$ = 56.0 kg) and in excellent condition, judging from condition scores (Gerhart et al., 1996) and their visible appearance. Several calves had forked or 3-point antlers, and several had already shed the velvet from their antlers. During composition counts in October 2000, we found 21 calves:100 cows and 40 bulls:100 cows, including many trophy-class bulls.

Kilbuck Herd (KCH)

During the early 1980s, biologists noticed about 200 calving caribou in the Kisaralik drainage of the Kilbuck Mountains (Machida, 1984). At the time, hunting pressure was heavy, there was debate about the origin of the animals, and some people suggested they were feral reindeer. Surveys in the mid-1980s confirmed the animals were caribou (late calving date and appearance) and determined there were only about 60–70 remaining (Patten, 1987). Subsequently, a cooperative management plan was written, local people agreed to stop hunting, and the herd increased to about 685 caribou in 1987–1988 (Kacyon, 1995). By 1991 the KCH numbered over 2584 (Kacyon, 1995). In October 1994, about 35 000 MCH began using the Kilbuck Mountains as winter range, and over the next few years, MCH cari-

Table 3. Estimates of herd size, fall calf:cow ratio, and calf weight in the Southern Alaska Peninsula Caribou Herd, 1975–2002.

Year	Estimate of herd size	Autumn calf:cow	Autumn bull:cow	Estimated harvest[a]	Mean calf weight[b], $s_{\bar{x}}$, n
1975	3000				
1980	6500			700	
1983	10200			900	
1984	7500			1000	
1985	4000			650	
1986	4500	20	32	200	
1987	4700	26	36	230	
1988	3500	19	41	200	
1989	3500			200	
1990	3400	12	19	100	
1991	2500	19	28	75	
1992	2500	22	22	65	
1993	2000	24	30	no hunting	
1994	2000	28	29	no hunting	
1995	1500			no hunting	
1996	1500			no hunting	
1997	1800	19	42	53	48.9(A), 1.0, 13
1998		35	32	38	52.2(O), 1.2, 13
1999	3600	25	51	50	
2000	2860	37	42	40	
2001		38	57	40	
2002		16	38	40	

[a] Harvest estimates combined the reported harvest from Harvest Ticket Report Cards and an estimate by the Area Biologist of unreported harvest for nonresident, nonlocal resident, and local resident hunters. Prior to 1991 harvest was estimated to be about 50% males and 50% females. From 1991 to 2001, harvest was estimated to be about 95% males.

[b] Weight in kilograms. Letter in parentheses after mean calf weight indicates month of collection: A = April, O = October.

bou invaded the entire range of the KCH during summer, autumn, and winter. Radiocollared KCH caribou that had previously used only the KCH calving area began using calving areas of the MCH. By the late 1990s the MCH had almost completely assimilated the KCH, and the 2 herds were no longer distinguishable (Seavoy, 1997). In early June 2000 we surveyed the entire previous calving area of the KCH and surrounding areas (i.e., virtually the entire Kilbuck Mountains) after the MCH had moved eastward to its calving area, and we found <50 adult female caribou with newborn calves. Therefore, although there is little calving in the Kilbuck Mountains today, the calving tradition is still being maintained by a small number of caribou, and the KCH could re-emerge.

Nushagak Peninsula Herd (NPCH)

In 1988, caribou were translocated from the NAP to previously ungrazed range on the Nushagak Peninsula southwest of Dillingham (Hinkes & Van Daele, 1996; Valkenburg et al., 2000b). The population grew rapidly (annual finite rate of population growth $\lambda = 1.38$) and reached about 1200 by the mid-1990s (Table 4). During the first few years after the transplant, population growth exceeded the theoretical maximum for caribou because of the preponderance of females. Caribou in the NPCH were on a high plane of nutrition and 10-month-old calves were the heaviest recorded for caribou in southwestern Alaska (Table 4). All radiocollared 2-year-old females produced calves, and survival of calves and adults was initially high (Hinkes & Van Daele, 1996). During 1996–2001 herd growth slowed for largely unknown reasons, although unreported harvest may have equaled or exceeded reported harvest. So far, there has been no documented dispersal of radiocollared Nushagak females to the MCH, and MCH caribou have not begun using the primary range of the NPCH.

Discussion

Population trajectories and data on natality rate and body weight of newborn, 4-month-old, and 10-month-old calves in the MCH, NAP, and the SAP provide strong evidence that density-dependent limiting factors significantly affect caribou herds in southwestern Alaska. For the caribou herds on the Alaska Peninsula and Unimak Island, there is evidence for periodic population fluctuations with population highs occurring every 40–50 years (Fig. 2). During the early 1900s, and also recently, population highs progressed from south to north, with the UCH peaking first, followed by the SAP and the NAP thereafter. Without the recent high harvests of NAP caribou during the high population from the late 1970s to the late 1990s, the herd probably would have increased to higher levels and perhaps declined sooner. The decline of the NAP, when it finally did occur, was clearly related to nutrition and perhaps to disease. Both poor nutrition and disease were likely related to the high densities of caribou. Pneumonia was prevalent in calves during the decline, but it probably was facilitated by the high population density and relatively poor condition of the caribou. Ten years prior to the decline, biologists had already been concerned about depleted winter range, a problem that was exacerbated by an influx of caribou from the MCH (Sellers, 1987). However, it is also likely that summer range is limiting in the NAP because natality in June, and weight and condition of calves in October has also been low, and these factors are generally considered to be more affected by summer nutrition than by winter nutrition (cf. Skogland, 1984; Reimers, 1997).

The transplant of caribou to the Nushagak Peninsula also has provided evidence for a nutrition-related population response in caribou in southwestern Alaska. Although the caribou were transplanted from a high-density population (the NAP), body size of 4-, and 10-month-old calves increased and the herd reached maximum productivity (Hinkes & Van Daele, 1996; Valkenburg et al., 2000b).

Predation is also a significant factor that strongly limits caribou on the Alaska Peninsula, but it apparently does not keep caribou population low for extended periods as it does in some Interior herds in Alaska (Mech et al., 1998; Boudreau, 1999; Gardner, 1999). Although brown bears (Ursus arctos) are abundant on the Alaska Peninsula (density about 200 bears/1000 km^2, Miller et al., 1997), and wolves (Canis lupus) probably fluctuate around a density of about 4/1000 km^2 (similar to many areas of Interior Alaska), patterns of neonatal calf mortality on the Alaska Peninsula differed significantly from those in the Interior (Adams et al., 1995; Valkenburg, 1998; Sellers, 2000; Boertje & Gardner, 2001; Sellers et al., 2003, this volume). Alternate prey for wolves are also more limited on the Alaska Peninsula than in Interior Alaska because moose (Alces alces) are confined to local areas with sufficient willow (Salix spp.), and Dall sheep (Ovis dalli) and other ungulates are absent. Tundra hares (Lepus othus) have been recorded, but most of the area probably has not sustained a breeding population in recent times. In addition, wolf numbers on the Alaska Peninsula seldom remain high for long because, during winters with persistent snow cover, they are heavily hunted, and they are probably also periodically reduced by rabies. Rabies is prevalent in red foxes and likely is transferred to wolves (cf. Ballard et al., 1997). In 1998 we also found a dead coyote (Canis latrans) near Port Heiden, that was positive for rabies.

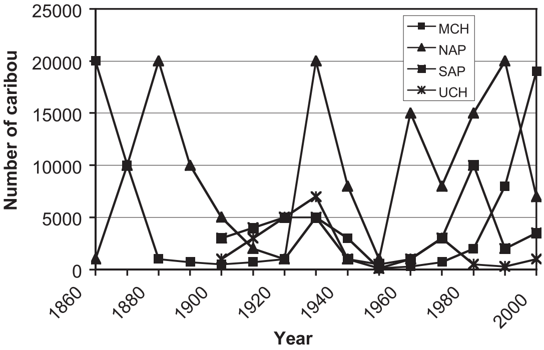

Fig. 2. Population trajectory of caribou herds in southwestern Alaska (MCH = Mulchatna Herd, NAP = Northern Alaska Peninsula Herd, SAP = Southern Alaska Peninsula Herd, and UCH = Unimak Herd). Population size of Mulchatna Herd is divided by 10.

Previously, biologists have commented on the lack of lichens on the Alaska Peninsula and the ability of caribou there to thrive on a winter diet composed primarily of sedges (cf. Skoog, 1968). To the casual observer, lichens do appear to be scarce. However, in 3 fecal samples collected in the range of the NAP in late winter 1995, lichens composed 38–55% and sedges composed 9–35% of discerned plant fragments. We believe the primary reason for the obvious lack of lichens on the Alaska Peninsula is the virtually continuous grazing pressure to which the area has been subjected. Around the settlement of King Salmon, where caribou are excluded by human activity, lichens are abundant. In addition, lichens are widespread on the uplands south of Port Moller

Table 4. Estimates of herd size, fall calf:cow ratio, and calf weight in the Nushagak Peninsula Caribou Herd, 1988–2002.

Year	Estimate of herd size	Autumn calf:cow	Autumn bull:cow	Estimated harvest[a]	Mean calf weight[b], $s_{\bar{x}}$, n
1988[c]	146		12	no hunting	
1988	202			no hunting	
1989	268			no hunting	
1990	383			no hunting	
1991	561			no hunting	
1992	734	72	60	no hunting	
1993	1007			no hunting	
1994		65	71	no hunting	
1995				81	57.1(A), 1.3, 15
1996	1304			110	
1997	1429	62	64	44	50.9(A), 1.9, 10
1998	1381	63	57	133	55.8(O), 1.6, 5
1999		53	48	106	
2000	1037	38	52	136	49.2(A), 0.7, 10
2001		35	46		51.3(A), 1.6, 10
2002	900	36	43		49.1(A), 1.0, 10

[a] Actual harvest was estimated to be at least twice the reported harvest during 1995–2002.

[b] Weight in kilograms. Letter in parentheses after mean calf weight indicates month of collection: A = April, O = October.

[c] Herd was introduced in February.

although they grow primarily between sedge tussocks, their biomass is low, and they are not readily apparent from the air. During the recent population low in the SAP, lichens became more noticeable than they were during and shortly after the population decline. The moist climate, high winds, and new soils provide ideal growing conditions for lichens in the uplands of the Alaska Peninsula.

During the last several decades we are not aware of icing conditions that may have contributed to population declines of caribou on the Alaska Peninsula. There have been significant ash falls, however, and in April 1998, many of the caribou calves we handled in the range of the SAP had incisors worn to the gum line. We only observed these extremely worn incisors in one year, and these calves were still in moderately good condition. Whether this single event of extreme tooth wear in calves had an effect on mortality is unknown, but ash falls are a stochastic event that would only occasionally be of significance to the populations.

The MCH is much larger than the Alaska Peninsula herds and has many more options for range expansion, but it too appears to be strongly limited by nutrition. Brown bears are abundant, and wolves are common in some areas within the range of the MCH, but predation obviously was not a severely limiting factor during the period of rapid population growth from 1980 to 1995. Hunting pressure on the MCH has been lighter than on the NAP and apparently was not a major restraint to herd growth during the 1980s and 1990s. However, during the late 1990s, as recruitment declined and the harvest of bulls remained high, the bull:cow ratio in the MCH declined. The recent severe outbreak of hoof rot and the prevalence of pneumonia in the MCH indicate that disease could be a limiting factor, although we have not been able to quantify the effects of these diseases on recruitment and survival.

The increase and subsequent decline of the KCH is interesting because it demonstrates the effectiveness of cooperative management programs in restraining harvest and promoting conservation of caribou. Additionally, as far as we are aware, it is only the second documented instance in which a caribou herd has been assimilated by a larger, expanding herd. This was previously documented with the Delta and Yanert herds in the central Alaska Range (Davis et al., 1991).

Conclusions

1 Nutrition had a significant effect on the size of 4-month-old and 10-month-old calves in the NAP

and the NPCH and probably also on population growth in at least 4 (SAP, NAP, NPCH, and MCH) of the 6 caribou herds in southwestern Alaska. Data were insufficient to determine the influence of nutrition in the remaining 2 herds.

2 There is evidence for long-term periodic (i.e., 40–50 year) population fluctuations in the UCH, NAP, and SAP caribou herds.

3 Predation does not appear to be sufficient to keep caribou herds in southwestern Alaska from expanding, probably because rabies is endemic in arctic foxes and is periodically transferred to wolves and other canids.

4 Pneumonia and hoof rot may result in significant mortality of caribou in southwestern Alaska.

5 Cooperative conservation programs, such as the Kilbuck Caribou Management Plan, can be successful in restraining traditional harvest and promoting growth in small caribou herds.

6 Small caribou herds can be swamped and assimilated by large herds, and fidelity to traditional calving areas can be lost.

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Population growth, movements, and status of the Nushagak Peninsula Caribou Herd following reintroduction, 1988 - 2000

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Abstract: Barren ground caribou (Rangifer tarandus) were reintroduced to the Nushagak Peninsula, Alaska in February of 1988 after an absence of more than 100 years. Since reintroduction, herd growth and population dynamics have been monitored closely. At this time, there has been no significant dispersal from the herds' core range. The Nushagak Peninsula Caribou Herd (NPCH) grew rapidly from 146 reintroduced individuals to over 1000 in 13 years. Dramatic mean annual growth during the first 6 years (1988-1994) of 38% ($r = 0.32$) can be attributed to the high percentage of females in the initial reintroduction, high calf production and survival, exceptional range conditions, few predators, and no hunting. However, the populations' exceptional growth (peak counts of 1400) slowed and stabilized between 1996-1998 and then decreased between 1998 and 2000. Size, body condition and weights of calves captured in 2000 were significantly lower than those captured in 1995 and 1997. Although calf production also decreased from close to 100% (1990-1995) to about 91% (1996-2000), overall calf survival continued to be high. Legal harvest began in 1995, and harvest reports have accounted for approximately 3% of population mortality annually. Although brown bears (Ursus arctos) and wolves (Canis lupus) are present, the extent of predation is unknown. Mean home range of the NPCH was 674 km^2 and group sizes were greatest during post-calving aggregation in July ($\bar{x} = 127$). Caribou population density on the Nushagak Peninsula reached approximately 1.2 caribou/km^2 in 1997 before declining to about 1.0 caribou/km^2. A range survey in 1994 noted only trace utilization of lichens on the Nushagak Peninsula by caribou. A subsequent survey in 1999 found moderate to severe utilization in 46% of plots, suggesting the reintroduced herd was beginning to alter range condition. Between 1997 and 2000, both calf production and condition of 10-month-old calves declined. Calving has also been delayed in recent years. However, we suspect the reduced herd growth can be attributed to increasing hunting pressure and some dispersal of caribou from the Peninsula, not reduced range condition.

Key words: aerial radio telemetry, barren ground caribou, calf production, condition, distribution, home range, mortality, range condition, Rangifer tarandus, subsistence.

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Introduction

Historically, a large caribou population occupied the coast of the Bering Sea from Bristol Bay to Norton Sound and archaeological investigations suggest that caribou were important to the native population (Kotwa, 1963). While still numerous in the upper Kuskokwim drainage, caribou were noted as absent from the Togiak and Goodnews drainages as early as 1900 coinciding with a period of human population growth and intense commercial trade (Capps, 1929). Reindeer were introduced into Bristol Bay in the early 1900s to provide the native communities with an economic base, however, the industry failed by the 1940s (Alaska Planning Group, 1974).

Togiak National Wildlife Refuge (Togiak Refuge) in southwest Alaska, established in 1980, was directed to reestablish wildlife populations to historic levels (U.S. Fish and Wildlife Service, 1986). As a result, barren ground caribou were reintroduced to the Nushagak Peninsula in February 1988 (Fig. 1). The reintroduction was intended to reestablish caribou in an area where local residents had been depen-

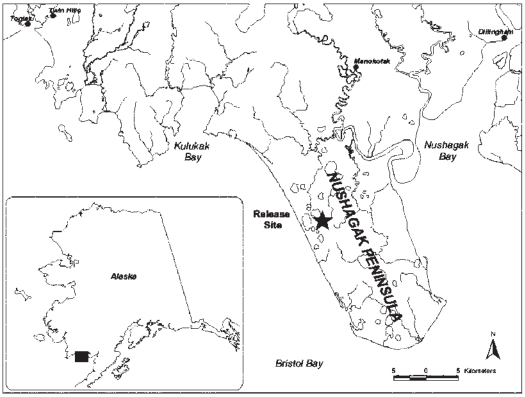

Fig. 1. Release site of the reintroduced NPCH, southwest Alaska.

dant on them for thousands of years. The principle goal was to maintain an expanding population with sustainable subsistence harvest. The nearest caribou herds to the Togiak Refuge were the Mulchatna Caribou Herd (MCH), the Kilbuck Caribou Herd (KCH) and the Northern Alaska Peninsula Caribou Herd (NAPCH). However, it should be noted that in 1994, the KCH was assimilated by the larger MCH (Patten, 1996) and the two herds remain indistinguishable. Previously, hunting pressure, natural barriers, and human settlements appeared sufficient to prevent these herds from expanding onto Togiak Refuge; recently the MCH has begun expanding onto Togiak Refuge in large numbers.

Study area

The Nushagak Peninsula is located in the southeast corner of the Togiak National Wildlife Refuge in southwest Alaska and encompasses approximately 1050 km^2. It is almost entirely lowland tundra with increasing elevation toward the northern portion. The climate is arctic maritime with temperatures ranging from an average minimum of –16 °C to an average maximum of 15 °C. The frost free period averages 120 days. Normal annual precipitation is 63.5 cm, including 186.7 cm of snow annually. Autumn is generally the wettest season of the year, while spring is generally the driest (U.S. Fish and Wildlife Service, 1986).

Methods

Radio-collaring

Details of the reintroduction of the NPCH are discussed in Hinkes & Van Daele (1996). Additional radio-collars were added in 1992, 1995, 1997, and 2000. Data collected during capture operations included weight, neck girth, total length, heart girth, metatarsus, hindfoot and mandible length. Body condition scores (condition index) were also taken. The condition index was determined by palpating the withers, ribs, and rump of captured animals and giving a subjective rating of 1 (emaciated) to 5 (obese) (Gerhart, 1995); an overall condition score was used in this analysis. We tested for differences in calf weights, heart girth, hindfoot length, metatarsus length, and mandible length over time using a one-way ANOVA. When differences existed, a Fisher's least significant difference test was used to identify which means differed significantly at the 95% confidence level. A Chi-square test was used to test for differences in condition index between years.

Monitoring

Monthly flights to monitor radio-marked caribou began in 1988. Weekly flights during the calving period were initiated in 1991. When possible, visual confirmation of association with a calf was made. However, to avoid disturbance, visual observations were not made during post-calving aggregations. Sex and age composition counts were conducted by helicopter in the fall of 1992, 1994, and 1997 - 1999. Population censuses were conducted in 1990 - 1993, 1996 - 1998, and 2000 using a total-count technique. Transects were flown at 1.0 - 1.5 km intervals depending on snow, light, and wind conditions. For 1994, 1995, and 1999 (years when a population census was not conducted), herd size was estimated using the formula: $N_{t+1} = (N_t – H)S + N_c \times R \times 0.90)$ where N_{t+1} is the estimate, N_t is the most recent population count or estimate; H is the reported harvest during the calendar year; S is the previous 5 year average survival rate for radiocollared caribou; N_c is the most recent estimate of the number of females ≥ 2-years-old; and R is the previous 5 year average fall calf recruitment rate for radiocollared females ≥ 2-years-old. We assumed that male survival equaled that of females or 0.90, whichever was less, and that calf survival from fall to the end of the year was 0.90 (Aderman & Woolington, 2001). Separate counts of caribou on and off the Nushagak Peninsula were conducted in 1996 through 1998 when substantial numbers of caribou were noted to the west (total population counts). However, a proportion of those individuals were suspected to be part of the dispersing MCH.

Home range, movements, and population growth

The Animal Movement Analysis extension (Hooge & Eichenlaub, 1997) for ArcView (ESRI, 2000) was used to determine MCP (minimum convex polygon) home range size and calving distribution

Table 1. Mean body measurements of captured NPCH 10-month-old female calves.

	1995			1997			2000		
	$\bar{x}$	n	(SD)	$\bar{x}$	n	(SD)	$\bar{x}$	n	(SD)
Weight (kg)	56.6	15	(5.0)	50.5	10	(6.1)	48.8	10	(2.1)
Condition Index	3	13	---	4	13	---	2	10	---
Heart Girth (cm)	98.1	13	(3.6)	96.5	13	(5.3)	95.0	10	(2.7)
Mandible (cm)	23.4	14	(0.9)	22.7	13	(1.1)	22.5	10	(0.8)
Hindfoot (cm)	51.1	13	(5.1)	53.3	13	(2.9)	51.4	10	(3.1)
Metatarsus (cm)	36.9	15	(1.2)	37.6	12	(1.8)	35.3	10	(0.7)

(Valkenburg et al., 1988), and distances moved between relocations. The MCP home range was grouped for all years due to small sample sizes. Distances moved between relocations were calculated as the distance moved between successive locations and were grouped for all individuals. Linear regression was used to identify relationships between home range size and distances between relocations, and the number of relocations. There was an indication of nonnormality in the data, therefore, a Kruskal-Wallis (KW) was used to test for differences between the medians for successive distances moved and group sizes. All statistical analyses were performed using STATGRAPHICS Plus (Manugistics, 1998).

The population was modeled in a Lotus 1-2-3 (Lotus, 1997) spreadsheet. Estimates of natality (% radio-collared cows observed with calves), survival (% radio-collar survival), and harvest rates were calculated each year from observed values. Projected population numbers were calculated by estimating the number of male and female calves (# females * % calves * 50% sex ratio) and adults (((# calves * % survival) + (# adults_{t-1} * % survival)) – harvest))). The average radio-collar natality and survival rates were used for population projections and survival rates were assumed to be equal between the sexes.

Range condition

Severe overgrazing by caribou was well documented in western Alaska during the early 1900s (Palmer & Rouse, 1945). Because lichen communities are known to be sensitive to over-grazing and trampling (Klein, 1967), a range condition study was initiated in 1989 to assist in management (Johnson, 1994). Permanent transects and / or exclosures at 5 sites on the Nushagak Peninsula were established in 1993 and visited in 1994 and 1999 to monitor changes in vegetation production and cover over time. In addition, selected lichen – rich upland sites were surveyed in 1994 and 1999 and classified into eight utilization classes ranging from trace to extreme (Swanson & Barker, 1992).

Results

Radio-collaring

A total of 146 caribou were reintroduced to the Nushagak Peninsula in February 1988 (Hinkes & Van Daele, 1996). In 1988, 20 radio-collars were deployed and, since reintroduction, an additional 56 radio-collars have been added (16 in 1992; 10 in 1995; 20 in 1997; 10 in 2000).

Body Measurements

Adult caribou captured in 1992 (2-year-olds) were larger and appeared to be in better condition than 2-year-old caribou originally transplanted to the Peninsula in 1988 (Hinkes & Van Daele, 1996). In contrast, Nushagak Peninsula caribou calves (approximately 10-month-old) captured in 2000 were smaller and appeared in poorer condition than those captured in both 1995 and 1997 (Table 1). NPCH calves captured in 2000 had significantly smaller metatarsus lengths compared with both 1995 and 1997 captures (F (2, 34)=8.21, P=0.001). Calf mandible lengths were also significantly larger in 1995 (F (2, 34)=3.40, P=0.045) than during subsequent captures. The mean spring weights of calves captured in 1997 and 2000 were comparable ($\bar{x}$=50.5 kg, SD=5.0, n=10; $\bar{x}$=48.8, SD=6.1, n=10, respectively), but both were significantly (F (2,32)=9.49, P < 0.001) lighter than calves captured in 1995 ($\bar{x}$=56.6 kg, SD=2.1, n=15). Further, the overall body condition index was significantly lower (x^2_6=29.97, P < 0.001) for NPCH calves caught in 2000 compared to those caught in both 1995 and 1997. Other body measurements (heart girth and hindfoot length) did not differ significantly between the years.

Calf production and survival

Peak calving for radio-marked NPCH caribou

Table 2. Average progression of calving for NPCH radio-collared cows, 1992-2000.

Calved By:	Average Percent
May 15th	7%
May 22nd	33%
May 27th	74%
May 30th	88%
June 10th	98%

occurred in late May which is consistent with other caribou herds at similar latitudes in Alaska (Skoog, 1968; Hemming, 1971). Peak calving is defined as the date by which 50% of calving has occurred. The mean calving date from 1992 to 2000 was 24 May (Table 2). From 1992-1995, mean calving occurred by 21 May. Between 1996 and 2000, the mean calving date was 26 May. Calving in 2000 was delayed with no radio-collared cows noted with calves by May 22nd and only 80% with calves by May 30th.

Calving grounds are perhaps the most predictably used portions of caribou annual ranges (Valkenburg et al., 1988), however, there is no apparent distinct calving area for the NPCH. The total calving distribution for the NPCH for all years combined was 760 km^2 (75% of the Peninsula). Annual calving areas were approximately 330 km^2 (SD=114 km^2, n=11) and appeared to be expanding north since 1993. Other than one individual, all radio-collared females calved on the Peninsula until 1994. Between 1994 and 1999, four radio-marked females have been observed calving off of the Peninsula, though not consistently.

Natality estimates derived from radio-collared females have been found to be similar to estimates of the herd at large (Davis et al., 1991). In 1990, 1992, 1993, and 1995 all radio-collared females in the NPCH produced calves (100%). The natality rate has since decreased (1996 - 2000), overall averaging 91% (Table 3). All five females estimated to be 2-years-old during the 1992 NPCH capture effort produced calves (Hinkes & Van Daele, 1996). Subsequently, 2-year-old radio-collared cows (captured as 10-month-old calves in 1995 and 1997) had lower incidences of calf production; none produced calves (0%) in 1996 and 3 out of 13 (23%) produced calves in 1998. The mean fall survival of calves associated with radio-collared cows from 1990 to 1999 averaged 62% (SD=9.8; n=9) (Table 3). Calf survival in 2000 dropped dramatically to 30%, though this may be due to a small sample of collared cows (n=10), bringing the overall mean fall survival to 60% (SD=13.7, n=10).

Mortality

Legal harvest of NPCH caribou began in January 1995 with 38 caribou reported killed. From 1995 to 2000, 3%-4% of the Peninsula population has been taken each year during the reported subsistence harvest. Mortality causes of radio-marked caribou from 1988 to 2000 were: 49% from unknown causes (n=25), 16% taken by hunters (n=8), and 6% by predation (n=3). Two other caribou were also documented as dead (4%), including one from birth related causes and another that locked antlers with another bull. An additional 25% were missing or had collars fail (n=11) or were capture related mortalities (n=2). The average age for caribou that died from unknown causes was 8.9 years (SD=4.4, n=25), from hunting was 5.4 years (SD=2.6, n=8), and from predation was 7.2 years (SD=3.3, n=3) suggesting no age specific mortality. Of note is one radio-collared female that lived approximately 15 years before dying of apparently natural causes.

Table 3. Production and survival of calves associated with NPCH radio-collared cows, February 1988 to October 2000.

Year	Production[a]	Calf Survival[b]
1988	---	---
1989	---	---
1990	100	62
1991	---	---
1992	100	64
1993	100	54
1994	96	75
1995	100	78
1996	86	67
1997	76	52
1998	80	54
1999	79	53
2000	91	30
Mean	91	60
SD	11	14
N	10	10

[a] Production = % of 3-years or older radio-collared cows observed with calves in the spring.

[b] Calf Survival = % of calves associated with radio-collared cows observed in October.

Home range, movements, and distribution

From March 1988 to March 2000, we obtained over 3000 relocations on 62 radio-collared caribou. The total number of relocations per radio-collared caribou averaged 59. Home range size was related to the

Table 4. Herd composition of the NPCH, 1988-2000.

Regulatory Year	Bulls:100 cows	Calves:100 cows	Calves (%)	Cows (%)	Bulls (%)
Feb 1988[a]	12	10	8	82	10
1992/1993	60	72	31	43	26
1993/1994	---	---	---	---	---
1994/1995	71	65	27	42	30
1995/1996	---	---	---	---	---
1996/1997	---	---	---	---	---
1997/1998	64	62	28	44	28
1998/1999	57	63	28	46	26
1999/2000	48	53	26	50	24
2000/2001	52	38	20	53	27

[a] Original reintroduction.

number of telemetry locations at n < 30 (r^2=0.55, P=0.009), therefore caribou with fewer than 30 locations were excluded from further analyses. Two radio-collared caribou with ranges to the village of Togiak (Fig. 1), beyond the Nushagak Peninsula (1551 km^2 and 1479 km^2), were also excluded. With those exclusions, the average home range of NPCH caribou between 1988 and 2000 was 674 km^2 (SD=173, n=48). The mean home range was similar to that previously reported for NPCH caribou with 64-74 locations ($\bar{x}$=606 km^2, SD=98, n=11) (Hinkes & Van Daele, 1996). The age of NPCH caribou was not significantly related to home range size (r^2=0.09, P=0.842).

Mean distances moved each year between successive relocations during 1988 - 1999 ranged from 9.2 km (1988) to 15.7 km (1998) ($\bar{x}$=12.4 km). There was a significant linear relationship between average overall distances moved and home range size for individuals (r^2=0.30, P<0.001). However, there was no relationship between the number of and distance between relocations (r^2=0.07, P=0.069) suggesting samples were representative of movements. Differences in movements between years were significant (KW=175.3, df=12, P<0.001) and generally increased through time as the herd expanded its range along the Peninsula. Mean distances moved each month were also significantly different (KW=292.8, df=11, P<0.001) and ranged from a low of 9.4 km during the calving period (May) to a high of 17.7 km in December ($\bar{x}$=12.5 km).

Seasonal variation of group sizes in the NPCH was significant (KW=531.9, df=11, P<0.001). Group size was greatest in July during post-calving aggregation ($\bar{x}$=127) and decreased through Sep ($\bar{x}$=15), remaining stable throughout the winter months (October – March) ($\bar{x}$=25). The lowest mean group size was observed in the spring (April – May) ($\bar{x}$=12) as pregnant females dispersed to calve. Group sizes for the NPCH were significantly different between years (KW=127.9, df=12, P<0.001) with the group size increasing on average from 1988 to 1999 (range 13 to 28 caribou, $\bar{x}$=21) as the population increased.

Caribou observations were plotted by month and season, with no significant pattern noted. The caribou did concentrate more in the center of the Peninsula during the calving and summer seasons and then expanded their range towards the coast during the winter months. No significant dispersal from the herds' "core range" on the Peninsula has occurred. Of over 3600 radiolocations during tracking flights and surveys, 92% were observed on the Nushagak Peninsula. This is compared to over 99% noted earlier (Hinkes & Van Daele, 1996).

Population growth and composition

The NPCH grew rapidly in the first 6 years following reintroduction (1988 to 1994) with a mean annual growth of 38% (SD=7.3, n=6) or an exponential rate of increase r=0.32 (Hinkes & Van Daele, 1996). After 1996, the NPCH's exceptional growth slowed; between 1996 and 1998, the NPCH only grew about 1% (Fig. 2). The herd's Nushagak Peninsula population level then dropped 19% between the 1998 and 2000 counts. The population density of the NPCH was estimated to be 1.0 caribou/km^2 in 1993. By 1997, the estimated density had reached 1.2/km^2 on the Peninsula but had dropped to 1.0 caribou/km^2 by 2000. Though no known dispersal has occurred, there have been as many as 100+ individuals reported near the village of Twin Hills that are suspected to be from the NPCH. Also beginning in 1996, caribou were noted off the Peninsula to the west in greater numbers, and although several collared NPCH caribou have been observed in this area, many of those individuals are suspected to be from the dispersing Mulchatna Caribou Herd. This is supported by confirmed locations of radio-collared Mulchatna (and Kilbuck) caribou near the village of Twin Hills.

Herd composition of the NPCH also changed dramatically in the first 5 years following reintroduc-

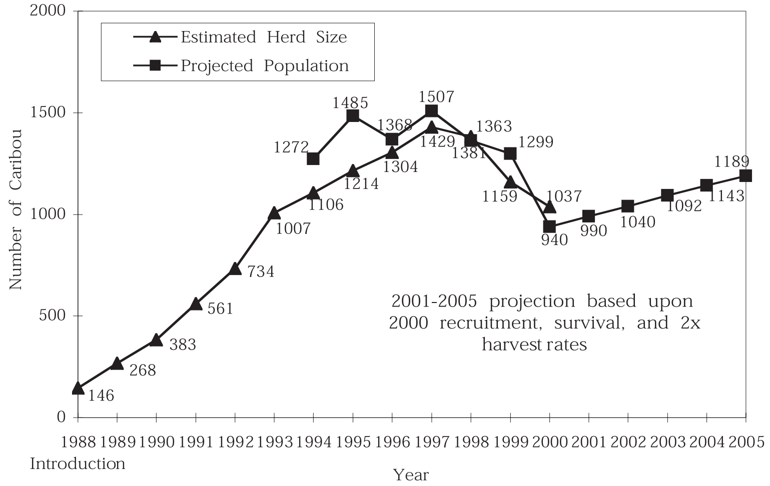

Fig. 2. Release site of the reintroduced NPCH, southwest Alaska.

tion (Hinkes & Van Daele, 1996). Initial herd composition was 82% cows, 10% bulls (12 bulls:100 cows), and 8% calves (10 calves:100 cows). Average herd composition from 1992 to 2000 (n=6) was 46% cows, 27% bulls (59 bulls:100 cows), and 27% calves (59 calves:100 cows) (Table 4). Although average bull:cow ratios in the NPCH continued to exceed that of most hunted Alaskan populations (45 bulls:100 cows) (Leib et al., 1991), bull:cow ratios in the NPCH have steadily decreased from a high in 1994/1995 (71 bulls:100 cows). By 2000, the ratio was 52 bulls:100 cows in the NPCH. Proportions of cows and calves remained constant between 1992 and 2000.

Range condition

A range condition inventory on the Nushagak Peninsula in 1994 noted only trace utilization of lichen tundra uplands by the reintroduced herd. In other areas, lichens appeared to be virtually ungrazed (Johnson, 1994). By 1999, however, obvious signs of grazing were prevalent and condition was beginning to be altered by the NPCH. Of 160 plots surveyed on the Peninsula in 1999, 54% were described as trace to slightly grazed, 44% were moderately to heavily grazed, and 2% were rated as severely grazed.

Discussion

Caribou do not generally come into estrus until 28 months of age (Skoog, 1968; Bergerud, 1971), although it has been noted that with good nutrition, caribou can conceive at 17 months (Bergerud, 1980). The initial observed increased production in young females (2-year-olds) in the NPCH has also been observed in several other transplanted herds in Alaska (Valkenburg et al., 2000). Despite a slight decline, the natality rates observed for the NPCH continue to be high; at least 91% compared to an average natality rate of 82% for other populations (Bergerud, 1980). The lighter calf weights in 1997 and 2000 of the NPCH are comparable to calves in the Northern Alaska Peninsula Caribou Herd ($\bar{x}$=50.9 kg, SD=3.0, n=19), the parent herd for the NPCH (Hinkes & Van Daele, 1995). The neighboring Mulchatna Caribou Herd also showed a marginally significant decrease in spring weights of 10-month-old calves (F (1,19)=3.14, P=0.09) between 1995 and 2000 ($\bar{x}$=49.8 kg, n=10; 46.6 kg, n=11, respectively) (P. Valkenburg, Alaska Department of Fish and Game, unpubl. data).

During 1988 – 2000, brown bears were common and wolves were rare on the Nushagak Peninsula; the effect of predation on NPCH herd dynamics is unknown. Incidental sightings of brown bears on the Peninsula have increased since 1997, especially of sows with cubs. Brown bears are known to be effective predators of ungulate calves (Adams et al., 1995; Valkenburg, 1997; Sellers et al., 2002) and sows with young have been shown to kill more caribou calves (< 2 weeks old) than other classes of bears (Young & McCabe, 1997).

The initial growth rate of the NPCH exceeded the maximum theoretical potential of r ≈ 0.30 or about 35% as described by Bergerud (1980) and Bergerud et al. (1983). Bergerud (1980) also surmised that Alaska caribou herds without predators show rapid growth approaching r=0.30, while those with predators showed little or no growth. However, Davis et al. (1991) stated that only transplanted caribou herds approach this level and that growth over 20% is uncommon even under optimum conditions. The initial impressive growth of the NPCH can be attributed to the high percentage of females in the reintroduced herd, high calf production and survival, pristine range conditions, few predators, and little hunting (Hinkes & Van Daele, 1996). Growth rates of other reintroduced caribou herds in Alaska have been more variable (Valkenburg et al., 2000). Expansion of range, including calving areas, has been documented in many herds across Alaska and

Quebec (Mercer et al., 1986; Couturier et al., 1990; Tobey, 1999; Woolington, 1999). Haber & Walters (1980) suggested that competition for food at densities approaching 2.0 caribou/km^2 will cause such dispersal, although dispersal (i.e. movement of caribou from one calving range to another) has not been documented in caribou as a response to increasing densities (Valkenburg et al., 1996; Valkenburg, 1997).

While the population dynamics of the NPCH continue to be similar to other reintroduced herds with high quality forage and few predators (Hinkes & Van Daele, 1996), growth rate of the herd has slowed. Decreased calf condition and size, reduced calf production, and a decline in range condition all suggest that the population has reached a plateau. In addition, delayed calving may further be symptomatic of poor nutrition (Skogland, 1985; Boertje & Gardner, 1999). Although, it should be noted that the winter of 1999/2000 was one of exceptional snow accumulation and winter severity is an important factor affecting caribou survivorship and condition (Russell & Martell, 1984); it is possible the observed effects were a result of short term weather conditions. However, while there can be annual fluctuations in body condition, increasing herd size in the Delta Caribou Herd also coincided with reduced calf weights and condition which, subsequently, have not returned to the levels of the 1980s when herd size was low (Valkenburg et al., 1999). Valkenburg et al. (2000) also noted that similar declines in body weight and natality in other transplanted herds occurred after relatively short periods of grazing pressure as densities within herds increased.

Modeling the NPCH using current estimates for natality, survival and harvest (~ 3%) results in a population increase to over 2000 caribou by 2005. However, we suspect that unreported harvest may be as much as 2 to 3 times the reported rate for the reason that a minimum of 16% of all radiocollared caribou mortalities between 1988 and 2000 could be attributed to hunting. Models using twice the reported harvest rate closely resemble observed total population counts for 1996 (1368 vs. 1304), 1997 (1507 vs. 1429), and 1998 (1363 vs. 1381) (Fig. 2). Movements of caribou off the Nushagak Peninsula are becoming more common. In addition, an increased number of caribou are also being counted off the Peninsula; however, a portion of those individuals may be from the expanding MCH. The neighboring Mulchatna Caribou Herd increased by over 10% annually from 1992 to 1994 and it continued expanding onto new range (Van Daele, 1995). The NPCH may also continue to grow if it disperses off the Peninsula. Although continued growth of the NPCH will verify the success of the reintroduction, changing densities and movement patterns, and higher potential for overgrazing will present managers with increasingly difficult decisions.

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Population demography of high arctic caribou on Banks and Melville Islands

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Abstract: Caribou numbers, *Rangifer tarandus pearyi*, (excluding calves) on Banks Island were estimated (standard error of the estimate) at 1005 (SE±133) in 1992, 709 (SE±128) in 1994 and 436 (SE±71) in 1998; no paired estimates were different ($P<0.05$). On Melville Island caribou numbers were similar in 1987 and 1997 with estimates of 729 (SE±104) and 787 (SE±97), respectively. We conducted annual sex and age classification surveys during July on Banks Island from 1994-2000 and on Melville Island from 1998-2000. The number of calves per 100 ≥two-year-old females ranged from 24.0 in 1994 to 74.3 in 1998 on Banks Island, and from 44.8 in 1999 to 80.0 in 1998 on Melville Island. Recruitment rate ranged from 18.6% during 1997/1998 to 27.5% during 1999/2000 on Banks Island and from 16.7% during 1997/1998 to 25.0% during 1999/2000 on Melville Island. There has been an increasing trend in the rate of recruitment on both islands during the last three years of the study.

Key words: calf production, population size, *Rangifer tarandus pearyi*, recruitment.

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Introduction

Peary caribou (*Rangifer tarandus pearyi*) inhabit the Canadian High Arctic and were designated as an endangered subspecies by the Committee on the Status of Endangered Species in Canada (COSEWIC) in 1991. Current estimates of Peary caribou numbers are lower than the first estimates determined in the 1960s and 1970s. Severe winter weather has been associated with die-offs throughout the High Arctic and is believed to be the major cause of the reduction in numbers (Parker et al., 1975; Gunn, 1992). Unfortunately, data to critically assess causes are lacking. Over much of the Peary caribou range few systematic population surveys have been conducted and the periods between surveys can be measured in decades. Data on estimates of calf production, survival and recruitment are limited (Larter & Nagy, 2000a). Data from Banks Island are a notable exception.

Nagy et al. (1996) described population demography of Peary caribou on Banks Island from 1982-1992. The decline in numbers over this 10-year period was attributed to the cumulative effects of a combination of factors including human harvest, wolf predation, interisland movement, severe winters, and possible competition from an increasing muskoxen (*Ovibos moschatus*) population. Systematic population surveys for Banks Island caribou continued through the 1990s, and since 1994, annual sex and age classification surveys have been conducted. An annual quota of 36 male only caribou has been in effect for the community of Sachs Harbour since 1992. This quota was met during 1993-94 but harvest has never exceeded 23 animals in any other year.

There are fewer data on the caribou population of neighbouring Melville Island. Although the Melville and Banks Island caribou populations represent two different recovery units in the national Peary caribou recovery strategy, these two populations have little genetic differentiation (Zittlau et al., this issue). Annual sex and age classification surveys of the Melville Island caribou population were initi-

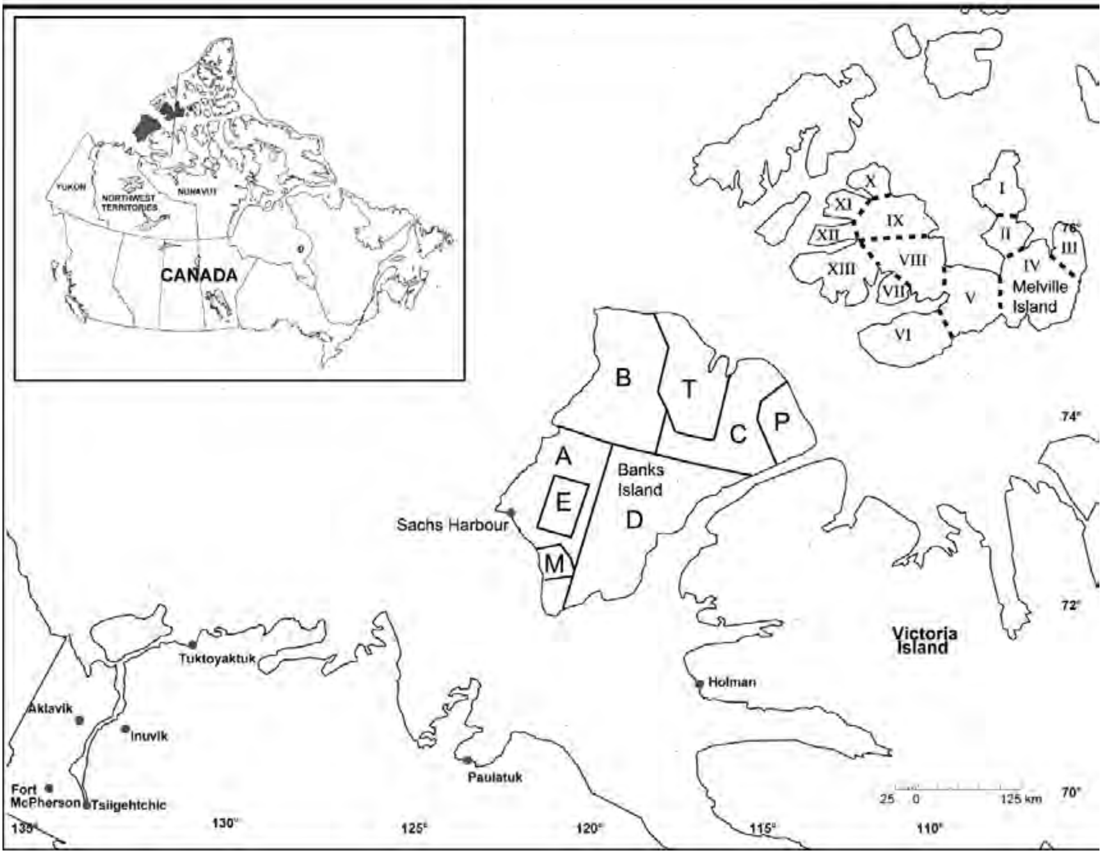

Fig. 1. The study area, Banks and Melville Islands in the western Arctic Archipelago. Note: Banks Island is delineated into the eight survey strata: A, B, C, D, E (Egg), M (Masik), T (Thomsen), and P (Parker). Melville Island is delineated into the 13 survey strata.

ated in 1998. The most recent population survey of Melville Island caribou was conducted in 1997, ten years after the previous survey. There are plans for systematic population surveys to be carried out on Melville Island every five years. There is no settlement on Melville Island and neither caribou nor arctic wolves (Canis lupus arctos) are hunted. This paper documents estimates of calf production and recruitment for Banks Island Peary caribou from 1994-2000 and for Melville Island from 1998-2000. The results are discussed in relation to current population estimates.

Study Area

Banks Island is the most western island in the Canadian Arctic Archipelago and covers an area of approximately 70 000 km^2 (Fig. 1). The climate is Arctic Maritime along coastal areas where weather stations are situated, tending toward Arctic Desert inland (Zoltai et al., 1980). Winters are long, with mean monthly temperatures below 0 °C from September through May, and cold, with mean minimum daily temperatures of -30 °C to -40 °C from December to March. Summers are short and cool; mean maximum daily temperatures of 5 °C to 10 °C from June through August. There is little precipitation, annual mean nine cm (Zoltai et al., 1980). Sachs Harbour (population 153 in 2000; N.W.T. Bureau of Statistics) is the only permanent settlement. Zoltai et al. (1980) provided a general overview of the geology and glacial history of Banks Island.

There are four major terrestrial habitats: wet sedge meadow (WSM), upland barren (UB), hummock tundra (HT), and stony barren (SB). WSM are generally level lowlands dominated by sedges (Carex aquatilis and Eriophorum scheuchzeri). UB and HT are well-drained sites found on slopes. Vegetation is dominated by mountain avens (Dryas integrifolia) and willow (Salix arctica). HT is characterized by individual vegetated hummocks. SB are sparsely vegetated with a gravely substrate and are found on wind blown areas, ridges, and gravel and sand bars. A more detailed description of the flora of Banks Island can be found in Wilkinson et al. (1976), Porsild & Cody (1980), and Zoltai et al. (1980).

Muskoxen and caribou are resident ungulates. In 1994 the muskoxen population was at a historic high, estimated at 64 608 (SE ± 2009) ≥one-year-old animals. Arctic wolves, arctic foxes (Alopex lagopus), and polar bears (Ursus maritimus) are resident predators.

Melville Island, located northeast of Banks Island, is the largest island of the Parry Islands group and covers an area of approximately 42 000 km^2 (Fig. 1.). Winters are long and summers cool and short. Although there are no weather stations on Melville Island, records from Mould Bay (76°14'N; 119°20'W) and Resolute Bay (74°43'N; 94°59'W) show that the mean maximum daily temperature is below 0 °C starting in September with mean monthly temperatures of -34 °C in February and 4 °C in July, the coldest and warmest months. The island is geologically divided into three distinct structural provinces (Tozer & Thorsteinsson, 1964). Eastern and central Melville Island (east of 112 °W) is generally low, <150 m above mean sea level (amsl), and flat. Western Melville Island is mainly plateau ranging from 300-600 m amsl with steep walled drainages and some peaks rising to 1100 m amsl.

Vegetation cover is prostrate and generally sparse consisting of lichens, bryophytes, graminoids, herbs, cushion plants and shrubs (Babb & Bliss, 1974; Edlund & Alt, 1989). Babb & Bliss (1974) describe four general cover types: polar desert, polar semi-desert, diverse terrain, and wet sedge-moss meadows. Polar deserts are devoid of woody shrubs and have 0-10% plant cover. Polar semi-deserts may have some moister areas and 5-20% cover of vascular plants including Luzula spp., Papaver spp., Saxifraga spp., and Draba spp. Diverse terrain areas are more mesic than polar semi-deserts. Mats of woody species (Cassiope tetragona, Dryas integrifolia, and Salix arctica) are interspersed throughout and in moist depressional areas patches of moss-graminoid meadows occur. Wet sedge-moss meadows are large areas dominated by a continuous layer of mosses and sedges or grasses. A more detailed description of the flora of Melville Island can be found in Thomas et al. (1999).

Muskoxen and caribou are resident ungulates on Melville Island. In 1997 the muskoxen population was estimated (standard error of the estimate) at 2258 (SE ± 268) ≥one-year-old animals (A. Gunn & J. Dragon, unpubl. data), and had declined since the previous estimate of 4761 (SE ± 372) in 1987 (Miller, 1988). Arctic wolves, arctic foxes, and polar bears are resident predators.

Methods

Population Estimates

Banks Island

Islandwide surveys were conducted during summers 1992, 1994, and 1998 and were designed to estimate muskox and Peary caribou population sizes. Surveys were conducted in July-early August, except in 1992 when the survey was conducted in late August. Censuses were conducted using fixed-wing aircraft (Helio-Courier and Cessna 185) and strip-transect techniques with a stratified design; the transect was the sampling unit (Norton-Griffiths, 1978). Banks Island was stratified into eight strata based upon a combination of geographic area and muskox density determined from previous surveys (see Fig. 1). Transect lines were flown at fixed altitudes. We attempted to maintain an altitude of 150 m above ground level (agl). Animals were counted within fixed strips on either side of the aircraft. Markers were placed on the aircraft wing struts to bound the strips (following Norton-Griffiths, 1978). Strip width was 500 m on each side of the aircraft. We attempted to maintain an airspeed of 160 km/hr.

Each stratum was flown at 20% coverage except for the Egg (E) and Masik (M) (Fig. 1) where coverage was 40%. After the initial islandwide survey was completed, areas of high caribou density were blocked off and reflown at 40% coverage. Population estimates (animals ≥one-year-old) for all years were derived by the Jolly (1969) method for unequal sized sampling units. We present estimated population number and the standard error of the estimate (Norton-Griffiths, 1978). Observations from the reflown blocks of high caribou density were used for the population estimate. Observations from the original coverage of areas blocked off as high density caribou areas were not included in the population estimate being replaced by the reflown observations.

We tested for differences in population estimates between years following the formula described in Norton-Griffiths (1978) and adapted from Cochran (1954).

Melville Island

Islandwide aerial surveys were conducted in 1987 and 1997 to estimate caribou and muskox populations (Miller, 1988; A. Gunn & J. Dragon, unpubl. data). Both surveys used a strip-transect technique with a stratified design; the transect was the sampling unit (Norton-Griffiths, 1978). The island was stratified into 13 strata based upon geographic area

Table 1. The number of calves, yearlings, adult (≥two-year-old) females, males, and unclassified adults from each classification survey conducted in July on Banks and Melville Islands.

	Banks Island					Melville Island				
	calves	yrlngs	ad. fem.	ad. mal.	unk. ad.	calves	yrlngs	ad. fem.	ad. mal.	unk. ad.
1994	6	9	25	7	0					
1995	3	2	5	3	16					
1996	8	4	12	10	0					
1997	6	4	15	23	4					
1998	52	16	70	18	0	12	3	15	16	0
1999	55	25	78	16	0	13	9	29	22	0
2000	21	14	37	8	0	17	9	27	4	0

(Fig. 1). In 1987, a Bell 206B helicopter was used. Transect lines were flown at 90 m agl and an airspeed of 160 km/hr. Parallel lines were flown 6.4 km apart; animals were counted within fixed strips of 857 m on each side of the aircraft resulting in an overall coverage of 27% (Miller, 1988). In 1997, a fixed-wing aircraft (Helio-Courier) was used. Transect lines were flown at 100 m agl at an airspeed of 160 km/hr. Parallel lines were flown that provided an overall coverage of 20% with animals being counted within fixed strips of 500 m on each side of the aircraft (A. Gunn & J. Dragon, unpubl. data). Population estimates (animals ≥one-year-old) for both surveys were derived by the Jolly (1969) method for unequal sized sampling units. We present estimated population number and the standard error of the estimate (Norton-Griffiths, 1978).

Classification Surveys

Banks Island

Surveys were conducted annually during July from 1994-2000. Three to six h flights were made by helicopter aircraft (Bell 206B or 206L) over the major historical calving and summer range located to the northwest of Banks Island (Urquhart, 1973). Caribou were spotted from the air and the survey crew, generally an observer and a recorder, was positioned on the ground in such a way as to minimize disturbance of the animals. The survey crew moved into a position where the animals could be observed with a spotting scope (15-45x) or binoculars (7x24). Caribou were classified into calves, yearlings, adult females (≥two-years-old), and adult males (≥two-years-old). Occasionally, small groups of adult males (one-three) or dam-calf pairs were classified from the air. In 1994 and 1998, aerial reconnaissance by fixed-wing aircraft involved in the Banks Island population survey identified areas of local caribou concentration in the summering grounds prior to the classification survey and the helicopter flew directly to these areas.

Melville Island

Surveys were conducted annually in mid-July from 1998-2000. In 1998, the survey was based on opportunistic observations made during flights with a rotary aircraft (Bell 206L) concentrated over the Dundas Peninsula (Fig. 1; VI). This was in an area where Miller et al. (1973) had reported high densities of Peary caribou in August, 1972. In 1999, we flew over a much larger area of central and western Melville Island in an attempt to confirm that the majority of caribou were distributed on Dundas Peninsula during mid-July (Larter & Nagy, 2000b); the flight confirmed this. We blocked off a survey area bounded by 74°46'N to the north and 74°32'N to the south and flew eight parallel line transects, 26 km in length and spaced ca. 5.6 km apart, from 113°40'W eastward to 112°23'W. All groups of caribou observed within this area and during flights to and from the survey area were classified as described above. During the 2000 survey we added a ninth parallel transect to the east of the survey area on 112°12'W.

Demographic characteristics

We estimated calf production as the number of calves per 100 adult females determined in the July classification surveys. We realize that this estimate does not address neonatal mortality but surveys were conducted during the same three-week period in July and we believe any biases would be similar for each survey. We used the number of yearlings per 100 adult females divided by the sum of 100 plus the number of yearlings per 100 adult females to estimate annual recruitment rate, which we expressed as a percent. Because fewer than 15 animals were classified during the 1995 survey on Banks Island (Table 1), we made no estimates of pro-

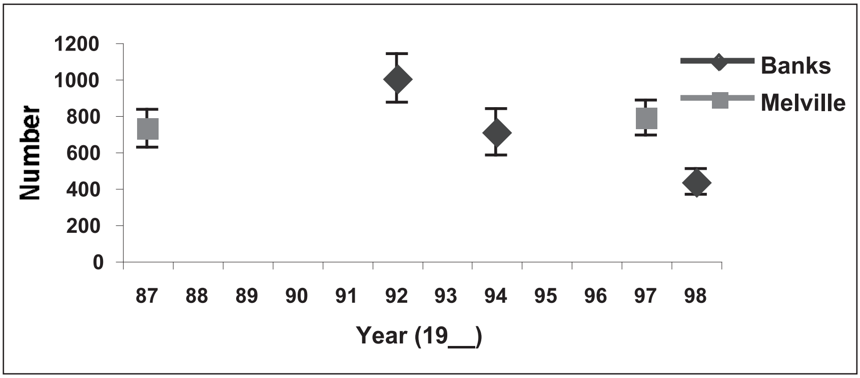

Fig. 2. Population estimates (±SE) of Peary caribou ≥one-year-old for Banks and Melville Islands.

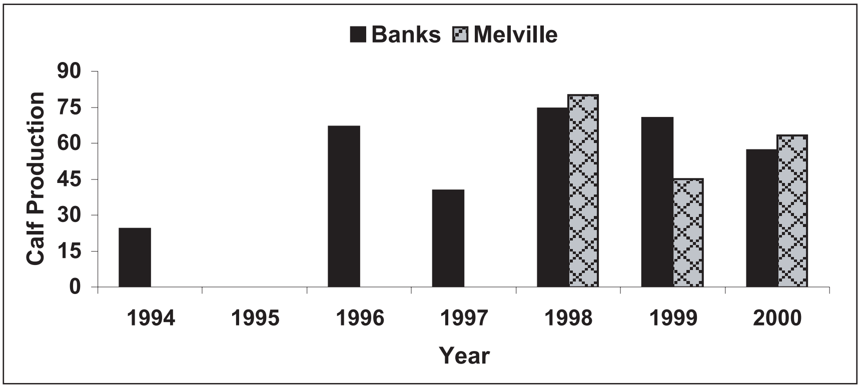

Fig. 3. Calf production (number of calves per 100 females ≥two-year-old) for caribou on Banks and Melville Islands.

duction or recruitment for this year. The four unknown adults from the 1997 survey on Banks Island (Table 1) were also excluded from the calculations. We used correlation analysis to assess any potential trends in calf production and recruitment rate over time for Banks and Melville Islands.

Results

Population estimates for Banks Island caribou were 1005 (SE±133), 709 (SE±128), and 436 (SE±71) for 1992, 1994, and 1998, respectively (Fig. 2). None of the three estimates were different ($P<0.05$). Population estimates for Melville Island caribou were 729 (SE±104) and 787 (SE±97) for 1987 and 1997, respectively (Fig. 2).

From 1994 to 2000, excluding 1995, we classified 34-174 animals per survey on Banks Island, and from 1998 to 2000 we classified 46-73 animals per survey on Melville Island (Table 1). Calf production on both Banks and Melville Islands had considerable variability, showing a slight increasing trend ($r=0.64$; $P=0.17$) from 1994-2000 on Banks Island but a slight decreasing trend ($r=-0.48$; $P=0.68$) from 1998-2000 on Melville Island (Fig. 3). Recruitment rate varied less than calf production, showing no trend on Banks Island from 1993/1994 to 1999/2000 ($P=0.90$; Fig. 4) but a strongly increasing trend on Melville Island from 1997/1998 to 1999/2000 ($r=0.93$; $P=0.24$). A strongly increasing trend in recruitment rate occurred during the same three-year period for Banks Island ($r=0.99$; $P=0.10$).

Discussion

Although current population estimates of Banks and Melville Island caribou are lower than those of 20 years ago, both populations have remained relatively stable since 1987 for Melville and since 1991 for Banks Island (Nagy et al., 1996). Annual calf production has been highly variable for both populations. The slight increasing trend in calf production on Banks Island is likely a result of low calf production in 1994. Larter & Nagy (2000a) documented 11 years of calf production on Banks Island and production in 1994 was the lowest recorded. The decreasing trend in calf production on Melville Island is likely a result of small sample size (three years) in combination with annual variability. Values reported for Melville Island fall well within those reported for Banks Island and other high arctic caribou and Svalbard reindeer populations reported elsewhere (Tyler, 1987; Miller, 1992).

High calf production does not necessarily translate into high recruitment. Calf mortality is one of the main factors affecting population growth of caribou and reindeer populations (Bergerud, 1971; Parker, 1972; Skogland, 1985; Tyler, 1987). Calf production and calf survival are both components of recruitment rate, therefore recruitment rate may provide better information on the potential for population change

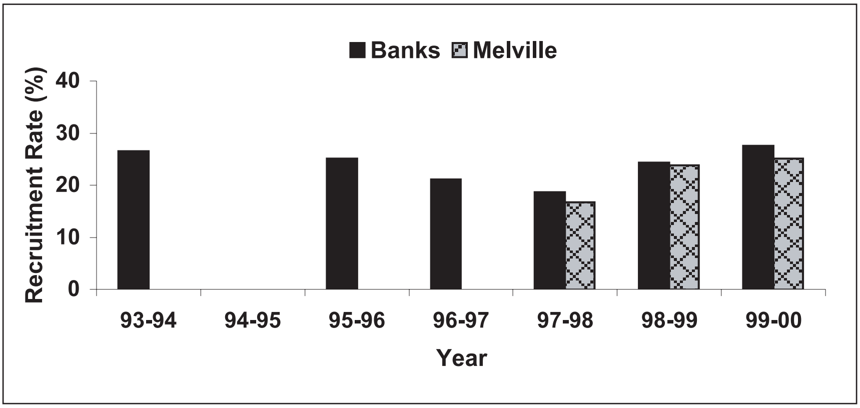

Fig. 4. Annual recruitment rate (%) of caribou on Banks and Melville Islands.

as our data suggest. Since 1998, the recruitment rate for both populations has shown a positive trend. Winter 1997/1998 was one of the mildest in recent years and had the least severe snow conditions, particularly snow depth, recorded on Banks Island during the period 1992/1993 to 1997/1998 (Larter & Nagy, 2000c; 2001a; R. Kuptana pers. comm). Whether snow conditions on Melville Island were of lesser severity during winter 1997/1998 is unknown.

During winter, legumes (Astragalus spp. and Oxytropis spp.) are an important dietary item for Banks Island caribou with their proportion in the diet being greater during years of shallower snow depth (Larter & Nagy 1997; N. Larter & J. Nagy unpubl. data). Shallower snow likely increases legume availability. During winter legumes remain highly digestible, and have a high crude protein content (ca. 13%), much higher than sedge and mountain avens which make up much of the remaining proportion of the winter diet (Larter & Nagy, 2001b). Improved access to a high quality winter diet may have had a positive effect on overwinter survival and/or calf production, which translated into increased recruitment. Whether improved access to a high quality winter diet continued during winters following 1997/1998 is unknown as comparative snow data collection ended.

The effect of wolf predation on these caribou populations remains unknown. Both Banks Island and neighbouring Victoria Island have a substantial alternate prey source, i.e. large muskoxen populations, which could sustain substantial wolf numbers. Harvest records and observations from local residents of both Sachs Harbour (Banks Island) and Holman (NW Victoria Island) indicate that wolf numbers have been increasing throughout the 1990s (Nagy & Larter, 2000; N. Larter & J. Nagy, unpubl. data). Between 40 and 50 wolves are generally observed on whole island surveys of Banks Island and it is not uncommon to observe groups of 15-20 individuals. The alternate prey source is not as substantial on Melville Island, however during the whole island survey in 1997, 20 adult wolves and 12 pups were observed (A. Gunn & J. Dragon, unpubl. data).

Limited information on wolf diet from Banks and Melville Island shows that muskoxen predominates (Nagy & Larter, 2000). However, wolf diet has been determined from opportunistic collections of wolf scats and the stomachs from harvested wolves, mostly collected during winter. Such sampling may not address wolf diet at key times of the year and from key locations. For example, on Banks Island, when caribou make their southerly migration from the calving and summer range (NW Banks Island), they pass adjacent to a high wolf density area. Non-selective predation on calves, yearlings, and adult females as caribou migrate through this area could go undetected by the current sampling regime. Nor would this type of predation be noticeable in our estimates of production or recruitment. Therefore, it is crucial that whole island population surveys be conducted at regular intervals so that production and recruitment estimates can be evaluated in their proper context.

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Natality and calf mortality of the Northern Alaska Peninsula and Southern Alaska Peninsula caribou herds

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Abstract: We studied natality in the Northern Alaska Peninsula (NAP) and Southern Alaska Peninsula (SAP) caribou (Rangifer tarandus granti) herds during 1996-1999, and mortality and weights of calves during 1998 and 1999. Natality was lower in the NAP than the SAP primarily because most 3-year-old females did not produce calves in the NAP. Patterns of calf mortality in the NAP and SAP differed from those in Interior Alaska primarily because neonatal (i.e., during the first 2 weeks of life) mortality was relatively low, but mortality continued to be significant through August in both herds, and aggregate annual mortality was extreme (86%) in the NAP. Predators probably killed more neonatal calves in the SAP, primarily because a wolf den (Canis lupus) was located on the calving area. Despite the relatively high density of brown bears (Ursus arctos) and bald eagles (Haliaeetus leucocephalus), these predators killed surprisingly few calves. Golden eagles (Aquila chrysaetos) were uncommon on the Alaska Peninsula. At least 2 calves apparently died from pneumonia in the range of the NAP but none were suspected to have died from disease in the range of the SAP. Heavy scavenging by bald eagles complicated determining cause of death of calves in both the NAP and SAP.

Key words: Aquila chrysaetos, bald eagle, Canis lupus, coyote, golden eagle, grizzly bear, Haliaeetus leucocephalus, pneumonia, predation, Rangifer tarandus granti, Ursus arctos, wolf.

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Introduction

The Northern Alaska Peninsula (NAP) and Southern Alaska Peninsula (SAP) caribou (Rangifer tarandus granti) herds have been important to local subsistence hunters for centuries and to guides and recreational hunters since the 1950s (Murie, 1959; Skoog, 1968; Sellers, 1999). Caribou from these 2 herds are widely known for their large antlers and have attracted hunters from all over the world (Boone & Crockett Club, 2000). However, these herds have fluctuated in size, and recent population declines have caused economic hardships for local residents and guides.

The SAP reached a peak population size of 10 200 in 1982 and then declined continuously to about 1500-2000 by 1995 (Valkenburg et al., 2003a). Hunting was gradually restricted during the late 1980s and all hunting was closed in 1993. The NAP reached a peak population size of 20 000 caribou during the early 1980s but remained relatively stable between 16 000-20 000 during 1981-1994 when it began declining (Valkenburg et al., 2003a). Hunting by nonresidents was severely restricted in 1998 and a year later only 600 permits were issued to subsistence hunters.

There has been considerable speculation about the causes of declines in caribou on the Alaska Peninsula, including predation, disease, icing of winter ranges, and emigration (Skoog, 1968; Valkenburg et al., 2003a). Because the adjacent NAP and SAP caribou

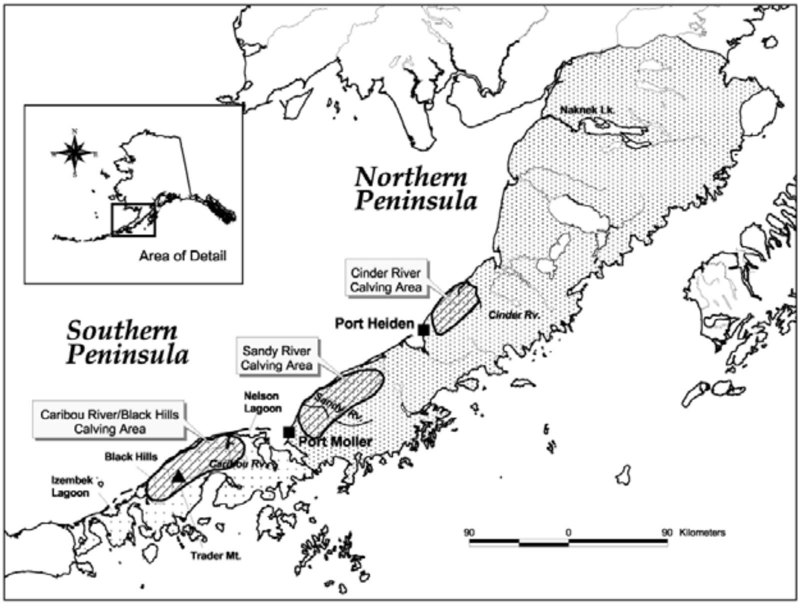

Fig. 1. Location of calving areas and annual ranges of the Northern Alaska Peninsula (NAP) and Southern Alaska Peninsula (SAP) caribou herds.

herds were in different phases of population fluctuation, we investigated natality and mortality to evaluate how differences in these factors might be responsible for differences in population growth rates. Therefore, in 1995 we increased the intensity of annual surveys and began collecting female calves to assess body condition and the prevalence of disease. We also began radiocollaring female calves to determine age-specific natality rates and mortality rates. In addition, we conducted calf mortality studies in the NAP in 1998 and the SAP in 1999. In this paper, we report results of the calf mortality studies and compare mortality and natality patterns in the NAP and SAP with patterns in other Alaskan herds.

Study areas and populations

NAP

The NAP ranges throughout the Alaska Peninsula from Naknek Lake to Port Moller (Fig. 1). Caribou calve primarily on the flat, poorly drained coastal plain of the Bristol Bay side of the Alaska Peninsula from Port Moller to Cinder River Flats north of Port Heiden, and some scattered calving occurs throughout the Aleutian Mountain Range. Most caribou spend the summer south of the Ugashik River but migrate north in autumn to spend the winter between the Ugashik drainage and Lake Iliamna on lichen ranges in tundra and open spruce (*Picea* spp.) woodlands.

Grizzly bears (*Ursus arctos*) are abundant on the Alaska Peninsula (estimated at 191 bears/1000 km^2 near the center of the NAP's range, Miller et al., 1997) and wolves (*Canis lupus*) are periodically abundant but susceptible to rabies that is endemic in red foxes (*Vulpes vulpes*) (Ballard et al., 1997; Sellers, 2000). Bald eagles (*Haliaeetus leucocephalus*) are also abundant, but golden eagles (*Aquila chrysaetos*) are uncommon. Wolverines (*Gulo gulo*) occur throughout the ranges of both herds. We detected no denning activity by wolves on the calving area of the NAP.

During the mid-1990s, as the population began to decline, there were indications that NAP caribou were chronically undernourished, their winter ranges shifted, and the caribou were probably more vulnerable to parasitism, disease, and predation (Sellers, 1999). During 1996-1998, 14 of 30 4-month-old calves that were collected to assess body condition had lesions on their lungs consistent with lungworm (*Dictyocaulus* spp.) infestation or pneumonia (Sellers, 1999).

SAP

Unlike the NAP, the SAP now appears to be recovering from a population low, and body condition and weights of calves captured in autumn 1998 were excellent (Valkenburg et al., 2002).

Southern Alaska Peninsula females calve on low-lying sedge flats in the Caribou River drainage southeast of Nelson Lagoon and on uplands in the Trader Mountain/Black Hills area (Fig. 1). Caribou remain on and around the calving areas for the summer, but most move south in October to winter in the vicinity of Cold Bay and Izembek Lagoon. Unlike the range of the NAP, there are no native trees in the range of the SAP, and caribou winter primarily on sedge flats and heath-covered uplands (Post & Klein, 1999). Lichens are present in the uplands but have never been described as abundant (Skoog, 1968; Post & Klein, 1999). Fauna of the SAP range is similar to the NAP range, but we discovered an active wolf den with at least 5 adult and yearling wolves located along the Caribou River in the calving area of the SAP. In the ranges of both the NAP and the SAP, severe weather is common at all

Table 1. Natality of females surveyed on the calving areas of the Northern Alaska Peninsula (NAP) and Southern Alaska Peninsula (SAP) herds in 1998 and 1999.

Herd and area	Year	Number parturient (%)	Total females surveyed
NAP — Cinder River	1998	95 (69)	137
NAP — South of Port Heiden	1998	402 (84)	480
NAP — Cinder River	1999	275 (68)	405
NAP — South of Port Heiden	1999	395 (86)	461
Total NAP — 1998 and 1999		1167 (79)	1483
SAP — Caribou River Flats	1999	129 (88)	146
SAP — Black Hill/Trader Mountain	1999	189 (96)	196
Total SAP — 1999		318 (93)	342

times of the year and high winds, low clouds, and intense snowstorms make flying difficult.

Methods

During late May 1997-1999, we observed 35 radiocollared, known-aged, NAP females from fixed-wing aircraft or a Robinson (R-44) helicopter to determine age-specific natality rates (Bergerud, 1964; Whitten, 1995). The females were captured as 4-month-old or 10-month-old calves beginning in 1995. On the Bristol Bay side of the Alaska Peninsula we monitored pregnant radiocollared females daily during 1998 to determine birth dates and locations. Also in 1998, from 30 May to 9 June we radiocollared and weighed 39 1- to 2-day-old calves. Calves were caught by hand after a close approach with the helicopter (cf. Adams et al., 1995). To reduce chances of abandonment, we generally only caught calves that were dry (i.e., at least several hours old), and ones that were not in groups with other caribou. We monitored calves daily through 12 June to determine timing and causes of mortality. We also recorded observations of predators on the calving area and surveyed caribou to determine the proportion of parturient females in the herd. To assess the prevalence of lungworm and pneumonia, we collected samples of lung and liver from calves that were found dead during the calf mortality study. In addition, 30 fresh fecal samples from caribou older than calves were collected from the calving area to assess prevalence of lungworm in the herd. Follow-up telemetry flights were made on 19 June, 25-28 June, 3-8 August and 30 September 1998. On 30 June a Robinson R-22 helicopter was used to investigate deaths of calves that occurred after 15 June and to collect 2 unmarked calves that were debilitated. The carcasses of these 2 calves and an intact collared calf were sent to the Washington Animal Disease Diagnostic Laboratory in Pullman, Washington for complete necropsy. In October 1998, we collared 19 additional female calves with adult-sized radio collars and monitored their mortality through June 1999.

Table 2. Mean kg weights (with standard error of the mean) of newborn caribou calves of the Northern Alaska Peninsula (NAP) and Southern Alaska Peninsula (SAP) caribou herds, during 1998 and 1999.

Herd and year	Males ($s_{\bar{x}}$, n)	Females ($s_{\bar{x}}$, n)
NAP 1998	8.44 (0.24, 19)	7.17 (0.30, 20)
NAP 1999	8.35 (0.25, 22)	7.41 (0.24, 22)
SAP 1989	6.67 (0.67, 8)	5.44 (0.57, 9)
SAP 1999	7.70 (0.28, 25)	7.14 (0.16, 29)

In 1999 we conducted a similar study on caribou in SAP, and we also captured and weighed (but did not collar) calves in the NAP to compare their weights with the previous year and with weights of SAP calves. Capture and monitoring methods were identical except we collared 52 calves in the SAP during 3-12 June and continued daily monitoring through 18 June. Follow-up flights were made on 26-29 June and on 23 August. We compared natality rates of radiocollared caribou using chi-square (χ^2) tests, and we used t-tests to compare weights of newborn calves. We compared ratios of uncollared parturient to nonparturient cows on the calving areas of the NAP and the SAP by calculating binomial confidence intervals for the ratios. For these comparisons, we report only the P-value. For calculating mortality rates of calves from late June to late September in both the NAP and the SAP, and for calculating total annual mortality rates, we used Kaplan–Meier survival estimates because it was necessary to account for censored caribou that were not found during incomplete survey flights (Pollock et al., 1989).

Table 3. Causes and timing of mortality of caribou calves that were radiocollared as newborns in the Northern Alaska Peninsula (NAP) and Southern Alaska Peninsula (SAP) herds in 1998 and 1999 respectively.

	Number of calves collared as newborns that died through 28 June							
Herd and year	Brown bear	Wolf	Eagle	Wolverine	Drowning	Disease (pneumonia)[1]	Unknown	Total dying (%)
NAP 1998	3[2]	none[2]	1	none	1	2	6[2]	13/37 (35)
SAP 1999	3	6	1	1	2	none	9	22/49 (45)

[1] Two calves were found dead in late June. There were no visible subcutaneous marks on them. Carcasses were sent to Washington Animal Disease Diagnostic Laboratory and pneumonia was diagnosed.

[2] Two calves included as unknown were killed either by bears or wolves.

Results

Natality

There was no difference (P=0.20) in natality rates of uncollared females surveyed in 1998 and 1999 in the NAP. We therefore lumped these data and compared them with similar data from the SAP for 1999. In aggregate, females surveyed on the calving areas of the NAP were significantly less fecund than those surveyed on the calving areas of the SAP (79% vs. 93%, P<0.01) (Table 1).

Radiocollared 3-year-old females in the NAP were also significantly less fecund than those in the SAP (χ^2=9.9, P=0.002, df=1). Six of 18 3-year-olds were parturient in the NAP, whereas 8 of 8 were parturient in the SAP. We suspect that natality in older radiocollared females was similar between herds, but sample sizes were too small for meaningful comparison (14/17 in the NAP and 4/5 in the SAP). No 2-year old females were parturient in either herd (n=25 for the NAP, and n=12 for the SAP).

Weights of newborn calves

There was no difference in weights of NAP calves in 1998 and 1999 (for males, t=0.27, P=0.79, df=39; for females, t=0.64, P=0.52, df=40). We therefore lumped NAP data from 1998 and 1999 for comparison with the SAP data from 1999. Male NAP calves were somewhat heavier than male SAP calves (t=2.25, P=0.03, df=64) (Table 2). There was no difference in weights between herds for females (t=0.57, P=0.57, df=69). Weights of calves from the SAP were significantly heavier (for males, t=1.70, P=0.09, df=31; for females, t=2.72, P=0.01, df=36) in 1999 than recorded by Pitcher (1991) in 1989 (Table 2).

Calf mortality in the NAP

In 1998, of 39 newborn calves collared, 2 did not reunite with their mothers and were censored from the study, and 13 of the remaining 37 died by 28 June (35% mortality) (Table 3). During the first 2 weeks of life, 19% (7/37) of the radiocollared calves died; during 12-19 June only 1 calf died; and during the following week, 5 of the remaining 29 calves died. Two of the calves that died in late June had no subcutaneous marks and apparently died of pneumonia. One of these was diagnosed with bacterial pneumonia. No lungworm eggs were found in the fecal samples collected from the calving area, and lungworm did not appear to be prevalent in the NAP.

Follow up flights in August and September 1998 were less intense and status was determined by the radio collar mortality sensor. Coverage of the caribou range was incomplete and 9 of 24 calves known to be alive in late June were not located and thus were censored. In early August, 13 live and 2 dead calves were found. On 30 September only 7 live and 1 dead calf were located. Therefore, the Kaplan-Meier survival estimate from birth through 30 September was 49.5% (50.5% mortality). The mortality rate of 19 claves collared in October 1998 was 71% by June 1999, but causes of death were not determined. Thus the total annual calf mortality rate was 86% in the NAP during 1998-1999.

Sample size was too small to determine the relative importance of individual predators or disease in the NAP calves, but brown bears killed the most collared neonatal calves. During 29 May-12 June, we observed 88 brown bears on the calving areas of the NAP. Brown bears were not likely involved in the high overwinter mortality.

Calf mortality in SAP

Of the 52 newborn calves collared in the SAP in 1999, 4 did not reunite with their mother and were censored from the study. Also, we discovered 1 calf the day after capture in a steep-sided stream with its mother nearby. We rescued the calf, considered it a mortality for the purposes of the study, and reentered it as a new calf. Therefore, there were 49 calves in the study. Of these, 45% were dead by late June, and 66% were dead by late August. Brown bears and wolves killed most calves that died, but sample size was inadequate to distinguish which of these predators was most important to herd mortality (Table 3). As in the NAP study in 1998, a high proportion (61%) of deaths occurred late in the calving period (i.e., after 18 June). Because of the high cost of keeping the helicopter available to determine cause of death of calves, we were only able to determine the cause of death of the 11 calves that died before 18 June (Table 3). Eleven more died by 26 June and eagles scavenged 9 of them so much that cause of death could not be determined. Wolves killed the other 2. We could not determine cause of death of the 10 that died between 26 June and 23 August. Of 13 calves collared in October 1998, only 1 died by June 1999. Therefore, total annual mortality rate for SAP calves was at least 69%.

Discussion

Natality

Natality of female caribou in the SAP was higher than in the NAP primarily because most 3-year-old females did not produce calves in the NAP. Similar differences in natality have been shown for Interior caribou herds where summer nutrition (i.e., weight gain of calves over summer) varies (Valkenburg et al., 2003b). In the NAP, survival of calves to 1 year was low during the mid- to late 1990s and, therefore, there were few 1-, 2-, and 3-year-olds in the population.

Weights of newborn calves

Weights of newborn male NAP and SAP calves during this study were similar to weights of newborn calves from other herds in Alaska (except the Porcupine herd and SAP in 1989) in most years (Whitten et al., 1992; Whitten, 1995; Valkenburg et al., 2002). Southern Alaska Peninsula calves were exceptionally light in 1989 (Table 2) during the precipitous population decline, when they were lighter than any other calves weighed in Alaska (Pitcher, 1991; Valkenburg et al., 2002). The relatively low weight of SAP males compared with NAP males in 1998 and 1999 may indicate that SAP caribou are more limited by winter nutrition than NAP caribou (cf. Reimers, 1997). In contrast, summer nutrition appears better in the SAP than the NAP judging from the higher natality rates in 3-year-old females (see Natality), and the slightly higher weights of female calves in autumn in the SAP (Valkenburg et al., 2002).

Calf mortality

Although neonatal calf mortality did not differ between the NAP and the SAP ($\chi^2=0.83$, $P=0.36$, df=1), it appeared that predation was a more significant factor in the SAP than in the NAP. This may primarily have been because a wolf den was located within the calving area of the SAP, and no den was present on the calving area of the NAP. It may also be significant that 2 neonates died from pneumonia in the NAP, particular because pneumonia was also found to be prevalent in 3 collections of 4-month-old female calves during autumn 1996-1998. We hypothesize that NAP calves were in generally poor condition during the mid- to late 1990s, and that diseases became more prevalent.

In contrast to mortality patterns in other herds that have been studied in Alaska, in both the NAP and the SAP high mortality continued through August, and golden eagles were rare and were not major predators of caribou calves (Adams et al., 1995; Boertje & Gardner, 2000; Valkenburg et al., 2002). Also, despite their high density (mean density of about 180 bears per 1000 km^2 within the range of both herds, ADF&G unpublished data), brown bears killed surprisingly few calves in the NAP and SAP compared with other studies on newborn moose and caribou in Interior Alaska (Adams et al., 1995; Miller et al., 1997; Boertje & Gardner, 2000; Bertram & Vivion, 2002; Valkenburg et al., 2002). Also, despite the high density of bald eagles on the calving area, they were not significant predators of calves. In contrast to golden eagles, bald eagles appeared to primarily be scavengers. The extensive scavenging of carrion by bald eagles did make documenting cause of death more difficult on both the NAP and the SAP.

Although neonatal and summer mortality of caribou calves was similar in both herds (albeit for different reasons), the extreme winter mortality in the NAP caused recruitment in that herd to be low and insufficient to prevent the population from declining.

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Session five

Inuit Elder's Story:

Willie Emudluk, Kangiqsualujjuaq, Québec

Willie Emudluk, a respected elder from Kangiqsualujjuaq, was born January 24, 1924 in Old Fort Chimo (across the Koksoak River from Kuujjuaq). He is married to Emily, with whom he has raised six children (two by adoption). Willie started working at an early age for the Hudson's Bay Company. In 1969 he was asked to manage the fuel distribution in Kangiqsualujjuaq for Shell Canada and has held exclusive distribution rights since then. Willie is currently deputy mayor of Kangiqsualujjuaq (his daughter Maggie Emudluk is mayor). He is also president of the Qiniqtiq land holding corporation and a member of the local Hunting, Fishing and Trapping Association. Despite his many responsibilities, Willie continues to take every opportunity to hunt, fish, and practice his traditional lifestyle as a respected Nunavik Inuk.

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Predation risk and optimal foraging trade-off in the demography and spacing of the George River Herd, 1958 to 1993

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Abstract: The behavior options of feeding animals lie on a continuum between energy maximization and minimization of predation risk. We studied the distribution, mobility, and energy budgets of the George River herd, Ungava from 1974 to 1993. We arranged the annual cycle into 6 phases where we argue that the importance between the priorities of optimal foraging and predation risk change between periods. At calving, risk is more important than foraging for females but males take more risk to optimally forage. During the mosquito season, insect avoidance takes priority over risk and foraging. Optimal foraging takes precedent over risk in the late summer and fall and it is at this time that the herd expanded its range relative to numbers and forage abundance. In the winter (December to mid-March) animals sought restricted localized ranges with low snow cover to reduce predation risk. The spring migration of females may have increased risk during the interval the females were moving back to the tundra to give birth to their neonates on the low risk calving ground. In May, females sought early greens near treeline, which may have increased risk in order to provide maximum nutrition to their fetuses in the last weeks of pregnancy. The ancestors of the George River Herd during the Pleistocene, 18 000 yr. BP may have reduced predation risk by spacing-out in the Appalachian Mountains, removed from the major specie of the megafauna in the lowlands. With global warming, it is argued the major problem for caribou will be increased wolf predation rather than changing forage and nutritional regimes. It is essential that First Nation residents of the North maintain their option to manage wolf numbers if excessive predation in the future adversely affects the migratory herds of the Northwest Territories and Ungava.

Key words: caribou, climate change, Labrador, Québec, Rangifer tarandus.

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Introduction

The George River Herd in Ungava increased from less than 5000 animals in the 1950s (Banfield & Tener, 1954) to approximately 650 000 animals in the 1980s and was the largest herd in the world (Williams & Heard, 1986; Bergerud, 1988a). This was the greatest eruption that we know of for an ungulate. For some 20 years 1974 to 1993 the junior author monitored the demography, physical condition, and movements of the herd. The senior author censused the herd in 1958, conducted calving studies in 1978 and 1988, and supervised optimal summer foraging studies 1988 to 1992 (see Camp & Linders, 1989).

From this data backdrop we wish to evaluate how caribou balance the trade-off between predation risk and optimal foraging in their annual use of space and its effects on demography. There is a growing concern among caribou biologists about the impact of global warming on caribou. But the concerns voiced (Russell, 1993; Gunn, 2000; Griffith et al., 2000) relate solely to optimal foraging considerations to the exclusion of how predation risk will be altered as temperature increases in the Arctic. We feel a more balanced approach is needed for certainly predation risk will be affected by climatic change and predation impacts will be the primary means by which survival rates will be altered.

Lima & Dill (1990) stated that the behavior options to a feeding animal lie on a continuum between energy maximization and minimization of risk (Fig.1). Animals are free to choose and their choice may affect their survival and reproductive fitness. Belosky (1991) stated that insect and predator avoidance will "constrain" optimal foraging but Lima & Dill say there is nothing constraining a free choice of the two options; neither choice is more fundamental than the other. Clearly neither option is desirable and optimal behaviour will lie somewhere in between (Lima & Dill, 1990).

Table 1. Weather statistic recorded at Schefferville 1955-56 to 1992-93 by students of the McGill Sub-Arctic Research Laboratory (Snowfall statistics based on biological year June to May, Julian dates for Y in freeze-up and break-up). Mean with standard error of the mean ($s_{\bar{x}}$) in parenthesis.

Weather parameter	Mean ($s_{\bar{x}}$)	Maximum	Minimum	Annual trend
July temperatures °C	12.4 (0.16)	14.4 (1959)	9.8 (1965)	Y=34.116-0.011X r=0.121, P=0.46
January temperature °C	-23.1 (0.61)	-15.9 (1958)	-30.4 (1991)	Y=184.814-0.104X r=0.312, P=0.05
Annual temperature °C	-5.0 (0.15)	-2.7 (1981)	-7.9 (1972)	Y=49.179-0.027X r=0.355, P=0.04
Annual snowfall (cm)	382.5 (16.50)	612.8 (1980-81)	209.0 (1992-93)	Y=-4877.641+2.666X r=0.287, P=0.085
Fall freeze-up (Knob L.)	Oct 29.1 (1.87)	Nov 16 (1978)	Oct 3 (1956)	Y=175.348+0.064X r=0.056, P=0.76
Spring break-up (Knob L.)	Jun 12.0 (1.14)	Jun 29 (1992)	Jun 1 (1956)	Y= -91.963+0.129X r=0.212, P=0.20

Bergerud (1996, fig. 9, p. 111) has noted that habitat choices for caribou have a hierarchical scale in space. For example, for the George River herd, all the Labrador tundra was a low risk habitat within which the animals could select smaller scale habitats to optimally feed. In fact, the animals on the calving grounds generally shifted locations between years in response to a degraded flora from a previous grazing.

Caribou ecology could be described and understood by balancing predation risk and optimal foraging in this hierarchical space and habitat framework.

Predation risk versus optimal foraging: a synthesis

We have divided the annual cycle into 6 phases where we argue that the importance of risk vs. foraging changed from the previous phase:

1. Calving (June): Risk more important than optimally foraging for females but males optimally forage.
2. Mosquito season (July): Insect avoidance is more central than risk or foraging
3. Late summer and fall (August through November): Optimal foraging takes precedent over risk.
4. Winter pause (December to mid March): Risk is a greater problem than foraging
5. Spring Migration (mid March and April): Females may increase risk to return to the calving ground.
6. May: Optimal foraging is the priority within the constraints of having made the return migration to the low risk tundra.

All would agree that in the absence of predators, caribou will optimally forage especially at times that will influence reproductive fitness. Again if a range is overgrazed animals may be prepared to take greater risks especially if the reproductive fitness of conceiving and or producing viable neonates is involved.

The sequences we discuss for the George River Herd 1958-1993 should act as a "control" relative to global warming. The weather in Ungava has remained relatively constant in temperatures in the past 40 years compared to the warming trends that have and are taking place in Alaska and western Canada (Table 1).

In comparing risk vs. foraging choices the density of caribou or total numbers are needed in some analyses. Three regressions of numbers (Y=1000s of animals) on years (X=last two year digits) were calculated. (1) The first regression was based on census results 1954 to 1988 (1993 censuses excluded) ($Y=750/(1+1614718e^{-0.177X})$) (r=0.972). (2) The second regression was calculated based on the ages of 2267 caribou aged by annulations 1973-74 to 1987-

88 using the Cagean program (Deriso et al., 1981) commencing with a population estimate of 176 000 in 1973-74 (expanded from Wetmore, 1973) and excluding declining estimates in 1985,1986, and 1987 ($Y=0.0078e^{0.137X}$) ($r=0.991$). (3). A third regression was based on the conifer scar data of Morneau & Payette (2000) for the years 1943 to 1988 and excluded their last tally for 1988 to 1992 that showed a decline in scarring ($Y=0.002e^{0.114X}$) ($r=0.967$).

We also calculated the expected population size in 1993 based on adult mortality and spring recruitment statistics annually commencing with the 1984 census (Crête et al., 1991). The expected population based on the M/R procedures gave an estimate in 1993 of 400 000 (Bergerud, 1996). This estimate was in agreement with the root scar data 1988-92 from Morneau & Payette (2000) and consistent with a decline since 1984 based on the Cagean program.

We argue that the censuses in 1993 (Couturier et al., 1996; Russell et al., 1996) were too high to represent internal growth of the George River Herd and that animals from the Leaf River Herd were present and counted in these estimates; we did not include these counts in our equations of population growth of the herd. In both 1988 and 1993 Leaf River animals were associated with George River calving females (Bergerud, 1996). More recently a news release at this conference showed 5 of 23 satellite George River animals associated with Leaf River satellite animals (April 17-22) and Couturier et al. (this conference) gave a paper titled "Is the metapopulation theory useful in conservation?--A test with the Quebec-Labrador caribou". When we have two large adjacent migratory herds that winter in the same areas at high numbers, one with a severely degraded low risk calving range and the other with a much larger above treeline, low risk calving habitat, (Crête & Huot, 1993; Crête et al., 1990; Bergerud, 1988b; 1996; Manseau et al., 1996), might not we expect exchange?

1. Calving (June)

Female caribou migrate to calving grounds in North America to reduce predation risk for their neonates (Bergerud, 1974a; Whitten & Cameron, 1980; Bergerud & Page, 1987; Bergerud, 1996; Heard et al., 1996). Predators are less common on the calving grounds than winter ranges as documented for the Porcupine Herd (Garner & Reynolds, 1986) and the herds in the Northwest Territories (Kelsall, 1968; Fleck & Gunn, 1982; Heard et al., 1996). Males lag behind females in spring migration while foraging on early greens (Whitten & Cameron, 1980; Russell et al., 1993; Heard et al., 1996).

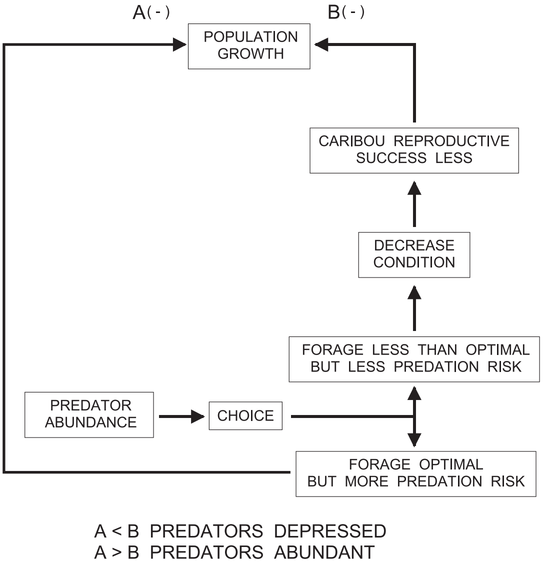

Fig. 1. Caribou optimal foraging/predation risk trade-off model.

The per cent nitrogen in the feces of females on the Caribou House calving ground of the George River Herd in 1988 was 24% less than that of males who were foraging in the Lac Champdoré area (Bergerud, 1996), a former calving ground of the George River Herd (Wetmore, 1973). Males were seeking *Menyanthes trifoliata* with 3.98% (standard error of the mean $s_{\bar{x}}=0.35$) nitrogen whereas females 130 km further NE were utilizing *Scirpus cespitosus* 2.54% ($s_{\bar{x}}=0.26$) nitrogen and *Arctostaphylos alpina* 2.80% nitrogen.

The Naskapi of Schefferville in 1958 (then called Knob Lake) told Bergerud that caribou calved in the taiga between Knob Lake and Indian House Lake. A calving ground, Lac Champdoré, was found in this area at the headwaters of the Wheeler and Whale Rivers in 1970 (Westmore, 1973). Thus some George River cows in the 1960s were calving south of the treeline and where the growing season commenced about June 5 or just as calving commenced. On June 4, 1972 Westmore (1973) also located a much larger concentration of cows calving on the Québec-Labrador provincial boundary southwest of Hebron Fiord; this ground we named Caribou House in respect of Naskapi mythology. The growing season at Caribou House commences about June 20, 15 days later than that at Lac Champdoré. By 1980 all the females had deserted Lac Champdoré and moved to Caribou House but males continued to graze there in May and June. It was at Lac Champdoré that we found males in 1988 and recorded their much higher fecal nitrogen than the cows at Caribou House.

We believe that a change in wolf predation pressure was responsible for the females moving to Caribou House. In the 1960s wolves were nearly extinct in Labrador. Some excerpts in 1958 from hunters that traveled inland extensively by dog team seeking the few remaining caribou were:

> Hopedale hunter: abundant when a boy, none for about 20 years.
>
> Nain hunter: 50 years ago there were plenty, have never seen any.
>
> Davis Inlet hunter: none for 15 years, plentiful 45 years ago.

We postulate that in the absence of wolves in the 1960s [the wolverine (Gulo gulo) had also disappeared (Novak et al., 1987)], a major portion of the herd calved below treeline dispersed in the taiga at Lac Champdoré. The growing season commences earlier at Lac Champdoré than any other area in central Québec and Labrador. This hypothesis is consistent with the greater abundance of root scars from caribou hooves in this region in the 1950s than further north (Morneau & Payette, 2000). Without predators the cows were able to optimally forage prior to calving. By the 1970s the herd exceeded 100 000 and wolves were becoming more abundant. Luttich saw three on his first spring trip in 1974. As the herd increased and attracted more attention from wolves the cows deserted their prior calving ground and moved as far northwest from treeline as snow-cover permitted (to Caribou House). Possibly the presence of bears along the Labrador coast influenced the extent of their eastern shift. They traded optimal foraging for reduced risk.

By 1988 they had severely overgrazed Caribou House compared to the western tundra where the Leaf River Herd calved in the 1970s (Fig. 2; Bergerud, 1988) while forage was still abundant at Lac Champdoré (Table 2). They remained above treeline in the low risk tundra even though the habitat continued to be degraded especially from trampling (Table 2). The physical condition of the females was reduced (Couturier et al., 1988; 1990). The pregnancy rate declined from 93% ($s_{\bar{x}}$=0.55) (1976 to 1982, 7 counts in 6 years, n=16 819 females) to 69.3% ($s_{\bar{x}}$=2.28) for the interval 1983-1993 (13 counts in 10 years, n=25 421 females. The body size of fall calves was reduced which increased their vulnerability to wolf predation (Bergerud, 1996). It was this trade-off of risk over foraging that more than any single other factor started the decline of the George River Herd in the mid 1980s.

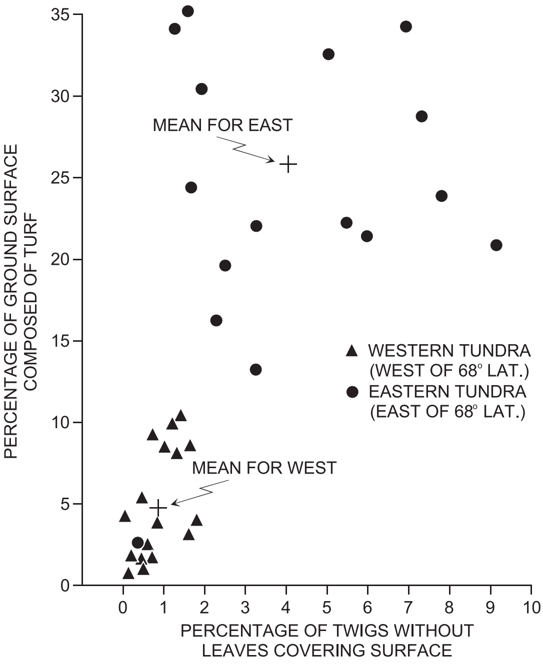

Fig. 2. Grazing and trampling on the Québec-Labrador Peninsula.

Note: The eastern tundra on the Labrador Peninsula was more heavily grazed and trampled in 1988 than the western tundra that was generally north of the Koksoak River and west of 68°W. Data based on 34 range stations. Each station centered in a 60' x 30' longitude x latitude grid. Each grid approximately 3500 km².

In the later stages of degrading of the above treeline range, the animals did compromise risk by mov-

Table 2. Comparison of the range destruction in % (standard error of the mean in parenthesis) between the deserted Lac Champdoré calving ground and the Caribou House calving ground, 1988.

Weather parameter	Mean ($s_{\bar{x}}$) at Lac Champdoré	Sample size	Mean ($s_{\bar{x}}$) at Caribou House	Sample size
The ground covered with broken twigs	0.74% (0.62)	3	5.8% (1.02)	9
Turf cover created by caribou hooves	3.00% (0.62)	4	23.0% (2.87)	9
Percentage of birch dead	10.0%	1	37.7% (5.57)	9
Percentage ground lichens shattered	11.5% (0.76)	4	94.4% (2.98)	9

Table 3. Phenology dates (month/day) relative to summer energy budgets (1988-92). (Standard error of the mean in patenthesis).

Phenology parameter	1988	1989	1990	1991	1992*
First mosquito bite	6/27	6/24	7/4	7/9	nd
Peak mosquitoes	7/22-29	7/12	7/12-15	7/25-8/3	nd
Mosquitoes downwind sweep	20.9 (3.25)	5.2 (2.17)	4.6 (1.26)	4.7 (1.59)	nd
First warble fly	7/25	7/11	7/7	7/22	nd
Insect relief acts/minute	1.2 (0.18)	0.5 (0.16)	0.6 (0.14)	0.2 (0.11)	nd
Days caribou observed	18	13	12	21	nd
Date birch full leaf	6/28	6/18	6/28	6/29	7/8
Per cent birch (July diet)	34 (4.4)	58 (7.0)	66 (7.6)	41 (6.8)	58 (6.4)
Feeding days observed	17	15	14	15	6

ing nearer the treeline but remained on the tundra. On average 32% ($s_{\bar{x}}$=6) (n=16, 1974 to 1990, 1983 missing) of the calving ground each year resulted from range extensions that were not within the perimeters of earlier calving distributions. These annual percentage additions were not correlated with the annual size of the calving ground each spring, r=-0.107 (Y=annual addition, X=annual size of ground, km^2 in 100, Y=31.176-0.0256X) nor with year, r=-0.294 (Y=annual addition, X=year, last two digits, Y=110.453-1.005X). The regression of the perpendicular distances of the annual centers of the calving grounds to the George River (approx. treeline) on year (last two digits) was significant, Y=426.714-4.420X, r=-0.849, n=21, 1973 to 1993).

In the years when pregnancy rates were reduced (1984 to 1993) this range rotation nearer treeline was not followed by increased risk since calf mortality to autumn was not significant (Y=33.089+0.081, r=0.251, n=10 fall recruitment, Y=calves/100 females) regressed on distance from the George River (X=km). Also these shifts closer to treeline with greater forage may have stabilized physical condition since there was no detectable decline in pregnancy rates 1984 to 1993, r=-0.067, (Y=pregnancy/parous) on X (year last two digits, Y=84.720-0.172X, C.V. of annual tallies of pregnancies 12%).

The other large herd in Ungava, the Leaf River Herd, also calved near treeline when first discovered in 1975, both males and females were present and the overall density was less than 1/km^2 (Le Henaff, 1975). In the 1980s as this herd increased it contracted the size of the calving ground by increased aggregating and shifted north. By 1999, it was calving 425 km farther north than 1975 (Couturier, pers. comm.). As it increased it shifted from an area where the growing season commenced June 15 to that of June 30 and like the George River the males, optimally foraging, had been left further south. This shift north may be a movement to reduce risk since if the animals were seeking a greater green phytomass they should have moved closer to tree line as the George River females did.

2. Mosquito season (July)

The mosquito season for the George River Herd commenced at the end of June or early July (Table 3). However peak harassment of caribou generally occurred in the last half of July when the major species (*Aedes punctor*) hatched. Lewis & Weber (1984) indicated the peak abundance of *Aedes punctor* should occur in the last week of July and this was the case in 1988 and 1991 (Table 3). Mosquitoes were more abundant in 1988 than 1989-91 and caribou were bothered more in 1988 than in the three other seasons (Table 3).

Toupin et al. (1996) felt that insect harassment of George River animals was not serious and contributed little to the negative energy balance of females during the first month of lactation. Their studies were in 1992 and 1993; 1992 was the coldest spring since weather records have been kept at Schefferville. We feel mosquitoes have a major impact on July energy budgets (Table 4). The energy budgets of females in 1988 did not turn positive until the mosquitoes abated in the first week of August even though caribou walk more but lie less in daylight hours with oestrid harassment than mosquitoes (Fig. 3 and Camps & Linders, 1989). During the insect seasons 1988 to 1991 the combined activity budget of caribou was 12% lying, 19% standing, 37% walking, and 41% feeding between and 0600 and 2200 hours, 1988-91, n=49 410 caribou. In the absence of insects during the growing season their budget was 18% lying, 2% standing, 20% walking, and 60% feeding (n=43 515 animals). When insects

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* nd=no data.

were absent they fed more, walked less and reduced their travel speed (Fig. 3). Travel rates were greater in July and August than in any other month except November and in some years April (Fig. 4). The Porcupine Herd also has had its greatest travel rates in during the insect season when bothered by mosquitoes (Whitten & Fancy, 1990).

The males joined the females in forming large post calving aggregations in July when the mosquitoes became abundant. This same sequence occurs in all the other large arctic herds in North America (Kelsall, 1968; Skoog, 1968; Curatolo, 1975; Roby, 1978) and is the basis of the post-calving census technique developed in Alaska. The George River bulls by leaving the treeline and moving to the tundra in July left an area with better birch (Betula glandulosa) than that present on the tundra. The percentage of the birch dead on their vacated range was 26% ($s_{\bar{x}}=5$) (5 stations) vs. 38% ($s_{\bar{x}}=6$) dead on the female tundra range (8 stations). Birch was the dominant forage in July (Table 3). This male movement to the tundra was to gain insect relief; they had been in an area of greater predation risk along the treeline and also of greater forage, yet moved to the overgrazed and trampled range of the females.

Commonly the females in the latter half of June, after calving, moved north staying on the low risk tundra but following a green-up, moving from the calving ground where the growing season commenced about June 20 to more northern locations where the season commenced 10 days later. When the mosquitoes became bothersome at these higher elevations the animals generally returned south paralleling the north-south treeline travelling over the range they had previously foraged. They appeared channeled to open wind-swept relief habitat. But as soon as the mosquitoes abated in the last days of July or early August they turned immediately, moving

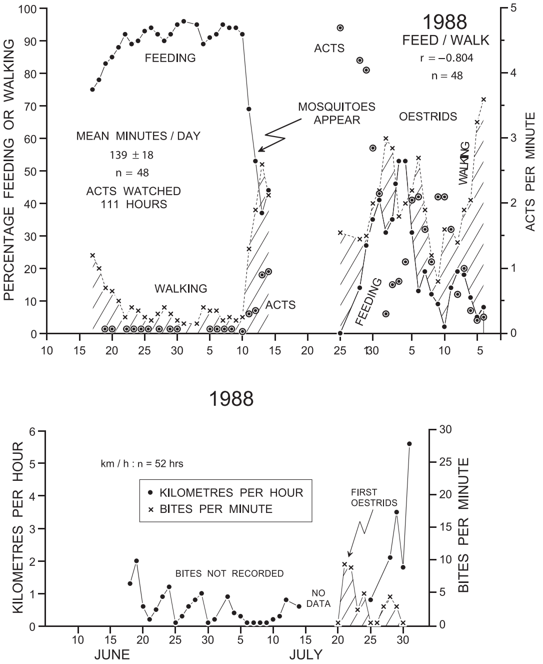

Fig. 3. Feeding and walking schedules and mobility compared with the biting of mosquitoes and the presence of oestrids in 1988.

Note: The majority of the camps were in the vicinity of the George River. Horizon scans generally at 8, 12, 16, and 20 hours as well as the bites received per minute on an exposed arm without repellant. Feeding and walking percentages based only on active caribou (not lying). Mobility rates based on observing caribou in small groups generally less than 5 animals for at least 5 minutes, noting their positions and then pacing the distance covered. Insect act per minute based on observing a single animal for one minute and counting head shakes, leg stamps, bites to the body, and tail/ear flicks. Similar data was gathered in 1989, 1990, and 1991.

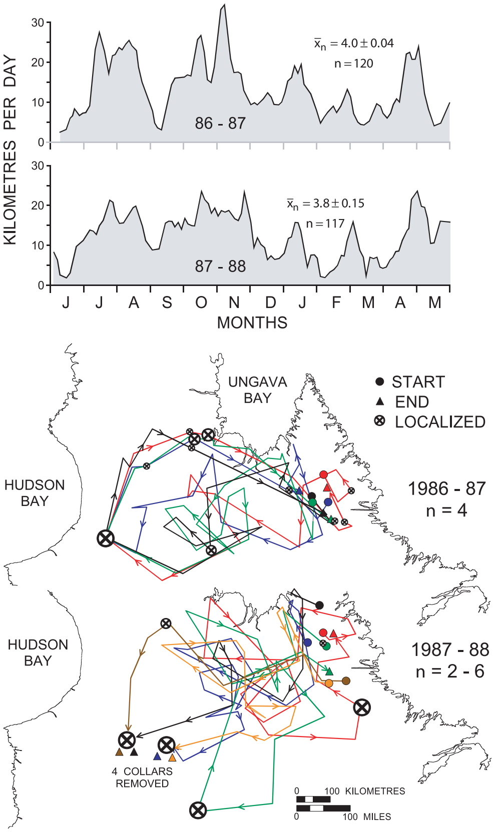

Fig. 4. a) Annual mobility cycle in 1986-87, and 1987-88 based on the biological year June 1 to May 31. (Below) b) Routes taken in 1986-87 and 1987-88 by the satellite collared females showing the localized ranges.

west towards the treeline where forage was more abundant and less trampled even though oestrids had taken up the chase. The mean date of crossing the George River going west was closely synchronized with end of major mosquito harassment, July 30 (Julian 211.4 ($s_{\bar{x}}$=4.04), n=7 years, 31 UHF radioed females involved). In July mosquito relief took precedence over optimal foraging even resulting in negative energy balances and applied to both sexes. The wind swept tundra provided mosquito relief and open habitat where the animals could aggregate to further mitigate mosquitoes. A bonus of remaining on the tundra was that risk was also lower, the trade-off was the insufficiency of forage. But reduced mosquito harassment was the primary incentive for choosing the wind-swept tundra, in insect season. The calving ground got a double whammy, first at calving and then a return visit to mitigate insects in July. The tundra area available to the George River Herd (47 000 km^2) is smaller than that of any of the other large herds in Canada (Bergerud, 1996): an unfortunate location for the largest caribou eruption in modern times to have occurred.

Table 4. Energy expenditures and intake compared between days insects were active and not active, George River 1988-90.

Dates observed (month/day/year) and insects	Energy budget (kJ in 1000s)		
	Expenditures	Intake	Difference
Mosquitoes present and active			
7/12/1988	18	3	-15
7/13/1988	16	1	-15
7/14/1988	20	5	-15
7/28/1988	23	11	-12
7/13/1990	24	11	-13
Means	20.2	6.2	-14
Mosquitoes present but not active			
7/29/1988	32	34	+2
7/30/1988	42	51	+9
7/31/1988	43	53	+10
Means	39.0	46.0	+7
Warble flies and tabanids active			
8/1/1988	12	2	-10
8/4/1898	12	2	-10
8/8/1988	25	13	-12
7/11/1989	20	5	-15
7/13/1989	29	21	-8
Means	19.6	8.6	-11.0
Warble flies & tabanids present but not active			
8/3/1988	42	50	+8
8/7/1988	41	52	+11
8/24/1988	39	56	+17
Means	40.7	52.7	+12.0

[1] Methods in Camps & Linders, 1989.

3. Late Summer and Fall (August through November)

The dispersal of the late July aggregations coincided with the end of mosquito abundance. In the words of Kelsall (1968) the animals were "released" when heavy mosquito harassment ceased. This August dispersal did not occur as proposed by Curatolo (1975) and Roby (1978) as a response to oestrid harassment (but see Dau, 1986). Our best disproof of the oestrid hypothesis occurred on July 27, 1990 when biologist Lo Camps visited an aggregation of >100 000 animals south of Indian House Lake. These animals

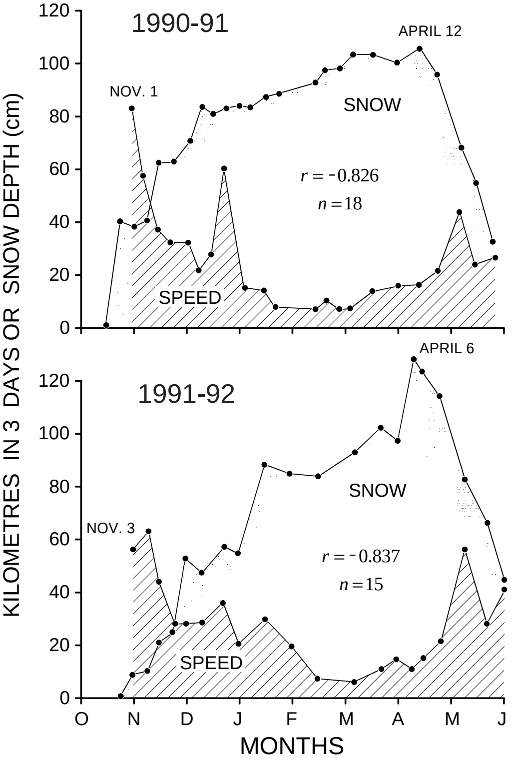

Fig. 5. Mobility rates and snow depths.

Note: Mobility rates declined as snow depths increased between the start of snow cover and the date of maximum depths 1990-91 and 1991-92. This data gathered in 6 years (see Table 7).

were severely bothered by mosquitoes, blackflies, oestrids, and tabanids. The animals remained massed milling about. The following four days were stormy and cold and the herd disbanded in the absence of all insect harassment and the mosquito season never resumed but oestrids reappeared after the stormy weather. In other years in late July a common observation was to see large herds disband when mosquitoes and oestrids abated due to inclement weather but again mass when both insects resumed their harassment. In each year, 1988 to 1992, we were unable to find large aggregations after the mosquitoes abated regardless of oestrid abundance. Also, Toupin et al. (1996) observed animals still aggregated between 19-30 July 1993 when oestrids were present. The rather abrupt abandonment of the late July aggregations coincided with the cessation of mosquito abundance and not with the arrival of oestrids, although the end of the mosquito season and the commencement of the oestrid season can occur within days of each other. One cannot use the term "insect harassment" without referring to a certain insect group. Oestrids and tabanids fly only in warm and mostly in sunny weather, whereas mosquitoes do not seem to like strong sunshine (Anderson & Nilssen, 1998; Anderson et al., 2001). Clearly, regional differences in insect abundance explain why study results differ. In Norway, mosquitoes had little influence on reindeer activity patterns, contrary to oestrids. Moreover, in the absence of oestrid flies, weather parameters had no influence on reindeer activity pattern. (Hagemoen & Reimers, 2002; Colman et al., 2003).

Without mosquito harassment the scattering bands left the overgrazed June/July tundra and moved toward more abundant phytomass west in the taiga. Their return to treeline increased their predation risk; 28 of 105 VHF collared females died primarily from predation adjacent to the treeline in this study. Risk increased but was not extreme since open water was still available for escape and snow cover to impede escape flights did not accumulate until mid November (Fig. 5). Their direction in August led them back to

Table 5. Activity budgets and frequency of insect related activity during attack of different numbers of oestrids ($s_{\bar{x}}$=standard error of the mean).

	Number of Oestrids per Caribou			
	1	2	3	≥4
PER CENT ACTIVITY				
Feeding	23.1	0.2	1.8	0
Walking	9.6	18.6	5.0	1.4
Standing	66.0	75.4	93.2	98.6
Running	1.3	5.9	0	0
FREQUENCY OF ACTIVITY	(min^{-1})			
Head shake	3.0	3.0	2.1	10.1
Body shake	1.8	2.6	1.1	6.9
Leg stamp	1.2	1.4	1.0	4.8
Bite body	0.3	0.6	0.4	0.9
(min:sec)	81:00	63:27	55:48	8:32
Mean Group Size ($s_{\bar{x}}$)	3.05 (0.77)	1.82 (0.56)	1.0	1.0
(n)	(20)	(17)	(6)	(6)

habitats where the larvae of oestrids had pupated that had emerged from male caribou in June. They also moved closer to the vast muskeg areas northeast of Schefferville (see Hare, 1959: Map 1) where tabanids (*Chrysops* spp. and *Hybomitra* spp..) pupate (McElligott & Lewis, 1996). These deer and horse flies are much more abundant in Ungava than on the ranges of more northern migratory herds in NWT. These tormentors caused severe landing and biting harassment when the animals were in the taiga on sunny warm days and trees blocked wind flow. The animals had not returned to the taiga to mitigate fly attacks but to forage now that mosquito attacks had ceased.

Fly attacks may hasten the August dispersal. Caribou often ran splitting from groups and acting more independently but animals in small groups were more bothered by oestrids than were the members of larger groups (Table 5). The explanation of Heard et al. (1996:42) for this August dispersal is the correct one: "When insect numbers decline [meaning mosquitoes] in August the large aggregations break-up and caribou amass large amounts of fat even though plants are senescing...we suggest caribou attempt to reduce competition for food by spacing out as widely as possible."

The most abrupt and consistent pause in the annual movement cycle occurred in the first week of September every year 1986 to 1992 on a mean date of September 5.2 ($s_{\bar{x}}$=1.78) resulting in a minimum mean speed of 5.4 km/day, $s_{\bar{x}}$=1.63 (Fig. 4) (see also Bergman et al., 2000). This pause happened exactly as the oestrids ceased. The last oestrid we saw in 1988 was on August 30. This pause was to accelerate forage intake. Interestingly this major feeding break did not occur for the Porcupine Herd in 3 years that Whitten & Fancy (1990) followed satellite caribou. In those years the June/July range of the Porcupine Herd was not heavily overgrazed (Russell et al., 1993). This pause then for George River females was a compensatory feeding period, again illustrating the adaptability of this species when faced with a food shortage.

Heard et al. (1996) had it right again when they said this fall feeding period could explain the density-dependent range expansions and contractions observed in migratory caribou populations. Each year as the George River Herd increased 1973 to 1984 the distance between the calving ground and the rutting range increased ($r=0.931$, $Y=-2241.11+32.063X$, Y=km between calving and rutting ranges, X=last two digits of year, n=12). After 1984 the distances commenced to retract. The size of the calving grounds also increased 1974-87 with numbers ($r^2=0.723$, n=13) but continued to increase with overgrazing after 1987 when numbers began to decline. It was the size of the fall range that expanded in a density-dependent manner 1978-79 to 1986-87, >300 000 animals to 644 000 animals, [expansion equation ($Y=14\,518.490/(773.612-X)$, Y and X in 1000s, $r^2=0.719$), the area of fall range was only available for 13 years]. The density-dependence was still apparent when the herd declined 1987-88 to 1991-92 ($Y=6.343e^{0.0044X}$, $r^2=0.752$, n=6).

The movements in this period in late October and November are classically called the fall migration. We believe this is a misnomer; the animals are not trying to reach a goal. They are trying to forage rapidly before snow level hinders forage intake and predation risk increases. The coldest temperatures in the subarctic are in the higher latitudes where leaf fall occurs earliest and snow becomes persistent first. Thus caribou in the NWT commonly cross the tree line in late summer moving south but in Ungava where the tree line runs north and south the George animals go west. Hence movements in this season are the reverse of following the advance of green forage north as temperatures moderate in the spring.

The mean monthly travel rates of the satellite females in October and November in 7 years were positively correlate with our population estimates for those years, but the travel rates were not correlated with herd numbers for August and September:

August: 18.7 km/day, $s_{\bar{x}}$=1.17, not correlated with numbers r=0.312, n=7

September: 14.7 km/day, $s_{\bar{x}}$=1.17, r=0.018, n=7

October: 17.5 km/day, $s_{\bar{x}}$=1.50, correlation coefficient, r=0.614 n=7

November: 16.6 km/day, $s_{\bar{x}}$=1.15, r=0.738, n=7

The November correlation is nearly significant ($r_{[P=0.05]}=0.754$). The lack of correlation in August might relate to differences between years in oestrid numbers. In September the lack of correlation between numbers and travel rates would be nullified by the September pause and in October another delay for breeding. However the correlations in mobility and travel rates in October and November suggest foraging interactions between animals and strengthen the view of the priority of maximum foraging in this interval.

Further evidence that the fall period was directed at foraging rather than reducing risk was the many turns the animals made (Vandal et al., 1989; Bergman et al., 2000). The frequency of turning peaked when the first frosts resulted in reduced greens in September and again in late October when lake ice formed (Table 6). Such major changes in direction in September might be to reach lower elevations and remaining greens. The increased frequency of changing travel directions in October

Table 6. The frequency of major turns made by satellite females >15° on moving azimuths.

Dates by weeks	Number of turns	Remarks
September 1-7	0	
September 8-14	7	Searching for
September 15-21	6	remaining
September 22-30	24	greens
October 1-7	7	
October 8-14	2	
October 15-21	4	Lakes freeze &
October 22-31	11	more searching
November 1-7	11	for forage
November 8-14	1	
November 15-21	7	More snow,
November 22-30	12	searching for low risk
December 1-7	3	areas of reduced snow
December 8-14	3	and localizing
December 15-21	2	
December 22-31	4	

when lakes formed a highway could have provided the opportunity to move in new directions seeking out forage still not covered by snow; the animals could take advantage of traveling on the ice surfaces where predators could be better detected and the reduced snow cover favored rapid escaped flights.

4. Winter pause (December to mid-March)

This period began with the localization of caribou on restricted winter ranges as snow cover increased. We define a localized winter range as a restricted area where travel rates were less than 10 km per day and the satellite animals made many acute angle turns within a restricted region (Fig. 4). Animals generally localized and reduced travel rates in late November or early December when snow cover reached >50 cm (Fig. 4 and 5, Table 7).

The herd was more widely scattered in winters when snow cover was low. The extent of the annual winter ranges (km^2) was negatively correlated with winter snow depths in 11 winters (r=-0.736). In shallow snow winters animals were further south where snow depths are usually deeper; in heavy snow winters they ranged further north often moving into the tundra beyond the treeline that generally parallels the Leaf River. The percentage of the annual winter distributions that was north of treeline varied from 75% in 1983-84, a hard winter, to less than 5% in 1992-93, a mild snow winter, and was positively correlated with snow depths in 12 winters (r=0.661).

The propensity of caribou to occupy areas of low snow profiles has been recognized since the earliest winter studies (Banfield, 1954; Skoog, 1956; Bergerud, 1963) and has recently been well documented for the Porcupine Herd (Russell et al., 1993). It has been assumed that this selection was for energetic considerations since digging craters to uncover forage has a significant cost (Thing, 1977; Russell et al., 1993).

We compared the distribution of caribou in 18 winters by tabulating their presence in 60x30 degree long. by lat. map-grids with: (1) estimates in the same grids of the general height of snow (based on the branchless part of spruce stems (see Hustich, 1951:Fig. 9) or the height of bushes and Krumholz) and (2) with the percentage of terrestrial lichen cover in the range station grids. The presence of caribou was not correlated with the abundance of lichen cover (r=-0.135, n=50) but with snow depths (r= -0.637, n=52 grid stations). Caribou selected regions of low snow rather than lichen biomass per se.

Two recent studies in Alaska have shown that wolves are more successful killing caribou in deep snows, even resulting in surplus killing (Dale et al., 1995; Mech et al., 1998). The winter mortality rate of VHF radioed females for the George River confirmed this predator advantage. The mortality rate of females in 8 winters increased with deep snows (r=0.824); these females did not have depleted fat reserves (Bergerud, 1996: Fig. 4). Additionally the annual mortality rates of females in the Delta and 40-Mile herds in Alaska were correlated with winter severity (Delta Herd r=0.634, n=17 years, 40-Mile r=0.792, n=8 seasons) (Boertje et al., 1995; 1996, Valkenburg et al., 1996; Valkenburg, 1997). These animals were also not predisposed to predation by reduced condition.

Caribou are the most cursorial of the surviving deer species (Geist, 1998). Their rapid escape rate is maximized with minimum leg and hoof lift on wind-swept frozen lake surfaces. Even a few centimeters of snow increase the cost of locomotion and reduce their high speed advantage over wolves.

Caribou should choose tundra landscapes in deep snow winters if they wish to reduce predation risk, but at a trade-off in reduced forage. Lichens are the primary winter food of the large migratory herds on the mainland of North America. These lichens are less common north of trees than in the taiga (Kelsall, 1968; Skoog, 1968; Bergerud, 1971; Russell et al., 1993, Thomas et al., 1996) and are especially limited on the high elevation tundra of Labrador (Bergerud, 1988b). Caribou may have forfeited weight and condition to occupy these wind-swept safer environments with less phytomass in both

Table 7. Role of snow cover on mobility rates and winter localizations.

Winter season	Correlation km/3 days vs. snow depth (n)	Winter localization dates	Kilometers/day before; after	Snow depth (cm) localized	Maximum snow date (cm)
1986-87	-0.730 (20)	Nov. 23 to 26	11.9; 9.3	49	March 23 (93)
1987-88	-0.521 (20)	Nov. 27 to 30	27.4; 6.17	56	March 22 (115)
1988-89	-0.432 (22)	Dec. 1 to 5	11.3; 6.18	45	April 9 (99)
1989-90	-0.752 (23)	Dec. 16 to 20	12.2; 7.8	89	April 23 (113)
1990-91	-0.826 (18)	Dec. 5 to 8	13.9; 8.5	84	April 12 (107)
1991-92	-0.837 (15)	Nov. 26 to 29	15.4; 8.8	53	April 6 (129)

Ungava and Northwest Territories (Tables 8, 9, and 10).

5. Spring migration (mid-March and April)

Guess the name of the species: "A herd of —roams over desolate snow-covered plains. With the onset of spring, most —migrate north. Males disperse to forage on herbs and grasses during a scant three-month growing season, while females trek to calving grounds. After giving birth, the females return south with their young, but nearly half the newborns perish on the way," (National Geographic inside front cover, Vol. 198, No 3). It is the chiru, *Pantholops hodgsoni* or Tibetan antelope that like the caribou and the Asian saiga (Saiga tatarica) (Bannikov et al., 1967) make long spring migrations of females to calving grounds with harsher environments to reduce predation risk.

Satellite females of the George River Herd left their localized winter habitat to return to the calving grounds (1987-1992) as early as February 26 and as tardy as May 6 (mean April 8, Julian date 98.4, $s_{\bar{x}}$=0.53, n=18). A number of these females were migrating prior to the accumulation of maximum snow depths. The releasing mechanism appeared to be knowledge of how far the females had to go to return to the Labrador tundra. The correlation between the initiation date and the distance to the George River was highly significant (r=-0.742, n=18, Y=1024.884-5.784X; Y=Julian date, X=straight line distance km to the George River). None of the females followed the shortest route to the Labrador tundra. The difference between the shortest route and the trail taken, averaged 55 km, $s_{\bar{x}}$=11. If the females were west of 73°W and north of 53°N, they followed the tree line northeast adjacent or between the Koksoak and Leaf Rivers, turning southwest as they passed Kuujjuaq. The snow on the ground in the central interior (Schefferville) that they avoided, averaged 85 cm at the end of March 1951-90 but was 19 cm shallower on the route they took by Kuujjuaq, 66 cm (1951-90) (Jacobs et al., 1996). The average depth of snow along the treeline, based on our measurements of the height of the branchless gap on spruce, gave a depth of 45.7 cm, $s_{\bar{x}}$=0.61 (n=10 stations) whereas a direct path east at 57°N gave a depth of 62.5 cm, $s_{\bar{x}}$=0.62 (n=10). Their indirect route had less snow cover.

Physiography may also influence the route chosen to return east. The Laurentide ice sheet finally melted at about 5500 BP in central Ungava--the last remnant was located northeast of present day Schefferville. The topography left in this core area in the central interior was linear ridges running north and south, bold hills and north-south oriented lakes; all at right angles to the shortest return route. In contrast the travel route the females commonly followed northeast between the Leaf and Koksoak rivers is a rocky plain with northeast-southwest parallel eskers (Hare, 1959). We do not argue for topographical funneling, a hypothesis of earlier decades (Bergerud, 1974a). Still the more uniform and reduced snow cover and improved visibility of travelling along the tree line may have facilitated less risk; the ecotone of tundra and taiga would provide a mix of lichens and alpine evergreen shrubs available under reduced snow cover.

Pregnant caribou that began the return to their calving ground at the end of March could be nutritionally stressed as were the females of the Kaminuriak Herd, NWT. in the 1960s (Dauphiné, 1976). However Huot & Goudreault (1985) showed that with high numbers and an overgrazed summer range George River animals were in better condition in April than September. But these long return migrations had an energy cost. The mean distance that the 18 satellite cows migrated 1987 to 1992 to reach the George River was >512 km (extremes from 245 to 1125 km). When cows had migrated a similar distance in 1982 (475 km) their mean Kidney Fat Index based on Huot & Goudreault's (1985) formula (FATP=-3.29+3.73lnKFIR) had declined from

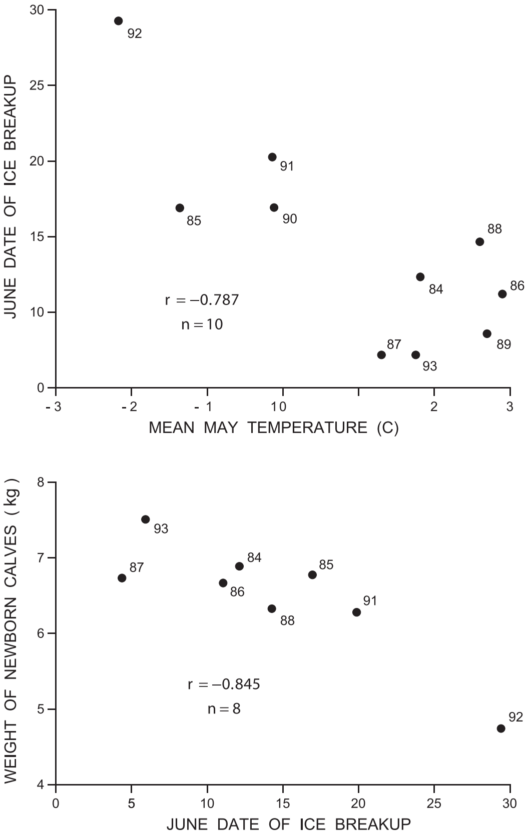

Fig. 6. a) The date of ice clearing Knob Lake, Schefferville was correlated with May temperatures. b) The weight of newborn calves was correlated with the date of ice break-up and spring phenology.

Note: The weight of calves listed only for the years after pregnancy rates declined (after 1982); weights in kg were also taken in 1978: 7.5, $s_{\bar{x}}$=0.35, (n=12), 1979: 7.4, $s_{\bar{x}}$=0.61, (n=3), 1980: 7.3, $s_{\bar{x}}$=0.25, (n=2), and 1981: 6.4, $s_{\bar{x}}$=0.29, (n=15). The correlation of the weights in these 4 latter years with ice break-up was r=-0.462. Newborn weights in 1991 and 1992 provided by S. Couturier, pers. comm.

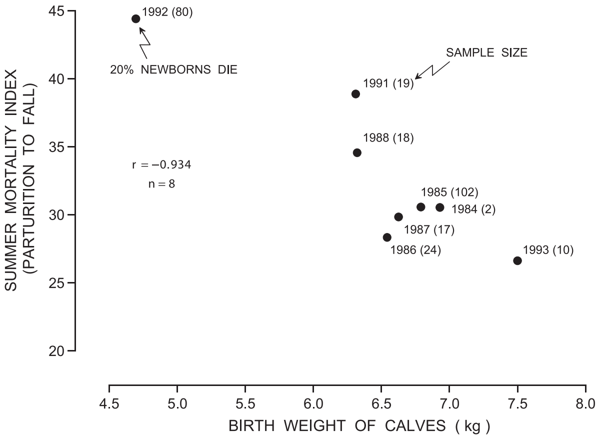

Fig. 7. Summer mortality and birth weight of calves.

Note: Summer mortality index (calves/100 females at birth minus calves/100 females in October) declined as calf birth weights increased for those years (after 1982) after the physical condition of females had declined (Fig. 6). Calves at birth based on mean 69.3% $s_{\bar{x}}$=2.27, per 100 females, (1984 to 1993); the regression of parous percentages 1984 to 1993, Y=84.712-0.172X, r=-0.067 (X last two year digits, 13 observations, 422 autopsies, 24 611 parous counts). Data from literature included. Newborn weights in 1991 and 1992 provided by S. Couturier, pers. comm. Data for 1991 are from Leaf River herd.

65.2 g, $s_{\bar{x}}$=13.27, (n=9) in March 1-10, to 35.7 g, $s_{\bar{x}}$=1.44, (n=36) by April 15-29, when the herd was again sampled. Backfat reserves from these same females had declined from 21.4 mm, $s_{\bar{x}}$=4.40, in March to 4.3 mm, $s_{\bar{x}}$=1.89, April 15-29. The regression of maximum back fat of pregnant females on spring migration distances for George River females during this study was $Y=-5.604X^{0.268}+32$, $r^2=0.982$, n=19 collection periods (data from 15 years between 1976 and 1993, total animals 1293, some data from the literature included). Animals that had a return distance >600 km could arrive on the calving ground with less than 1 mm of backfat.

The rate of travel of the herd in April in 7 years of following the satellite females (1987-1993) was positively correlated with our population estimates generated from mortality/recruitment schedules, r=0.794 ($P_{0.05,\,5df}$=0.754) (Table 11). Our 1988 range survey indicated that the migration routes were heavily grazed and the density dependence likely resulted from interactions between animals searching for reduced supplies rather than from social facilitation; the migrating columns are not readily distinguished by group sizes (Duquette & Klein, 1987). These authors showed that animals migrating long distances fed more and reclined less than herds with shorter migrations. It appears that routes followed provided a reasonable compromise between risk and optimal foraging and that both were involved in the choices made.

6. May

In April in the 1980s the George River females commonly returned to the Labrador tundra passing

Table 8. Weight (mean and standard error of the mean in parenthesis) of females in March or April compared to their location relative to tree line[1].

Year	Kilometers from tree line	Mean weight in kg	n
1976	160 km below tree line	101.0 (1.70)	21
1982	At tree line	95.9 (1.46)	36
1983	48 km below tree line	89.2 (0.73)	5
1984	132 km above tree line	84.1 (1.72)	11
1986	At tree line	87.0 (2.40)	12
1987	At tree line	96.3 (3.80)	11
1988	160 km below tree line	102.3 (3.29)	16
1993	152 km below tree line	97.6 (2.25)	20

[1] $Y=101.240-0.137X$, $r=-0.837$ (X coded: 175 km below=0, tree line=70, 150 km above=130).

southeast from the Ungava Coast (Parker, 1981). A common sequence was that the animals traveled through where they would later calve and moved further south pausing near treeline. Here they fed on early greening graminoids little affected by overgrazing. This sequence increased the risk of predation but allowed maximum energy intake in the last trimester of pregnancy.

Calf survival at parturition has been shown to be correlated with birth weight (Whitten et al., 1992; Adams et al., 1995) and Skogland (1984) proposed that forage at this stage of the fetus growth was critical. In 1992, the year of the latest phenology in Ungava since weather records have been kept at Schefferville (early 1950s), the calves born were extremely small (Couturier, unpubl. data; Fig. 6). We recorded a neonate mortality rate, from cows with a large udder not followed by a calf, of 20% (n=308) compared to the rate of 6.6%, $s_x=1.24$, in 8 other springs. Calf weights at birth were correlated with spring phenology based on May temperatures and ice break-up (Fig. 6) and also correlated with summer mortality (Fig. 7). Females improved their reproductive fitness by maximizing the weight of their calves at birth by optimally foraging in May.

A similar optimal foraging strategy may occur for the Porcupine Herd in Alaska. Calf survival in June in 10 years (1986-1995) was correlated with the abundance of green phytomass at calving as measured by the Normalized Difference Vegetation Index (NDVI) (Griffith et al., 1998). Hence early survival would also be correlated with the abundance of green phytomass in the latter stages of gestation. Cows in the Porcupine Herd, similar to the George River, calve in a low risk habitat on the coastal plain adjacent to the Brooks Mountains where predators are rare compared to the adjacent Brooks Mountains (Garner & Reynolds, 1986; see Bergerud, 1996: Fig. 1). But prior to parturition these Porcupine females are further south (Russell et al., 1992) foraging in an earlier NDVI and where the bulls forage optimally after the females move north to the less risky coastal plain for calving (Russell et al., 1993).

We regressed the parturition weights of cows from 24 herds in the world against calf birth weight (Y=

Table 9. Comparison of the body condition of caribou in the Beverly Herd, Northwest Territories in March 1984, above treeline (Sifton) and below treeline (Porter) taken from Thomas & Kiliaan (1998). Mean value, standard error of the mean ($s_{\bar{x}}$) in parenthesis.

Condition measurements sex and age	Porter 70 km below		Sifton 130 km above		Difference Porter-Sufton
Kidney fat in g ($s_{\bar{x}}$)					
Females >3 years	126.5 (4.6)	(n=63)	98.6 (9.5)	(n=14)	+27.9
Males >3 years	116.8 (10.2)	(n=10)	65.3 (4.4)	(n=6)	+51.5
Percent marrow femur ($s_{\bar{x}}$)					
Females >4 years	87.3 (0.5)	(n=52)	80.5 (3.5)	(n=6)	+6.8
Males 2-4 years	87.0 (0.8)	(n=13)	77.7 (3.1)	(n=9)	+9.3
Total body fat in kg ($s_{\bar{x}}$)					
Females >4 years	12.5 (0.2)	(n=60)	11.0 (0.6)	(n=9)	+1.5
Males >2 years	11.0 (0.2)	(n=17)	10.0 (0.3)	(n=11)	+1.0
Body weight in kg ($s_{\bar{x}}$)					
Females >4 years	87.8 (0.9)	(n=60)	77.8 (2.0)	(n=9)	+10.2
Males >5 years	117.8 (5.0)	(n=4)	92.7 (3.0)	(n=3)	+25.2
Back fat in mm ($s_{\bar{x}}$)					
Females >4 years	21.0 (1.1)	(n=60)	6.9 (2.9)	(n=9)	+14.1
Males 3-5 years	4.6 (2.0)	(n=14)	1.1 (0.4)	(n=9)	+ 3.5

[1] Animals in better condition when below tree line 1981, 1982, 1985, and 1986 except 1980 than above tree line 1983 and 1987 (Thomas & Kiliaan, 1998).

Table 10. Condition of female caribou collected in April 1980 between a sample mostly above treeline (Hebron) and tree line (Nain)[1]. Mean value, standard error of the mean in parenthesis.

	Hebron April 3-4			Nain April 5-15			Probability of No Difference
10 month-of-age							
Mean backfat (mm)	0		(n=3)	0.2	(0.15)	(n=13)	0.3370
Mean kidney fat (g)	20.1	(7.80)	(n=3)	22.1	(1.69)	(n=13)	0.8390
Mean femoral fat (%)	52.3	(9.61)	(n=3)	57.8	(3.84)	(n=13)	0.5845
Mean body weight (kg)	42.1	(1.40)	(n=3)	45.?	(1.04)	(n=13)	0.0944
Mean total warbles	119.7	(48.72)	(n=3)	59.0	(8.91)	(n=13)	0.3403
22 month-of-age							
Mean backfat (mm)	0		(n=4)	3.6	(1.18)	(n=14)	0.0100
Mean kidney fat (g)	22.9	(8.32)	(n=14)	40.8	(5.04)	(n=13)	0.1206
Mean femoral fat (%)	55.5	(17.89)	(n=4)	88.6	(0.86)	(n=16)	0.1612
Mean body weight (kg)	64.1	(3.54)	(n=4)	73.3	(1.88)	(n=15)	0.0711
Mean total warbles	146.0	(21.30)	(n=4)	53.7	(10.17)	(n=15)	0.0145
≥34 month-of-age							
Mean backfat (mm)	0		(n=10)	6.0	(0.72)	(n=87)	0.0001
Mean kidney fat (g)	39.6	(5.75)	(n=8)	84.8	(3.24)	(n=71)	0.0001
Mean femoral fat (%)	73.1	(6.13)	(n=10)	90.1	(0.42)	(n=88)	0.0214
Mean body weight (kg)	88.5	(2.33)	(n=10)	93.7	(0.82)	(n=91)	0.0602
Mean total warbles	50.3	(15.68)	(n=7)	39.1	(3.98)	(n=88)	0.5124
Fetus weight (kg)	2.1	(0.09)	(n=8)	2.5	(0.13)	(n=15)	0.0063

[1] Raw data sheets provided to A. T. Bergerud by G. Parker.

-0.104+13.543X, r=0.852). The weight of newborn calves for the George River herd was only 4.7 kg, s_x=0.13, (n=80) in the late 1992 year when calves died at birth and 3.2 kg greater the very next year, 7.5 kg, s_x=0.37, (n=10) in 1993 (Fig. 6). The predicted weights of their dams based on the calf/dam weight regression was 63.5 kg in 1992 and 101.5 in 1993. This weight disparity would have translated into major differences in milk supply. The neonate is the most vulnerable animal and requires the safest environment; the adult female is more able to cope with predators than her calf will be at birth and can afford the greater risk in May to produce a larger bodied calf in June.

By migrating early prior to green vegetation and then pausing to partake of the more nutritious forage relative near the lower risk birthing habitat she can contribute more resources to her fetus. One might predict the dates at which she abandons higher quality forage and moves to the calving area habitat, will be a product of the disparity in forage quality between the two locations assessed against the risk factor in both locations. In the mountains of British Columbia where predators were common and early calf mortality extreme, cows left forage of high quality in the lowlands to move to safer alpine birth sites with low phytomass only a few days before parturition (Bergerud et al., 1984). On the George River satellite females in 5 years moved to the vicinity of their calving sites more than two weeks prior to parturition (mean date May 21, s_x=1.93, n=15 females).

Predation risk in the Pleistocene

Did the ancestors of the George River Herd alter ranges in response to predation risk 18 000 yr. BP when caribou in eastern North America persisted only south of the Laurentide Ice sheet that extended south to 40°N? The megafauna at 18 000 BP existed in abundance with its huge mastodons, mammoths, stag-moose, woodland muskox and more, as well as an assortment of large predators including the sabertooth, dire wolf, timber wolf, great short-faced bear and other cat and bear species.

We compared the locations of dated caribou fossils (C14-normalized) (from the literature) with the forest habitat types existing in those times reconstructed by paleobotanists from pollen core samples. We examined the vegetative maps of Delcourt & Delcourt (1981) of 18 000, 14 000, 10 000 and 5000 yr BP to determine the major dominant arboreal vegetation existing during the span of fossils from the Pleistocene and Holocene. We also consulted the Pleistocene-Holocene vegetational analyses of Ritchie (1987), Davis & Jacobson (1985) and the Historical Atlas of Canada, Vol. I, Univ. of Toronto Press, Plates 3 and 4.

Most biologists probably assume, as we did, that caribou living 18 000 years ago and south of the Laurentide ice were inhabiting the tundra/taiga zone immediately adjacent to the ice sheet. Banfield (1961:34) said "we may conclude that at the height of the Wisconsin glaciation reindeer were distributed in a tundra belt across the south of the ice sheet." He also noted they might frequent taiga habitats in the winter. But the fossil locations are not consistent with this arctic tundra/taiga paradigm; there are no fossil liter-

Table 11. Mobility rates (standard error of the mean in parenthesis) of females in April to the Labrador tundra correlated with the population estimates based on mortality and recruitment calculations.

Year	Km/day[1] ($s_{\bar{x}}$)	Sample size	Herd size (in 1000s)[1,2]
1987	14.30 (2.16)	40	632
1988	11.53 (2.27)	30	644
1989	9.28 (1.63)	32	592
1990	6.33 (0.98)	18	575
1991	8.46 (1.10)	66	546
1992	5.80 (0.67)	84	492
1993	6.05 (0.88)	56	428

[1] Correlation coefficient, km/d vs. herd size, r=0.798, n=7.

[2] Herd size estimated from mortality recruitment schedules.

ature citations of Pleistocene animals dying in either the tundra or taiga zones for the interval 20 000 to 16 500 BP (Table 12). The 7 fossil caribou (5 locations) in this interval were all in the Appalachian Mountains: (1) New Trout Cave, Pendleton Co., West Virgina 29 500, 28 250, 17 600 yr. BP (Grady & Garton, 1982); (2) Beartown Cave, Sullivan Co, Tennessee, 20 000 BP. (Guilday et al., 1975); (3) Guy Wilson Cave, Sullivan Co., Tennessee, 19 700 BP. (Guilday et al., 1975); (4) Baker Bluff Cave, Sullivan Co, Tennessee 19 100 BP (Guilday et al., 1975); and (5) Yarborough Cave, Bartow Co., Georgia, 18 610 BP (Martin & Sneed, 1989).

For the period 16 500 to 12 500 BP caribou fossils were also predominately in the Appalachian Mountains (3 of 4 locations) (Table 12). Again there was a fossil bone (14 315) in Yarborough Cave , another in Saltville, Smyth Co., Virgina, 13 460 (Ray et al., 1967); a third in Darty Cave, Virgina, 14 650 (Faunmap, 1994), and the lowland exception was at Christensen Bog, Hancock Co., Indiana; the oldest fossil there 14 545 BP (Faunmap, 1994).

The Appalachian Mountains in those times was not an optimal foraging habitat. There was little altitudinal zonation in vegetation. The entire mountain chain was dominated by jack pine (Pinus banksiana) with spruce (Picea spp.) subdominant with a minor area of alpine tundra (Delcourt & Delcourt, 1981; Figs. 6 and 7). In this era more nutritious forage would have been available at lower elevations where there was a longer growing season. More mesic sites would also have been down below. Furthermore there was a large area of the forest type called the Mixed Conifer-Northern Hardwoods south of the Mountains, which would have been a richer habitat. This latter biotype was suitable habitat since caribou did move into these forests after 12 000 BP (Table 12). The floral mix in this association was analogous to the present day forest classification "The Lake State Forest." Caribou have been recently introduced to a Lake State Forest Association on Michipicoten Island, Lake Superior and are prospering in the absence of other ungulates and predators (Bergerud, A. T., unpubl. data).

Caribou began recolonizing habitats north of the Appalachian Mountains approximately 12 000 BP (Table 12). The distribution of animals 12 000 to 8500 BP did not suggest that they were selecting any major forest type (Table 12). Their range was shifting north as the ice retreated, but they could physically have made this move several millenniums earlier. This northward dispersal coincided with the disappearance of the Megafauna herbivores and predators. The last appearance dates of 45 megafauna species from fossil beds in North America based on ^{14}C dating showed a rapid extinction sequence between 12 000 and 10 000 BP (data from Kurten & Anderson, 1980: Table 19.6, pp. 364-365). Ten species had more than one last appearance date based on two or more fossil locations:

17 900 to 16 000 BP 2 disappearance dates
15 900 to 14 000 BP 1 date
13 900 to 12 000 BP 5 locations
11 900 to 10 000 BP 31 locations
9900 to 8000 BP 17 locations
7900 to 6000 BP 8 locations
5900 to 4000 BP 0 locations

We believe the caribou were in the mountains 20 000 to 13 000 BP spacing-out from most of the megafauna that were more common at lower elevations. Bergerud & Page (1987) refer to spacing-out as being dispersed from other caribou at calving and away from alternative prey species and their predators (Bergerud & Page, 1987). Dr. Dick Harington (Canadian Museum of Nature) indicated that the megafauna predators likely selected the young of the large herbivores in the Pleistocene (pers. comm.). Caribou were of the size to be selected. Montane caribou at present space-out from each other and alternative prey and their predators in the mountains of British Columbia (Bergerud et al., 1984; Bergerud & Page, 1987). The antler morphology of 8 of the 9 antlers of Pleistocene caribou described or depicted in the literature appear similar to present day montane antlers with the characteristics of some compression of the main beam (oval cross section), palmated high tops, and high bez tines (as described by Butler, 1986). These antlers conform to neither

Table 12. Locations of dated caribou fossils in the Pleistocene in Eastern North America compared between forest types existing at that time.

Time period and forest type	Size of area (km^2 in 1000s)[1]	Number of fossil locations Observed	(No. of ages)	Expected
20 500 to 16 500 BP				
Appalachian Mts.	150	5	(7)	0.43
Tundra	340	0	(0)	0.98
Open spruce (taiga)	105	0	(0)	0.30
Spruce and jack pine	530	0	(0)	1.52
Jack Pine and spruce	560	0	(0)	1.61
Mixed conifer and hardwood	55	0	(0)	0.16
Total	1740	5	(7)	5.00
16 500 to 12 500 BP				
Appalachian Mts.	150	3	(3)	0.31
Tundra	340	0	(0)	0.70
Open spruce (taiga)	565	2	(6)	1.17
Spruce and jack pine	900	0	(0)	1.87
Jack pine and spruce	345	0	(0)	0.72
Mixed conifer and hardwood	110	0	(0)	0.23
Total	2410	5	(9)	5.00
12 500 to 8 500 BP				
Appalachian Mts.	150	4	(6)	1.86
Tundra	110	1	(1)	1.36
Open spruce (taiga)	265	4	(5)	3.28
Spruce and jack pine	415	2	(4)	5.14
Jack pine and spruce	330	5	(16)	4.09
Mixed conifer and hardwood	425	5	(10)	5.27
Total	1695	21	(42)	21.00

[1] The distributions and areas of the forest types based on Delcourt & Delcourt (1981) Figs. 5, 6, and 7 and include the region from the Atlantic Coast west to 98 degrees west longitude, north to the Laurentide Ice Sheet and Gaspé and south to the southern boundary of the Mixed Conifer and Northern Hardwood type. The Appalachian Mountains encompasses the area classified as Oak-Chestnut at 5000 and 200 BP in Delcourt & Delcourt (1981), Figs. 8 and 9. The area of the Appalachians subtracted from the other forest types located there at 18 000, 14 000 and 10 000 yr. BP.

sedentary woodland or migratory barren-ground animals. There should have been only one common gene pool south of the ice in the Pleistocene. Which is consistent with genetic studies of present day caribou living in eastern North America by Røed et al. (1991) and subspecies classifications of Banfield (1961) made on the basis of extant skull measurements.

These southern mountains provided a stable and survivable environment during the period of maximum ice and even during the global warming trend of the Holocene. The fossils at Baker Bluff Cave spanned 19 000 years (19 100 to 555 BP, Faunmap, 1994); nearby Beartown Cave had a 20 000 year old fossil. There was still a ridge of spruce on these Blue Ridge sites at 200 BP (Delcourt & Delcourt 1981, Fig. 9). The Pleistocene animals put survival and risk first and optimal foraging second; a sequence we believe continues to the present.

Discussion

Females with neonates select low risk habitats. They did so for the George River Herd even when the calving range was sufficiently degraded that pregnancy percentages declined by 25 percent (cf. Parker, 1981 vs. Crête et al., 1996). For the past two decades, biologists in Alaska have tried unsuccessfully to prove that economic development of the Arctic coastal plain calving range would displace calving females. Caribou are not going to be displaced from economic developments simply because the constructs are there. The opposite is more likely. There are numerous examples in the literature that document how other ungulate species in the absence of hunting have sought benign human activity if their predators avoided these areas. Visit the "Down Town" elk (*Cervus elaphus canadensis*) of Jasper or Banff, Alberta. It is myth that caribou are wilderness species that cannot coexist with development in the North (Bergerud, 1974a).

We do not agree with Klein (1988:190) who argues that caribou researchers to be "ethical" should: "undertake an active role in preventing human-induced environmental degradation". To be professional we should remain removed from debates that assume that human activity is synonymous with degradation and remain committed to documenting without prejudice the life history traits of our beast, including their adaptability to their environment, regardless of the fall-out.

Our intent in this paper originally was to present some of the highlights of the research on the George River Herd 1974 to 1993. But on reading some of the conference proceedings on climatic change it was evident that caribou researchers were focusing on forage/energy considerations without discussing changes that warmer temperature might wrought on the interactions of wolves and caribou. We changed our emphasis to compare optimal foraging *vs.* predation risk observations 1974-93 and to provide control reference data on these contrary views. During our study there was no evidence of warming temperatures in Ungava. Our conclusions were that risk outweighed optimally foraging at calving and during the deep snow season (December through March). Forage considerations dominated from the end of the mosquito season (August 1) until snows generally exceeded 40 cm in early December and again foraging was foremost in May when early greens were available, prior to a last-minute shifts of cows to the low risk tundra range for parturition.

One major concern of arctic warming in the literature is that it will reduce the abundance of terrestrial lichens due to an increase in forest fires. Additionally with the predicted increase in snow depths it will require more energy for animals to dig feeding craters. Studies of lichen abundance have been legion during the past 40 years; some of us have spent endless field days looking in feeding craters and measuring lichen abundance (Bergerud, 1974c; 1971; 1988; Miller, 1976; 1980; Russell et al., 1993; Thomas et al., 1996). No demographic impacts have been documented in these investigations. Yet the attempts go on. (Arseneault et al., 1997) stated (page 66) "density-dependent limitation of winter forage... has not yet been described for large, lichen dominated, continental ranges of wild caribou." Their lichen studies for the George River encompassed Landsat imagery 1989 *vs.* 1992. For the George River Herd the range has historically been heavily burned repeatedly (Hare, 1959, Payette et al., 1989, Couturier & St-Martin, 1990). There was so much ablaze in July 1988 that we could not fly west of 72ºW for range studies.

The George River Herd has had the highest number of caribou of any of the major herds in North America and these animals have had to crater in the deepest snows of any migratory herd. Even with an overgrazed summer range, fat reserves of pregnant females in March 1982, 1986, and 1987 averaged 11.7 kg, s_x=0.63, of fat (1986 and 1987 from Couturier et al., 1989). These fat reserves are similar to that of females in the Beverly Herd and that projected for the Porcupine herd (Russell et al., 1993; Thomas & Kiliaan, 1998) and were greater than that for the Kaminuriak (Dauphiné, 1976). Thomas & Kiliaan (1998) showed that the condition of the Beverly herd in March of 8 years 1980 to 1987 was superior to the condition of caribou in the Kaminuriak Herd in early April in 3 years (1966-68). The superior condition of the Beverly Herd compared to the Kaminuriak occurred despite the finding that there were reduced lichen supplies on the Beverly Herd compared to the Kaminuriak in both the 1960s and 1980s as a result of forest fires, and despite the fact that densities were 3-4 times greater for the Beverly in the 1980s than the Kaminuriak in the 1960s (Parker, 1972; Miller, 1976ab; 1980; Thomas et al., 1996, Thomas & Kiliaan, 1998). We might rank these four major herds that have been investigated as to late winter body condition (Porcupine-1980s, George River-1980s, Kaminuriak-1960s, Beverly-1980s) as follows:

Snow Depths:
George>Kaminuriak>Beverly>Porcupine
Population densities:
George>Beverly>Porcupine>Kaminuriak
Lichen abundance:
George>or=Kaminuriak>Beverly>Porcupine
Body Condition:
Porcupine>or=Beverly>George>Kaminuriak.

There is no obvious relationship between snow cover, lichen abundance, animal densities or physical condition. The highest persistent density of caribou in North America (1974-1999) has been on the Slate Islands in Lake Superior (6 to 14/km^2) (Bergerud, 1996). These islands have a history of logging and forest fires; there are no terrestrial lichens and there are no arboreal lichens within reach of the animals except on blowdowns. Changes in lichen abundance or winter energetics should not be a first order priority when evaluating impacts of climate change.

The other area where caribou biologists have voiced concern that climatic change could impact caribou is alterations in their summer foraging regime and energy budgets. The most persuasive arguments are those of Russell (1993) who raised concern about possible foraging problems with climatic warming in the Arctic based on a 1986 conference where the following predictions were made: (1) a 2-4 week earlier period of snow melt, (2) a 2-4 ºC increase in summer temperatures. He reasoned that mosquito harassment might decrease foraging budgets and plant phenology and senescence could occur earlier in the growing season affecting the availability of nutritious forage when lactation demands were high.

Mosquitoes are a major problem for caribou, but the biology of these insects is so complex, it is difficult to predict how they will react to warming temperatures and water level change. Each mosquito species has evolved it own life history schedule. We have even been more bothered at times in the Arctic by mosquitoes than in doing waterfowl research in the Manitoba potholes. At Indian House Lake during our energy budget studies in the summer there were major differences in mosquito harassment between years (1988-92) in numbers and annual chronologies. Peak abundance occurred in 1988 at 10 to 11 ºC and in 1991 at 22 to 23 ºC. On June 23 1989 the temperature reached 33 ºC at Indian House Lake (44 ºC in the sun) and the entomologist operating from Schefferville (McElligott, E. K., pers. comm.) felt the larvae might die from physiological stress in the warm waters. We had far fewer mosquitoes in 1989 than 1988.

We view the early growing season predicted with climate warming as a plus for caribou. Cows will be in better condition at parturition and birth weights will increase. The body size of caribou is determined by the length of the growing season. The correlation of total body length (Y) with the length of the growing season (days) for 24 herds in North America for males: $Y=-82640/(X-518.84)$, $r^2=0.799$ and for females $Y=-72949.13/(X-506.16)$, $r^2=0.784$). We may have larger caribou. Klein (1970) has argued that that the flora of the arctic is of higher quality than that foraged by woodland caribou, but it is the days available to forage on growing vegetation that drive growth. In time, with climatic warming, calving dates may also advance which might advance lactation demands to keep abreast with the earlier phenology. The dates of calving also vary with the length of the growing season. The correlation between the Julian Date of peak calving (Y) in 23 herds in North America had a high coefficient of determination with length of growing season (X) $r^2=0.991$, $Y=129.680X/(-12.547+X)$. We believe caribou should benefit nutritionally with warming spring and summer temperatures.

Wolf predation is now accepted as the major limiting factor for moose and caribou in North America (see 24 references in Bergerud & Elliott, 1998). With global warming we can expect wolf numbers and their impacts to increase. We suggest four sequences of concern, and other workers would list other predation consequences. First, a warming Arctic could result in a decline in the tundra and with it the abundance of lemmings and arctic foxes (*Alopex lagopus*). Wolves inhabiting ranges overlapping arctic foxes are exposed to the Arctic fox rabies vector (MacInnes, 1987) and there have been serious outbreaks in Alaska (Weiler & Garner, 1987; Ballard & Krausman, 1997) and in Ungava (Bergerud, 1996). Rabies outbreaks in Labrador are documented back to the early 1800s (Elton, 1942). At that time it was called the arctic sled dog disease (MacInnes, 1987). The George River Herd exceeded the carrying capacity of its summer range about 1982 after the wolf population crashed; based on the mean pack size, the decline was 61% or on harvest statistics 81% (Bergerud, 1988). In the absence of this disease wolf populations in the Arctic would be limited by the prey biomass (Fuller, 1989) and might frequently exceed 7 wolves/1000 km^2 which could result in caribou declines (Bergerud & Elliott, 1986).

Second, with warmer winters we could expect greater snowfalls and depths. Caribou are more vulnerable to predation in deep snows, at times resulting in surplus killing (Mech et al., 1998). With excessive snow caribou might not reach the increased safety of their calving grounds. This happened in the case for the Nelchina Herd in 1964, 1965, and 1966 (Bergerud & Ballard, 1988) and recently for the Porcupine Herd resulting in major mortality. It is not that caribou can not cross 100% deep snow cover; in the mountains of British Columbia animals commonly move over extensive snow fields when brown substrates are available elsewhere; but in the Arctic extensive snow at lower latitudes may signal that calving grounds are still covered and lack brown substrates for concealment of newborns.

The caribou in the Northwest Territories and Ungava that winter in the relatively level physiography use frozen lake surfaces of the Canadian Shield to mitigate predation risk and enhance escape possibilities (Kelsall, 1968; Miller, 1976). They don't have the advantage of the reduced snow and open vistas in the mountains as does the Porcupine Herd or the advantage of being above an approaching predator. If climate change reduces the extent and duration of the frozen lake period this coupled with deeper snows in the forest would greatly enhance the effectiveness of wolf predation and caribou would be spending more time on the tundra in diminished physical condition.

Our fourth concern is the most serious. With increased warming and the advance of the tree line we can expect moose (*Alces alces*) to further extend their range north. Moose have been pushing north for decades increasing the prey base for predators and increasing the abundance of wolves. With the advance of the tree line this movement will be accelerated. This enhanced abundance of wolves, coupled with the loss of habitat that has reduced the spacing-out advantages of woodland caribou, has resulted in an alarming rate of extinction of local populations on the southern edge of their range (Bergerud, 2000). When caribou returned to Ungava during the Holocene they were not followed by moose--the moose were still dispersing south from Beringia (Kurten & Anderson, 1980). Now moose are at the door. It takes only 0.10 moose per km^2 to allow wolves to reach 7/1000 km^2, a number too high to maintain caribou numbers (Bergerud & Elliott, 1986).

Whereas there is little we can do to reverse the adverse affects of climate change on forage/energy considerations, we can manage wolf numbers if warming temperatures result in increased predation rates. The problem is that the timber wolf is the icon predator of North America. This species is the most revered mammal in the Southern continental United States of America, more books, more paintings, more calendars than any other mammal, the symbol of wilderness, the balance-of-nature monarch.

However recently there has been some movement in the sentiments of professional biologists towards predator management. Many ground nesting birds in the United States are losing the habitat to space-out to minimize nest predation (Bergerud, 1988c; 1990) and this has recently been recognized in a special section of the Wildlife Society Bulletin "Impact of Predation on Avian Recruitment" Vol. 29, No. 1. Also several biologists researching woodland caribou have recognized that their subspecies is losing their race with wolf predation as their habitat is alienated for spacing-out and moose populations spread north expanding wolf numbers (see Rangifer Special Issues 9 and 10). Additional insights involve the recent introductions of wolves to Yellowstone Park and the wilderness area of Idaho. Now biologists in the lower 48 have had more contact with wolves and have the opportunity to test their ideas and evaluate the data published by biologists that have worked with moose-caribou-wolf systems in Alaska and Canada. But it is one thing to undertake the reduction of opossums, raccoons for game birds and another to gain public support to manage wolf numbers. Anti-hunting, animal rights groups, and some environmental groups would rather the caribou go extinct than reduce wolf numbers or interfere with the "natural balance." They don't relate to the George River Herd lesson of the 1950s; if you lose your caribou you lose your predators.

In reality with the present negative public opinion on predator management there are only two places left in North America where wolves could be reduced if it is shown that caribou numbers are threatened, the Northwest Territories and the Ungava Peninsula. It is our dearest hope that the First Nation people of the north can maintain their option to practice wolf management if climate change results in excessive wolf predation. However some environmentalists will try and take this option away. Note the recent article in the Globe and Mail newspaper, berating wolf hunting in the Northwest Territories. The wildlife programs in the North need to be developed so that wolf management is not subject to economic blackmail. Who would have thought that the Newfoundlanders could have lost their seal hunt, or that the grizzly bear hunt might end in British Columbia after animal rights people in London, England, who knew nothing about bears, promised boycotts? The declines of caribou in North America have generally resulted from overhunting and wolf predation (Bergerud, 1974b). Both can be managed. Come what may, if the abundance of the icon of the North can be supervised the George River deer will continue to assemble at "Caribou House" in the spring and pass by the ancient tent rings at Indian House Lake going west as in past millenniums.

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The Sundrun population of wild reindeer

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Abstract: The Sundrun wild reindeer (Rangifer tarandus) herd was recognized as a separate population during the 1950s. Since then, the herd has ranged over an area of approximately 180 000 km^2 between the Indigirka and Kolyma Rivers in northeastern Yakutia. Population dynamics and movements were investigated between 1987 and 1997. During this period, the population estimates ranged from 25 000 to 45 000 reindeer, the sex ratio averaged 55 bulls:100 cows, and the percentage of calves in the herd ranged between 17% and 25%. The main routes of seasonal migrations, wintering areas, and the location of calving areas are discussed.

Key words: harvest, Indigirka, Kolyma, migrations, Rangifer tarandus, Russia, Yakutia.

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Introduction

According to historical literature, numerous populations of wild reindeer occupied the Kolyma-Indigirka region during the end of the nineteenth century and the beginning of the twentieth century (Wrangel, 1848; Argentov, 1860; Maidel, 1894; Buturlin, 1913; Shmidt, 1930; Naumov, 1933; Mikhel, 1938; Druri, 1949). However, wild reindeer were apparently largely absent from the area between the 1920s and the 1950s. Beginning in the late 1950s and early 1960s, reliable reports of wild reindeer between the Indigirka and Kolyma Rivers again emerged (Egorov et al., 1965). The population was subsequently studied (Obukhov, 1967; Kichinski & Flint, 1973), and eventually surveyed from the air in 1975, 1978, and 1982 (Pavlov et al., 1982). Between 1987 and 2000, personnel from the Institute of Biological Problems of the Cryolithozone also conducted aerial censuses and ground composition counts of the herd (1987, 1993, 1996, and 2000). Because information on the history, dynamics, and distribution of the Sundrun wild reindeer herd has not been widely available to biologists outside Yakutia (Sakha Republic), we reviewed the historical literature and recent studies of the population and presented the information at the 9th North American Caribou Workshop.

Distribution and movements

During the 1970s, wild reindeer from the Sundrun population migrated south in the fall to winter ranges on the Alazeya Plateau and the head of the Alazeya River, in the western portion of their range (Fig. 1). During the early 1980s, migration routes expanded east to the central part of the Kolyma lowland, encompassing a migration corridor approximately 100 km wide (Tikhonov & Koriakin, 1995). This migration corridor included the Ulakhan-Tas and Suor-Uyata ridges, and forest-tundra of the Rassokha River basin. From the Rassokha River basin, reindeer moved west across the Ilin-Uriakh and Arga-Uriakh Rivers to the Alazeya plateau. Migration routes also continued straight west to the Alazeya plateau from the Shangina River basin.

Spring migration of the Sundrun population usually begins early with pregnant females appearing on the Ulakhan-Tas and Suor-Uyata ridges, and Kondakov's plateau in early March. However, during the mid-1990s, movements of the Sundrun reindeer population changed (Fig. 1). In 1995 the spring migration was delayed 2 months to the end of April and beginning of May, and calving was also delayed. Calving reindeer were observed on the left bank of the Alazeya River, far to the south of the normal calving area. In October 1995, one large group of

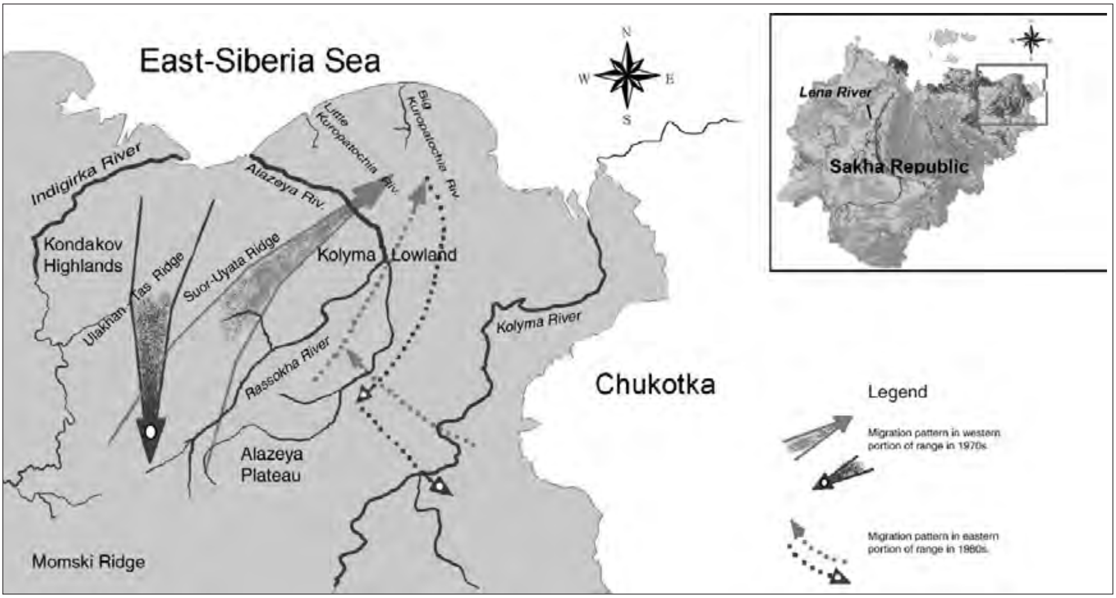

Fig. 1. Migration routes of the Sundrun wild reindeer population.

approximately 10 000 reindeer migrated to the east, and for the first time in 60 years, reached the head of the Konkovaya River. The animals then migrated east of the Kolyma lowland to the middle and head of the Alazeya River. An aerial survey in March 1996 found females on the right bank of the Chukochia River. During fall and winter 1996, about 1000 reindeer crossed the Kolyma River, the mouth of the Beriozovaya River, and traveled to the Ukagir plateau. During the rut (10 Oct through mid-Nov), the Sundrun population historically occupied the Ulakhan-Tas ridge region at the northern limit of the forest. However, since 1994, animals have been found in the Momski ridge area. It is also possible that, in this area, there was mixing of the Sundrun population with the Yana-Indigirka population, part of which winters on Momski ridge. The Sundrun population has also traditionally calved between the Big and Little Kuropatochia Rivers, with the postcalving concentration occurring on the arctic coastal plain or northward onto the Kondakov Highlands.

A separate, non-migratory herd of about 1000 reindeer can also be found on the arctic tundra in the vicinity of Big and Little Oler Lakes, the Chukochia River, and the head of the Big and Little Kuropatochia Rivers, where, during the winter, reindeer can be found in groups of 10–20 animals.

Table 1. Aerial counts of the Sundrun wild reindeer population, 1982–2000.

Year of census	Number of reindeer
1982	27 100
1987	29 200
1993	40 000
1996	34 200
2000	29 600

Herd composition

Between 1987 and 1997 the sex ratio of the Sundrun reindeer population averaged 55 bulls:100 cows. Between 1975 and 1993 percent calves in the herd in July averaged 26%. In July 2000 herd composition was estimated to be 17% calves and 21% bulls. The lower proportion of calves observed in 2000 is believed to be a result of lowered natality.

Population numbers

Sundrun reindeer population estimates ranged from 25 000 to 45 000 between 1987 and 1997 (Table 1). In July 2000, 29 500 reindeer were estimated in the Sundrun population using an aerial photo-direct count-extrapolation census (Hemming & Glenn, 1968; Safronov & Sivtsev, unpubl. data). This population estimate is comparable to the average estimates for the last 25 years.

Human impact on the population

In the Russian arctic, meat production from the harvest of wild reindeer accounts for about half of all local meat consumption (the remainder is either imported from the south or comes from semi-domestic reindeer). However, in some years and some areas, meat production from wild reindeer may comprise up to 70–99% of meat used. Wild meat production has thus become an important part of the economy of the far north. Hunters prefer to shoot males, and in the Sundrun reindeer population, male:female ratio has been reduced by hunting in recent years. In addition, large harvests under liberal hunting seasons have also exceeded the annual increment to the population in some years. Poor calf recruitment has also been an important contributing factor to the declining male:female ratio, and to a possible recent decline in herd size.

To optimize the harvest of reindeer from the Sundrun population, we recommend establishing specific annual quotas for the harvest of males and females. In addition, establishing reserve zones on the calving grounds and protecting the mass winter-spring migration of pregnant females may be necessary to conserve the population.

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Results of the 2000 census of wild reindeer on the Taimyr Peninsula

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Abstract: We conducted a census of wild reindeer (Rangifer tarandus) on the Taimyr Peninsula during 21-25 July 2000. This was the eighteenth aerial population census of wild reindeer on the Taimyr since counts began in 1959. Prior to the census, we conducted reconnaissance flights to identify areas of reindeer concentration. After the reindeer became aggregated, we estimated group size both visually and by photographing the larger groups. Unusually hot and dry weather (temperatures of 25-30 °C) and a high density of mosquitoes during the census likely forced the reindeer to group into unusually large concentrations. In late July most of the reindeer in the Taimyr population were distributed in two groupings that contained at least 450 000 animals, and one area that contained about 110 000. Smaller groups found during the census and the estimated 43 000 resident wild reindeer that were not counted during the census brought the total minimum population estimate to about 1 040 000. The maximum number of wild reindeer present could have been as high as about 1 100 000.

Key words: aerial photography, caribou, Rangifer tarandus, Russia, weather.

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Introduction

The Taimyr population of wild reindeer (Rangifer tarandus) has shown considerable change since 1959 (see Pavlov et al., 1996). Since, the herd has continued to grow, and it is now considered the largest in the world.

Historically, the number, distribution, and migration of wild reindeer was documented from both air and ground observations (Andreev, 1961; Pavlov et al., 1996). During the first aerial surveys, biologists noticed the tendency of wild reindeer to concentrate in western and central Taimyr during mid- to late July. Biologists conducted total counts and/or photographed wild reindeer in these areas of aggregation, and conducted selective surveys to estimate numbers of reindeer that were dispersed in other areas. As the number of wild reindeer increased, counting them became more difficult, but biologists continued to rely on a combination of visual estimation and aerial photography. Biologists realized that the degree of aggregation was dependent on weather and insect abundance, and structured surveys accordingly. Precensus reconnaissance flights allowed biologists to locate areas of concentration and document migration routes. In this paper we present results of the 2000 census that was conducted during late July.

Methods

In preparation for the July census, we began documenting the distribution and movements of wild reindeer on the Taimyr Peninsula in early July with periodic flights in an AN-2 biplane and by contacting pilots who were also flying in the area. From 21-25 July we conducted a total aerial count (census) of wild reindeer on the Taimyr Peninsula using an AN-2 biplane. During the census large concentrations of wild reindeer were estimated visually and photographed with a large format camera. Photographs were counted later and compared with visual estimates. To derive the total estimate for reindeer in the Taimyr population, we also added results of previous surveys of resident caribou that live year-round in the mountainous parts of the Taimyr Peninsula and on the arctic tundra of the northern Taimyr Peninsula.

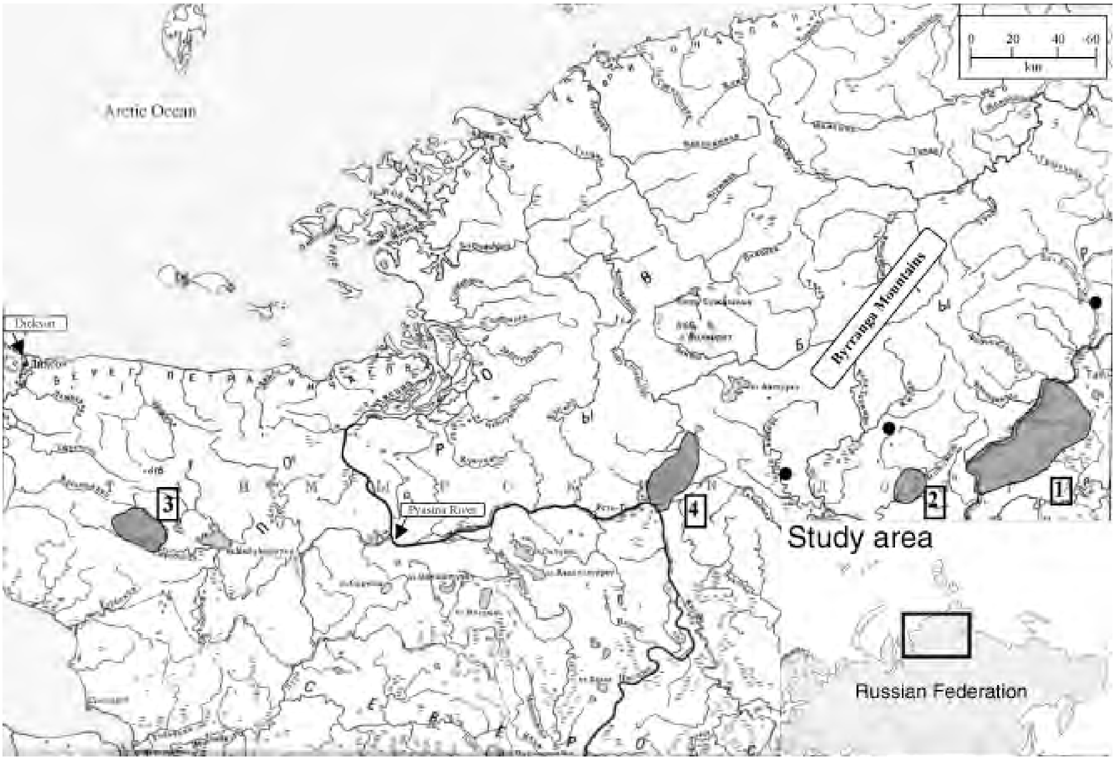

Fig. 1. Locations of concentrations of wild reindeer on the Taimyr Peninsula during 22-25 July 2000 (1 = Verhnetaimyrskaya, 2 = Deptumalskaya, 3 = Yeniseyskaya, 4 = Tareyskaya, ● = other, smaller groups).

Weather conditions during the second part of July were extremely favorable for an aggregation-type census; hot (25-30 ºC) and dry weather prevailed, and mosquitoes were abundant. The wild reindeer moved north quickly and grouped into compact aggregations. During the third week of July 2000, wild reindeer were more concentrated than anyone had ever observed. This significantly simplified our census efforts. It was under these conditions during 21-25 July that we conducted the census.

Most of the largest groups found during the census were photographed and also repeatedly estimated visually. Photos were taken at 200-300 m altitude. We used Kodak high-speed color and black and white film. More than 1500 frames of black and white and color films were processed, and about 400 photos, measuring 18-24 cm, were prepared for counting and classification of reindeer by sex and age. During the census, different observers estimated caribou numbers in groups and observers agreed on a final estimate. Only counts of experienced observers were used. Aggregations were numbered and located on topographical maps. The aircraft circled repeatedly to allow observers to visually estimate the number of wild reindeer in the aggregations.

Results

Precensus movements and distribution

Biting insects began to appear in large numbers at the end of the first week of July with the coming of the very warm weather. In early July, reindeer in the central Taimyr began moving north to the area west of Taimyr Lake. On the western Taimyr, animals moved to the mouth of the Yangoda River and the middle fork of the Gorbita River. The hot weather and a high density of harassing insects hastened the formation of postcalving aggregations and caused the period of rapid movement to be earlier than normal. The rapid movement of groups of females with calves caused the death of large numbers of calves as they attempted to cross the larger rivers. By the end of the first week of July, calves composed only 20% of postcalving aggregations. In most years, during early July, calves make up about 40% of these groups.

The 2000 census

The 2000 census was unusually successful because of the prolonged period of extremely warm weather that occurred during the second half of July. Between 21 July and 25 July, 4 large areas of concentration were found on the northern Taimyr Peninsula. These areas were designated Verhnetaimyrskaya, Tareyskaya, Yeniseyskaya, and Deptumalskaya (Fig. 1). Three other smaller groupings (20 000-50 000) were found away from these areas. The degree of mixing between these areas during summer and at other times of the year is unknown.

Surveys began on 21 July, when the average density in the areas surveyed was about 700 reindeer/10 km^2. However, the animals were aggregating quickly, and during the following days (22-25 July), the reindeer became much more densely aggregated. During 22-25 July almost all of the Taimyr Peninsula was surveyed during flights that averaged 11 hours per day (with refueling in the field).

The highest density of reindeer was found in the environs of Syrutaturku Lake. This large concentration area was originally observed on 21 July and named Verhnetaimyrskaya (Fig. 1). By 22 July reindeer in this vicinity had coalesced into groups of 40 000-50 000 in 5 areas. The largest concentration area was Fadyukuda (still labeled as Vernhnetaimyrskaya on Fig. 1) where we counted about 300 000 reindeer. In another concentration area immediately to the west, Deptumalskaya, we counted 82 000-85 000 wild reindeer in 12 loose aggregations. This area was in the foothills of the Byrranga Mountains and in the Deptumala River valley. Also to the north and west we counted reindeer in 3 smaller concentration areas near the Kyida (10 000-15 000), Ayatari (35 000-50 000), and Bolshaya Bootankaga (10 000-15 000) Rivers. Thus, in the 5 concentration areas of central and eastern Taimyr on 22 July, about 445 000-473 000 reindeer were counted.

In addition to the location and counting of the 5 groupings of wild reindeer in the Verhnetaimyrskaya area on 22 July, we also observed another large concentration forming to the west (Tareyskaya, Fig. 1). We continued to monitor this group until 25 July when it became sufficiently aggregated for counting. This was the largest single aggregation of wild reindeer found and it numbered 440 000-450 000. Also on 25 July, on the far western Taimyr Peninsula, we found and counted another relatively large, concentrated group of reindeer that we designated Yeniseyskaya. We estimated this aggregation to number about 110 000-115 000.

Thus, during the counts of wild reindeer on 22 July and 25 July, we estimated the migratory portion of the Taimyr Peninsula wild reindeer population to be about 995 000-1 038 000. In addition to these migratory wild reindeer, we had previously estimated that there are about 35 000 resident wild reindeer that live year-round on the arctic tundra north of the Byrranga Mountains, and about 8000 that live in the mountainous portions of central and eastern Taimyr. In summary, therefore, we estimated the total number of wild reindeer in the Taimyr population to be between 1 038 000 and 1 081 000 individuals in 2000.

Discussion

The distribution of wild reindeer during the second part of July differed from previous years. The weather conditions which resulted in high phytomass early, followed by high numbers of biting insects, and then by drying and early plant senescence were the most likely cause of the change in distribution of wild reindeer. The 50-day drought (early Jul-late Aug) and extremely hot weather caused reindeer to remain in relatively high concentrations until the end of August. The hot weather also delayed the fall migration of reindeer from the north of the Peninsula to the south by almost a month.

Distribution of reindeer during the 2000 census was also unusually compact. Almost all of the aggregations occurred in the ecotone between typical and arctic tundra. Tundra areas to the south were devoid of reindeer. The fact that the reindeer immediately moved south after the hottest weather abated indicates that it was the unusually warm weather that forced them all toward the arctic tundra. Without the extreme weather conditions, it would be difficult to obtain an accurate estimate of the Taimyr reindeer population with the resources available. One of the most difficult aspects of an aggregation-type census is ensuring that groups do not mix before the census is complete (Davis et al., 1979). During the 2000 census, although 2 days elapsed between counts of the Verhnetaimyrskaya groupings and the 2 other large groups to the west, ongoing reconnaissance ensured that there was no mixing of groups counted on 22 July with those counted on 25 July.

Management implications

Although the total number of wild reindeer on the Taimyr Peninsula is probably at an all-time high and the entire population is increasing, some groups of reindeer may be overharvested. The discreetness of various groups of wild reindeer on the Taimyr Peninsula needs further study. If these groups remain distinct from each other, throughout the year hunting must be more closely regulated to prevent overharvests of some groups and underharvests of others.

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Session six

Nutrition, Physiology, Diseases, Genetics and Taxonomy

Cree Elder's Story:

Andres Kawapit, Cree/Chisasibi, Waskaganish, Québec

Andrew Kawapit has been trapping all his life in the traditional lands of Whapmagoostui; indeed, hunting and trapping have been his main profession. As one of the few living members of the Community to have witnessed both the decline of the caribou and their return to the area, his knowledge of caribou habitat and migrations is extensive.

Body size of female calves and natality rates of known-aged females in two adjacent Alaskan caribou herds, and implications for management

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Abstract: We studied body mass of female calves and natality rate of adult females in two adjacent Interior Alaskan caribou (Rangifer tarandus granti) herds during 1991-2001. Mass of newborn calves was similar in both herds, but Delta calves gained significantly more mass over summer than Nelchina calves. In contrast, Nelchina calves consistently maintained their mass during winter while Delta calves lost mass. Metatarsus length was similar in both herds in 4-month-old and 10-month-old calves, and it increased over winter in both herds. Natality rates of females ≥3 years old were consistently higher in the Delta Herd than in the Nelchina Herd, primarily because natality in 3- to 5-year-old Nelchina females was low. Although body mass of Delta Herd calves consistently declined over winter, we concluded that nutrition was not significantly limiting herd growth. Managers are more likely to maximize harvest by maintaining the Delta Herd near its present size (i.e., 3500), or allowing it to increase only slightly. The only real option for increasing harvestable surpluses of caribou in the Delta Herd is reducing predation during calving and summer. In contrast, we conclude that summer nutrition significantly limits potential population growth and body mass in the Nelchina Herd, and managers are more likely to maximize harvest by maintaining herd size at or below 30 000 than by allowing the herd to grow to near historical highs (i.e., 60 000–70 000).

Key words: body mass, Delta Herd, metatarsus length, Nelchina Herd, predation, Rangifer tarandus granti, summer range quality, winter range quality.

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Introduction

During the late 1970s and 1980s most caribou herds in Alaska grew significantly, and many herds reached relatively high densities (Valkenburg et al., 1996). During this period, the emphasis in caribou research in Alaska broadened from primarily studying predation as a limiting factor to determining the influence of weather and population density on nutrition and productivity (Russell et al., 1993; Valkenburg et al., 1996; Adams & Dale, 1998; Lenart et al., 2002; Valkenburg et al., 2002, in press). This work has been of particular importance in the few caribou herds where the primary management goal is to maximize harvest and where managers have the ability to control herd size through harvest. In these few herds it is important to be able to estimate optimum population sizes that might provide the highest harvests over the long term. Therefore, in the early 1990s, Alaska Department of Fish and Game biologists began monitoring the mass and size of female caribou calves and natality rates of known-age females in several economically important herds (Valkenburg et al., 2002). We chose this approach because changes in body size and natality rate have been shown to be useful indices of nutrition in ungulates and sensitive to changes in climate and population density (McEwan & Wood, 1966; Klein & Strandgaard, 1972; White et al., 1981; Clutton-

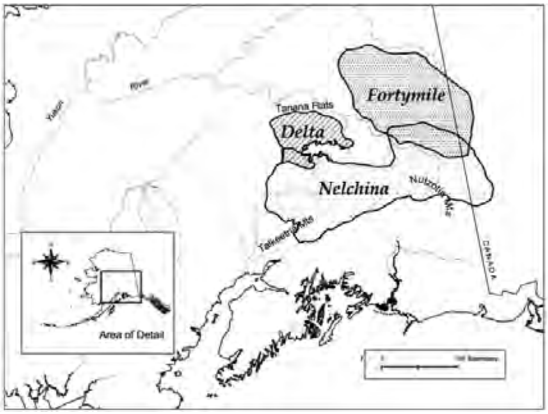

Fig 1. Location of Delta, Nelchina, and Fortymile caribou herds.

Brock et al., 1982; Peters, 1983; Reimers, 1983; Reimers et al., 1983; Skogland, 1983, 1984, 1985; Beninde, 1988; Crete & Huot, 1993; Gaillard et al., 1996; Reimers, 1997). We concentrated our efforts on female calves because they are inexpensive to handle, they can be collared with an adult-sized radio collar, and they are subsequently recruited into the population as known-aged females. Furthermore, the mass and size of 4- and 10-months old calves is largely a function of quality and quantity of available food during late gestation, and during the calf's first summer of life, so calves primarily reflect annual changes in nutrition (Skogland, 1983, 1984; Reimers, 1997; Valkenburg et al., 2000).

Research on calf size and natality has been particularly important to managers of the Delta and Nelchina caribou herds where access for hunters is good, there is a strong hunting tradition, demand for wild meat production is high, and where the caribou have approached or exceeded previous population highs. In 1995, we increased research emphasis on the Nelchina and Delta herds in the hope of determining the relative importance of summer and winter nutrition as limiting factors and providing managers with estimates of optimum population sizes for these herds. In this paper we compare changes in body size of female calves during summer and winter, and natality rates of females, and make inferences about the relative importance of winter and summer nutrition as limiting factors in these two herds. We also discuss management implications and provide initial estimates of optimum population sizes for these herds.

Study herds

Nelchina Herd

The Nelchina Herd has been relatively well studied since 1948, and it has fluctuated considerably in size since then (Van Ballenberghe, 1985; Tobey, 1999). During the late 1940s and early 1950s the herd numbered less than 10 000 but it increased rapidly to about 70 000 by the early 1960s following intensive wolf (Canis lupus) control. By the early 1970s the Nelchina Herd had once again declined below 10 000 and density dependent factors, predation, and overhunting were implicated in the decline (Doerr, 1979; Van Ballenberghe, 1985; Eberhardt & Pitcher, 1992). During 1975-1995 the Alaska Department of Fish and Game allowed the herd to grow while range conditions, and later, body condition, were being monitored. In the late 1980s, as the herd approached 30 000, Nelchina caribou began actively searching for new winter range. In 1987 many caribou moved northeast of traditional winter ranges in the Nelchina Basin to new winter ranges north of the Nutzotin Mountains (Tobey, 1999) (Fig. 1). This movement expanded, and within a few years a majority of the herd began using winter range on both sides of the Yukon–Alaska border (Tobey, 1993). Subsequently, most Nelchina caribou settled on winter range in eastcentral Alaska. These ranges are also used in some years by Fortymile Herd caribou. Until the mid-1990s, about 25–33% of the Nelchina Herd remained on traditional winter ranges in the Nelchina Basin, but since then, only about 10% of the herd continues to use this traditional winter range (Tobey & Scotton, 2001).

By the mid-1990s, the Nelchina Herd numbered about 50 000 and evidence of density-dependent effects on body size of calves and natality rate of adults began to appear (Tobey & Scotton, 2001). High caribou numbers obviously began to affect the distribution and biomass of lichens and other plants on primary summer range in the Talkeetna Mountains. After 1995 the Nelchina Herd declined from reduced calf production and survival and deliberately heavy hunting (Tobey & Scotton, 2001). From 1997 to 2001 the herd varied between 29 000 and 39 000 and hunting was greatly reduced. The newer winter ranges used by the Nelchina Herd after 1987 obviously have a much higher lichen biomass than traditionally used ranges in the Nelchina Basin. Proportion of lichens in the winter diet of caribou on these new ranges is also comparatively high (Valkenburg et al., 2002).

Delta Herd

The Delta caribou herd has been intensively studied since 1979 (Valkenburg et al., 2002). Like most other herds in Interior Alaska, numbers were low (<2500) in the early 1970s. Following wolf control in the mid-1970s, the herd increased rapidly and

Table 1. Mean mass with standard deviations (s) in kg of female newborn, 4-month-old, and 10-month-old caribou calves in the Delta caribou herd.

Birth year	Newborn mass, s, n	4 months Oct mass, s, n	10 months Apr mass, s, n	Mean mass Change Oct–Apr
1991		57.9, 2.6, 14	54.0, 2.6, 17	-3.9
1992		54.0, 2.6, 17	55.5, 2.9, 12	+1.5
1993		55.8, 3.0, 11	n.a.	
1994		59.6, 3.0, 15	55.8, 2.7, 15	-3.8
1995	8.31, 0.24, 19	59.5, 2.7, 15	54.8, 3.3, 15	-4.7
1996	7.40, 0.19, 28	55.8, 3.0, 14	53.7, 2.5, 14	-2.1
1997	7.99, 0.20, 35	58.2, 2.2, 20	56.1, 3.0, 12	-2.1
1998	7.70, 0.29, 15	56.4, 2.6, 16	52.9, 2.6, 13	-3.5
1999	7.89, 0.19, 35	57.1, 2.9, 14	52.1, 2.6, 12	-5.0
2000	7.76, 0.32, 16	56.6, 4.0, 14	55.4, 1.4, 11	-1.2
Mean	7.84	57.1	54.4	-2.6

Table 2. Mean weights and standard deviations (s) in kg of female newborn, 4-month-old, and 10-month-old caribou calves in the Nelchina caribou herd.

Birth year	Newborn mass, s, n	4 months Oct mass, s, n	10 months Apr mass, s, n	Mean mass Change Oct–Apr
1995		53.5, 1.5, 15	53.1, 1.2, 16	-0.4
1996	7.19, 0.19, 17	48.3, 2.1, 10	49.1, 1.0, 23	+0.8
1997	7.91, 0.21, 30	55.5, 1.8, 10	57.0, 1.1, 15	+1.5
1998	8.57, 0.18, 30	50.6, 0.9, 25	53.1, 1.2, 15	+2.5
1999	8.14, 0.21, 27	52.0, 0.8, 38	48.6, 0.8, 27	-1.4
2000	7.02, 0.15, 31	53.5, 1.1, 37	52.5, 0.9, 26	-1.0
Mean	7.77	52.0	52.2	+3.0

reached a historic high level of 10 700 in 1989 (Boertje et al., 1996; Valkenburg et al., 1996). Wildlife managers had deliberately allowed the herd to grow to determine if density-dependent factors would eventually regulate herd size. As the herd increased, caribou changed winter ranges frequently and used nontraditional winter range in the Tanana Flats. Following severe summer and winter weather in the early 1990s, the herd declined because of heavy predation and reduced calf survival (Valkenburg et al., 1996). Between 1995 and 2001 the herd remained relatively stable at about 3500-4500 caribou (Valkenburg et al., 2002). During the decline in the early 1990s, it was clear that nutrition was relatively poor compared with the late 1970s and early 1980s – body size and survival of calves was low, and natality rate in adults declined. After the population was reduced in the early 1990s and weather patterns moderated, nutritional condition of the herd largely recovered (Valkenburg et al., 2002). However, the proportion of lichens in the winter diet has remained relatively low compared with other Interior herds, and caribou have continued to pioneer new winter ranges (Valkenburg et al., 2002).

Methods

During 1991-1995 we monitored mass and skeletal measurements of samples of 4-month-old and 10-month-old female caribou calves in the Delta Herd, and during 1996-2000 we monitored mass of newborn calves and mass and skeletal measurements of newborn, 4-month-old, and 10-month-old female caribou calves in the Delta and Nelchina caribou herds. We located newborn calves (1-2 days old) with a Robinson (R-22) helicopter and captured them by hand after running them down. Older calves were darted from helicopters (Valkenburg et al., 1999). Four-month-old calves were captured during 27 September-14 October, and 10-month-old calves were captured during 1-25 April. Calves were weighed with calibrated electronic or spring scales, and metatarsus length of 4-month-old and 10-month-old calves was measured with calipers. We monitored natality rates of radio-collared female caribou during mid to late May by documenting the presence of hard antlers and/or distended udders (Bergerud, 1964; Whitten, 1995).

We used a linear model of mixed effects to examine potential differences in newborn, 4-month-old, and 10-month-old female calf mass. We used the same model to examine differences in metatarsus length in 4-month-old and 10-month-old female calves. The following model was used:

$$Z_{ijk} = \mu + \eta_i + Y_j + (\eta Y)_{ij} + \varepsilon_{ijk}$$

where Z_{ijk} is the mass (or metatarsus length) for the ith herd, i = Delta or Nelchina, for the jth year, and k indicates the replicate for the ith herd in the jth year; μ is an overall mean effect, η_i is a fixed effect for herd, Y_j is a random effect for year, and $(\eta Y)_{ij}$ is an interaction term that allows separate random effects among years for each herd. We used this model for each age class: newborns, 4-month-olds, and 10-month-olds. We compared age-specific natality rates of radiocollared females between herds by calculating confidence limits for the binomial distribution.

Results

During 1995-2000 mass of newborn female caribou calves in the Delta and Nelchina caribou herds did not differ (P=0.66) (Tables 1-3). Mass of 4-month-old Delta calves was greater than 4-month-old Nelchina calves (P=0.001), and remained higher than Nelchina calves at 10 months of age (P=0.03) (Tables 1-3). There was no difference in metatarsus lengths in either 4-month-old (P=0.77) or 10-month-old (P=0.33) calves between the two herds (Tables 4-6). Natality rates of radiocollared Nelchina females (≥3-years old) were lower than radiocollared Delta females (P=0.02) primarily because a majority of Nelchina females often did not produce their first calf until age 4, and natality was lower in 4- and 5-year-old females (P<0.04) (Tables 7 and 8). There was no difference in natality rates of radiocollared Delta and Nelchina females 6-years old and older (P=0.9).

Discussion

Even though female Delta caribou calves consistently lost mass over winter, at 10 months of age they remained heavier than Nelchina calves because Nelchina calves gained significantly less mass over summer, and they were not able to gain mass over winter. Because of the apparently superior winter nutrition of the Nelchina caribou we would

Table 3. Model predictions for mean mass and standard deviation (s) in kg of newborn, 4-month-old, and 10 month-old female caribou calves in the Delta and Nelchina caribou herds.

	Newborns		4 months		10 months	
Herd	Estimate	s	Estimate	s	Estimate	s
Delta	7.85	0.19	57.11	0.61	54.62	0.75
Nelchina	7.98	0.21	52.27	0.69	52.25	0.82

Table 4. Mean metatarsus lengths with standard deviations (s) in cm of female 4-month-old and 10-month-old caribou calves in the Delta caribou herd.

Birth year	4 months Oct length, s, n	10 months Apr length, s, n	Mean length change Oct–Apr
1991	35.6, 0.2, 14	36.3, 0.3, 16	0.7
1992	35.3, 0.2, 15	36.9, 0.3, 12	1.2
1993	35.1, 0.2, 14	n.a.	
1994	36.1, 0.2, 15	37.2, 0.2, 14	1.1
1995	35.7, 0.3, 12	37.0, 0.2, 15	1.3
1996	35.8, 0.2, 14	37.8, 0.4, 8	2.0
1997	36.0, 0.3, 15	36.7, 0.5, 12	0.7
1998	35.7, 0.2, 16	37.2, 0.2, 14	1.5
1999	35.7, 0.3, 13	36.6, 0.3, 12	0.9
2000	35.7, 0.3, 14	37.7, 0.3, 11	2.0
Mean	35.7	37.0	1.3

Table 5. Mean metatarsus lengths with standard deviations (s) in cm of female 4-month-old and 10-month-old caribou calves in Nelchina caribou herd.

Birth year	4 months Oct length, s, n	10 months Apr length, s, n	Mean length change Oct–Apr
1995	35.6, 0.3, 15	37.2, 0.3, 16	1.6
1996	35.5, 0.3, 10	36.8, 0.2, 18	1.3
1997	35.9, 0.3, 10	37.5, 0.1, 15	1.6
1998	35.4, 0.2, 25	37.1, 0.1, 15	1.7
1999	35.9, 0.2, 38	37.5, 0.2, 28	1.6
2000	35.5, 0.2, 36	37.2, 0.2, 25	1.7
Mean	35.6	37.2	1.6

Table 6. Model prediction for mean metatarsus length and standard deviation (s) in cm of 4-month-old and 10-month-old female caribou calves in the Delta and Nelchina caribou herds.

	4-month-olds		10-month-olds	
Herd	Estimate	s	Estimate	s
Delta	35.66	0.10	37.01	0.14
Nelchina	35.62	0.11	37.23	0.15

Table 7. Natality rates of radiocollared known-aged female caribou in the Delta caribou herd, 1991–2000.

	Proportion parturient (%) in late May						
Year	Yearlings	2-year-olds	3-year-olds	4-year-olds	5-year-olds	≥6-year-olds	All cows 3 years and older
1991	0/4 (0)		2/7 (29)	8/10 (80)	3/3 (100)	11/14 (79)	24/34 (71)
1992	0/16 (0)	0/5 (0)	0/1 (0)	6/7 (86)	8/8 (100)	12/12 (100)	26/28 (93)
1993	0/11 (0)	0/10 (0)	0/5 (0)	0/1 (0)	1/3 (33)	6/15 (40)	7/24 (29)
1994	0/10 (0)	0/12 (0)	2/9 (22)	4/5 (80)	1/1 (100)	13/15 (87)	20/30 (67)
1995	0/13 (0)	0/7 (0)	7/11 (64)	8/8 (100)	4/5 (80)	13/13 (100)	32/37 (86)
1996	0/16 (0)	1/11 (9)	5/5 (100)	9/10 (90)	6/6 (100)	15/16 (94)	35/37 (95)
1997	0/12 (0)	0/11 (0)	5/10 (50)	3/4 (75)	8/9 (89)	16/17 (94)	32/40 (80)
1998	0/17 (0)	1/8 (13)	9/10 (90)	7/7 (100)	3/3 (100)	18/22 (80)	37/42 (88)
1999	0/10 (0)	1/13 (8)	6/7 (86)	5/7 (71)	7/7 (100)	16/17 (94)	34/38 (89)
2000	0/9 (0)	0/10 (0)	8/12 (66)	5/5 (100)	6/6 (100)	14/18 (78)	33/41 (80)
2001	0/15 (0)	1/7 (14)	2/8 (25)	8/10 (80)	4/6 (67)	15/17 (88)	29/41 (71)
All years	0/133 (0)	4/94 (4)	46/84 (55)	52/65 (80)	51/57 (89)	149/176 (85)	309/392 (79)

Table 8. Natality rates of radiocollared known-aged female caribou in the Nelchina caribou herd, 1993–2000.

	Proportion parturient (%) in late May						
Year	Yearlings	2-year-olds	3-year-olds	4-year-olds	5-year-olds	≥6-year-olds	All cows 3 years and older
1993							19/29 (66)
1994							NA
1995							18/20 (90)
1996		0/7 (0)					10/15 (66)
1997		0/2 (0)	3/6 (50)	NA	NA	5/6 (83)	8/12 (66)
1998		0/2 (0)	5/11 (45)	6/8 (75)	NA	6/7 (86)	17/26 (65)
1999		NA	3/12 (25)	6/9 (66)	2/6 (33)	6/7 (86)	17/34 (50)
2000		NA	0/8 (0)	6/10 (60)	4/10 (40)	5/5 (100)	15/25 (60)
2001		0/5	1/6 (10)	6/6 (100)	7/8 (75)	9/14 (64)	23/34 (68)
All years		0/16 (0)	12/43 (28)	24/33 (73)	13/24 (54)	31/39 (79)	127/195 (65)

have expected to see consistently higher newborn calf mass (cf. Skogland, 1984), but mass of newborn calves was similar in both herds. Because of the apparently superior summer nutrition of Delta caribou we expected to see consistently higher natality in Delta females (cf. Reimers, 1997). Natality rates of 3- to 5-year-old Delta females were higher than natality rates of 3- to 5-year-old Nelchina females.

Despite higher natality and better summer nutrition in the Delta Herd, relatively few calves remained in the herd in autumn because of heavy predation by wolves, grizzly bears (Ursus arctos), and golden eagles (Aquila chrysaetos) (Valkenburg et al., 2002). Despite the higher natality of the Delta Herd, autumn calf:cow ratios in the Nelchina Herd were consistently higher than in the Delta Herd. During winter, mortality of the radiocollared calves was similar in both herds (i.e., about 40%) (Tobey & Scotton, 2001; Valkenburg et al., 2002).

Historically, the Nelchina Herd reached a population high of about 70 000 during the early 1960s, followed by a major decline to less than 10 000 by 1972 (Van Ballenberghe, 1985; Eberhardt & Pitcher, 1992). There has been much debate about causes of the decline, but there was clear evidence that nutrition was limiting (Eberhardt & Pitcher, 1992). In view of the strong evidence of nutritional limitation on summer range while the herd has recently fluctuated between 50 000 and 30 000, it seems even more unlikely now that the high caribou population present on the Nelchina range in the 1960s was sustainable. Similar strong evidence of limiting summer nutrition was not documented in the Delta Herd during its population high in 1989, although the herd peaked and declined so rapidly that there may not have been sufficient time for evidence of poor summer nutrition to become obvious (Valkenburg et al., 1996).

Management implications

At present, harvestable surpluses of caribou are relatively low in the Nelchina and Delta herds and harvest must be restricted largely to males to keep herd sizes from declining. To increase harvestable surpluses of caribou in the Delta Herd it may be desirable to increase herd size slightly (perhaps to about 4000-5000) even though there are indications that winter food is not abundant. At the present time there is no evidence that winter range is significantly limiting population growth either through production or survival. However, if herd size is increased we expect that body condition of females would decline during winter (particularly during severe winters), and neonatal calf survival would eventually decline (Adams et al., 1995). It appears therefore, that reducing predation is the only real option for increasing harvest -- the herd is currently stable or declining slowly because of high mortality of calves in summer and this mortality is not related to nutrition (Valkenburg et al., 1999; Valkenburg et al., 2002).

In the Nelchina Herd, reducing herd size further or maintaining it at about 30 000 may alleviate overuse of summer range and thus improve natality in 3- to 5-year-olds. The dilemma for managers of the Nelchina Herd is that predation is probably already a significant limiting factor, and reducing herd size further might exacerbate the problem. However, it seems inadvisable at present to allow herd size to increase because of the already strong effect of the heavily used summer range on natality.

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Session seven

Habitat Use, Movement and Activity

Naskapi Elder's Story:

Joseph Guanish, Kawawachikamach, Québec

Joseph Guanish was born on September 23, 1931, as his parents were travelling between Fort McKenze and Fort Chimo to get supplies. As a young adult, he transported supplies between those two trading posts for the Hudson's Bay Company. After the Naskapis settled in Schefferville, he started working for the Iron Ore Company on June 28, 1957, until the fall of 1982, when the IOC closed its operations in Schefferville. He was Chief for 27 years, and in that capacity he signed the Northeastern Québec Agreement in 1978 for the Naskapis. He was also a part-time police officer for two years and head of the rescue team for six years. He was appointed reviewer of the Naskapi Lexicon before its publication, and has been working on the development of a Naskapi curriculum for the past three years. Mr. Guanish is a member of the Naskapi Education Committee and a church warden. He has nine children. As a long time observer of the caribou, Mr. Guanish will talk of the activities of the caribou during the various northern seasons and of their feeding habits. He will also speak about the health status of the caribou.

The Ninth North American Caribou Workshop,
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Status, population fluctuations and ecological relationships of Peary caribou on the Queen Elizabeth Islands: Implications for their survival

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Abstract: The Peary caribou (*Rangifer tarandus pearyi*) was recognized as 'Threatened' by the Committee on the Status of Endangered Wildlife in Canada in 1979 and 'Endangered' in 1991. It is the only member of the deer family (Cervidae) found on the Queen Elizabeth Islands (QEI) of the Canadian High Arctic. The Peary caribou is a significant part of the region's biodiversity and a socially important and economically valuable part of Arctic Canada's natural heritage. Recent microsatellite DNA findings indicate that Peary caribou on the QEI are distinct from caribou on the other Arctic Islands beyond the QEI, including Banks Island. This fact must be kept in mind if any translocation of caribou to the QEI is proposed. The subspecies is too gross a level at which to recognize the considerable diversity that exists between Peary caribou on the QEI and divergent caribou on other Canadian Arctic Islands. The Committee on the Status of Endangered Wildlife in Canada should take this considerable diversity among these caribou at below the subspecies classification to mind when assigning conservation divisions (units) to caribou on the Canadian Arctic Islands. In summer 1961, the first and only nearly range-wide aerial survey of Peary caribou yielded a population estimate on the QEI of 25 845, including about 20% calves. There was a strong preference for range on the western QEI (WEQI), where 94% (24 363) of the estimated caribou occurred on only 24% (ca. 97 000 km^2) of the collective island-landmass. By summer 1973, the overall number of Peary caribou on the QEI had decreased markedly and was estimated at about 7000 animals. The following winter and spring (1973-74), the Peary caribou population declined 49% on the WQEI. The estimated number dropping to <3000, with no calves seen by us in summer 1974. Based on estimates from several aerial surveys conducted on the WQEI from 1985 to 1987, the number of Peary caribou on the QEI as a whole was judged to be 3300-3600 or only about 13-14% of the 1961 estimate. After a partial recovery in the late 1980s and early 1990s, Peary caribou on the WQEI declined drastically between 1994 and 1997 and were estimated at an all-time known low of about 1100 animals by summer 1997. The number of Peary caribou on the QEI in summer 1997 was likely no more than 2000-2400 or only 8-9% of the 1961 estimate. The four known major die-offs of Peary caribou on the WQEI between 1973 and 1997 occurred during winter and spring periods (1 Sep-21 Jun) with significantly greater ($P<0.005$) total snowfall, when compared to the long-term mean obtained from 55 caribou-years (1 Jul-30 Jun), 1947/48-2001/02, of weather records from Resolute Airport on Cornwallis Island. Of ecological significance is that the die-offs occurred when the caribou were at low mean overall densities and involved similar high annual rates of loss among muskoxen (*Ovibos moschatus*). All of the available evidence indicates that Peary caribou (and muskoxen) on the QEI experienced die-offs from prolonged, under-nutrition (starvation) caused by relative unavailability of forage-the forage was there but it was inaccessible to the caribou due to snow and/or ice cover. We cannot control the severe weather that greatly restricts the forage supply but we should try to reduce the losses of Peary caribou from other sources-humans, predators and competitors.

Key words: die-offs, ecology, genetics, population estimates, *Rangifer tarandus pearyi*, taxonomy.

Rangifer, Special Issue No. 14: 213-226

Introduction

The Peary caribou (Rangifer tarandus pearyi) occurs in the Canadian High Arctic. It was listed in 1979 as 'Threatened' and in 199l as an 'Endangered' form of wildlife in Canada by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC: cf. Gunn et al., 1981; Miller, 1990b; COSEWIC, 1991). It is a socially important and economically valuable part of Arctic Canada's natural heritage; the only member of the deer family (Cervidae) found in the Canadian High Arctic-the Queen Elizabeth Islands (QEI).

Peary caribou were listed as 'Threatened' on the basis of the decline in the total number on the western QEI (WQEI) between 1961 and 1974, then as 'Endangered' because of the continued overall decline in the 1980s. Only for Bathurst Island and its associated smaller islands was there evidence for recovery in numbers between, at least, 1985 and 1994, which was most likely initiated in the late 1970s (e.g., Miller, 1998). However, there was no aerial surveys of the other WQEI between 1988 and 1996, therefore, the lack of evidence is not proof that no recovery occurred there. We believe, it is most likely that some recovery was experienced within the Melville-Prince Patrick islands complex from about 1988 to 1994. Then those caribou probably also entered the 1994-97 decline phase, as documented in 1996/97 (Gunn & Dragon, 2002). All of that recovery from the late 1970s to the early 1990s and more was lost during the 3 most severe winters recorded in terms of total snowfall at Resolute Airport (1994-97). By 1997, the number of Peary caribou on the WQEI fell to an all-time estimated low of about 1100 caribou. The long-term overall decline together with the unknown status on the eastern QEI (EQEI) is a concern for Peary caribou conservation. Were those winters part of a human-induced trend consistent with the predictions for global warming or were they within 'normal' climate variability and how does either condition foreshadow future events for Peary caribou?

If the threats to Peary caribou were simply the natural consequences of high variation in weather in an extreme environment, then the need for recovery actions would be less as the caribou numbers would likely recover. However, recent trends in Arctic weather are consistent with the predictions for global climate change (Maxwell, 1997; Tynan & Demaster, 1997; and summarized in Weller, 2000). Some future predictions are ominous (e.g., Bradley, 2000), and we consider that the balance of scientific opinion is that human activity has contributed to global climate change. If the Peary caribou decline is a consequence of human activity, then we have a greater conservation obligation and in addition, the past would not necessarily be an accurate guide to the future. Thus, recovery to population sizes that will sustain meaningful levels of harvest will be slow at best. Most importantly, there is no guarantee of any large-scale recovery if climatic conditions unfavorable to caribou survival become more severe or prevalent (Gunn et al., 2000b).

The following is a summary review of (1) the unique status (taxonomy and genetics) of Peary caribou on the Queen Elizabeth Islands compared to caribou on the southern Canadian Arctic Islands; (2) population sizes and fluctuations that Peary caribou have experienced between 1961 and 1997; and (3) ecological relationships of the Peary caribou. Our aim is to point out the implications of these factors to the long-term survival and thus the conservation of Peary caribou, particularly with respect to an apparently changing climate in the western Canadian High Arctic (e.g., Weller, 2000). That is, to the potential detrimental effects on Peary caribou of climate change and resultant natural and/or anthropogenic warming in arctic regions.

The Queen Elizabeth Islands

The Setting

The Canadian Arctic Archipelago forms the remote and isolated northern apex of the North American continent and the QEI make up the northern point of that apex (Fig. 1). The QEI is collectively all of the islands that lie entirely to the north of about 74°N latitude, spanning about 62° of longitude from 61°W on the east to about 123°W on the west. The QEI include 2126 islands: 2092 are <137 km^2 in size; 16 are between 137 and 955 km^2; 11 are between 1059 and 6995 km^2; 6 are between 11 295 and 55 247 km^2; and 1 is 196 236 km^2 (Ellesmere Island, the 10th largest island in the world: data source, Natural Resources Canada, The National Atlas of Canada-Facts about Canada-Sea Islands http://atlas.gc.ca/english/facts/islands.htm1). The region is known for its extremely harsh climate and low plant growth forms and relative lack of vegetation compared even to mainland tundra ranges (e.g., Edlund & Alt, 1989; Bliss, 1990; Edlund, 1990). In this setting only two forms of large grazing animals have established themselves-the Peary caribou and the muskox (Ovibos moschatus).

The climate of the region is unpredictably variable and severe: summers are short, cool and winters are long and cold. Total annual precipitation normally averages <100 mm (Ecoregions Working Group, 1989). Air temperatures average below -17.7 °C from Dec to Mar and mean daily temperatures gen-

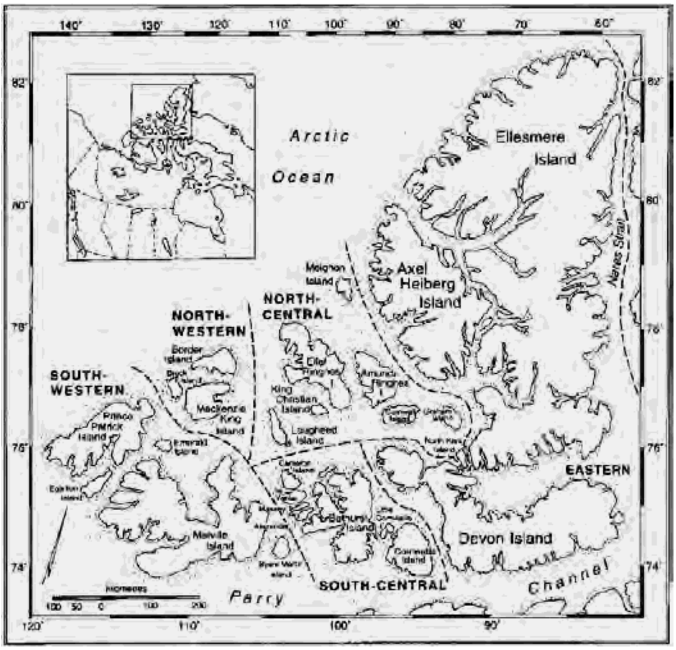

Fig. 1. Current range of Peary caribou (Rangifer tarandus pearyi) in the Canadian High Arctic: Queen Elizabeth Islands shown as five ecoregions (from Miller, 1990b).

erally do not rise above 0 °C until after 1 Jun on the extreme south of the region or 15 Jun on the north of the region (Meteorological Branch, 1970).

Snow cover usually begins melting in early to mid Jun, and often rapidly dissipates to bare ground from mid Jun through late Jun, except for snow banks in sheltered sites (Potter, 1965). In the most unfavorable years, however, considerable areas can remain snow- and/or ice-covered throughout Jun, and even rarely into the first few days of Jul. Summer is the period when the ground is generally essentially snow-free, and lasts from the beginning of Jul into the end of Aug. However, Aug is better thought of as autumn in terms of relative forage quality and supply with the initiation of plant senescence and common occurrence of snowfall. Winter starts when the mean daily temperature falls below 0 ºC, usually about or before 15 Sep. The stormiest months are Sep and Oct and much of the annual snowfall may occur in those months. Anticyclones from Dec to Mar dominate the weather causing frequent calms, clear skies, and light snowfall.

Established calendar dates for the seasons of the year do not relate well to the annually prevailing weather in the Canadian High Arctic. Therefore, on a whole calendar-month basis, winter can be considered as being from 1 Sep through 31 May, spring is essentially the month of Jun, summer is Jul; and autumn is Aug. Winter is subdivided into 'early-winter' (Sep-Nov), 'mid-winter' (Dec-Feb), and 'late-winter' (Mar-May) to allow better analyses of the temporal aspects of snow/ice conditions. In reality, most of Jun is wintry and sometimes, if not often, unfavorable to the survival of newborn calves and nutritionally debilitated yearlings and older (1+ yr-old) caribou. Thus, the springtime environmental "bottle-neck" for caribou on the arctic islands is of particular importance in the dynamics of population growth.

The Canadian High Arctic is a collection of island-landmasses with varied topography which contributes to regional climates (Maxwell, 1981). In the context of Peary caribou ecology, the WQEI of Prince Patrick, Melville, Bathurst, and Cornwallis and the north-central islands of Ellef Ringnes and Amund Ringnes fall into Maxwell's (1981) 'Northwestern Climatic Region' and the major EQEI of Ellesmere, Axel Heiberg and Devon are in the 'Eastern Climatic Region.' The above division approximates our major division of WQEI vs. EQEI, based on areas surveyed for Peary caribou, with the exception that we include Ellef Ringnes and Amund Ringnes islands in the eastern group. Weather on the WQEI is caused by cyclones originating from the Beaufort-Mackenzie area while cyclones from the Davis Strait-Baffin Bay-Baffin Island influence the EQEI. Also, in terms of differences in vegetation and relative numbers of animals, the QEI can be subdivided into five 'ecoregions' (Fig. 1: WQEI equals Northwestern, Southwestern and South-central ecoregions, plus Lougheed Island; EQEI equals Eastern and North-central ecoregions (minus Lougheed Island).

The 'Caribou-Year' (1 Jul-30 Jun)

We divide the caribou-year into six seasons on a whole month basis that have ecological significance in terms of range use by Peary caribou.

Summer (1-30 Jul)

All caribou should be in a positive energy balance. This is the annual period of highest quality vegetation, with maximum growth for bulls and high energy demands for maternal cows during early lactation. In general, it is the period of initiation of restoration of body reserves.

Autumn (1-31 Aug)
Caribou remain in a positive energy balance. Restoration of body reserves continues; however, quality of vegetation begins to decline with the initiation of plant senescence.

Early Winter (1 Sep-30 Nov)
Caribou can be in a positive or negative energy balance-depending on the severity of the year, timing of heavy snowfalls and ground-fast ice or icing on or in the snow cover. In some years, forage remains readily available throughout their range. However, in the most unfavorable years, forage becomes greatly restricted and the first stages of malnutrition are initiated among many caribou but they usually do not succumb to extreme undernutrition until mid winter or later.

Mid Winter (1 Dec-28/29 Feb)
Caribou are in a negative energy balance. It is a period of survival, with areas of range occupation depending on then prevailing snow/ice depths and conditions. Snow pack characteristics, depths, hardness and density, are do mainly to wind action but are largely determined by snowfall and icing that took place in early winter. In the worst years, mortality is accelerated by Jan/Feb but often mostly delayed to late winter or even spring.

Late Winter (1 Mar-31 May)
Caribou remain in a negative energy balance. It is usually a period of extreme stress for many caribou and in some years for all caribou. Areas of range occupation depend on then prevailing snow/ice conditions but are mostly tied to snow-free or shallow snow areas. Mortality is markedly elevated in the most environmentally stressful years.

Spring (1-30 Jun)
A period of negative energy balance for parturient or maternal cows. Those cows that were bred the previous year and carried their fetus to full-term likely remain in a negative energy balance throughout the month because the sites that they occupy for calving and early postcalving do not favor early initiation of plant growth. However, in most years bulls initiate body growth by tracking new growth (phenology) of vegetation which appears first on relatively low-lying coastal sites, apparently because they need more time for body growth (e.g., Russell et al., 1993). The condition of subadult females and males can vary among years from negative to positive as the month progresses. In the most severe years, mortality remains high through most of the month and there are major losses in calf crops, sometimes, to the point of near of total failures.

The caribou-year should be considered on a full 12-month basis in terms of range restriction and relative forage availability or relative forage unavailability. That is, adequate ranges (forage and space) are necessary during late winter (1 Mar-31 May) and spring (1-30 Jun) for Peary caribou to get through the most environmentally stressful times of the year. Then, during summer (1-31 Jul) and autumn (1-31 Aug) range conditions have to be adequate for the caribou to not only regain condition to breed but also to survive the following winter. Finally, adequate ranges during early winter (1 Sep-30 Nov) and mid winter (1 Dec-28/29 Feb) will maximize the probability of survival during the subsequent late winter and spring and promote successful initial calf production and early survival of the newborn offspring.

The overall range is only as good as its weakest seasonal link. That is, the protection of the caribou range during the stressful part of the year will be of little value if the caribou cannot subsequently make back their body condition, make new growth and build up their body reserves during the favorable time of the year. Thus, caribou need to have sufficient amounts of forge and space available during all seasons of the year to foster their year-round long-term survival. This is especially true if the population is to remain stable or expand while being harvested at a temporary sustainable level by Inuit hunters. Peary caribou populations are subject to abrupt changes in size. Therefore, sustainable harvesting of Peary caribou at a given level is feasible only on a short-term basis. When a major die-off occurs, the sustainable level decreases markedly, on occasion to zero, and harvesting should be stopped or a new lower rate established until the population has once again recovered sufficiently to support higher levels of annual harvest.

Status of Peary Caribou

Taxonomy and Genetics

The Peary caribou (*Rangifer tarandus pearyi*) was first described as a distinct species (*R. pearyi*) in 1902 by J. A. Allen (1902, 1908) from specimens obtained on Ellesmere Island by Lt. R. E. Peary, U.S. Navy (later, Admiral Peary of North Pole fame). The specific rank was later accepted by Jacobi (1931) in his classification of the genus-*Rangifer*. Subsequently, Flerov (1952) placed all reindeer and caribou in a single Holarctic species (*Rangifer tarandus*) and reduced Peary caribou to a subspecies-*R. t. pearyi*. In the late 1950s, Hall & Kelson (1959) followed Lydekker (1898) in arranging all New World forms as subspecies and accepted *R. t. pearyi* for the Peary caribou. In 1960, however, Manning (1960), still clinging to Richardson's (1829) use of *arcticus* for all New World forms, identified the Peary caribou as R.

arcticus pearyi. Most recently, Banfield (1961) returned the Peary caribou classification to-R. t. pearyi-in his revision of the genus Rangifer.

Manning (1960) and Banfield (1961) were the first to do or review the taxonomy of caribou on Banks Island and the caribou of the then supposedly extinct Dolphin & Union Herd. Both were classifying at the subspecific level; therefore, they were obligated to place specimens with clear phenotypic diversity below the subspecies into the subspecies that the specimen's taxonomical characters favored. As a result, both authors placed Banks Island caribou (and northwestern Victoria Island without the benefit of any specimens) in the pearyi subspecies and caribou of the Dolphin & Union Herd, from eastern Victoria Island, in the groenlandicus subspecies.

The important point to note for the conservation and especially the preservation of caribou on Banks Island and northwestern Victoria Island is that both Manning (1960) and Banfield (1961) never identified a single specimen from Banks Island as R. t. pearyi. Manning (1960:49) identified all of them as pearyi>groenlandicus, while Banfield (1961:63-64), using mainly the series of specimens from Manning (1960), identified them mostly as pearyi>groenlandicus but also identified a few new ones from southern Banks Island as groenlandicus>pearyi (possibly, from caribou of the Dolphin & Union Herd).

Manning (1960) identified all Dolphin & Union Herd specimens as groenlandicus>pearyi. Banfield (1961) relied on Manning's (1960) findings for the Dolphin & Union herd and discussed them under R. t. groenlandicus as 1 of 5 demes. Banfield (1961:54) noted "Those [5] demes showed no significant differences or clines but rather exhibited a mosaic type of variation. The Dolphin and Union Straits deme was small and pale, indicating some pearyi influence (Manning, 1960)." That is, "small and pale" relative to the other 4 demes of groenlandicus but relatively large and darker compared to pearyi.

Therefore, recognition of those groups as distinct from pearyi on the QEI and keeping them separate is an important consideration in the conservation and preservation of caribou on the Canadian Arctic Islands. Of course, this consideration extends further to include all of the other groups of caribou on the Arctic Islands and the island-type caribou found on Boothia Peninsula (Banfield, 1961; Manning & Macpherson, 1961; Thomas & Everson, 1982; K. Zittlau, pers. comm. 2002). All of these caribou groups can be identified as making a contribution to the biodiversity of caribou in Canada. In the case of these caribou, we believe, a solution relying on genetics and morphology and heavily on ecology should form the best basis for a conservation unit. The most obvious basic unit of conservation for an animal should be a naturally occurring one. Currently, we believe that the most basic and workable caribou conservation unit is the geographic population. We realize that much ecological diversity can and often does exist, however, within a geographic population. This diversity is initiated and most likely retained within an intermingling web of 'subunits': probably akin to 'subpopulations' or in the case of caribou on the Canadian Arctic Islands-'island populations'-with or without reproductive isolation. There could be functional ecological diversity that could greatly enhance the probability of short-term survival of certain groups of individuals and thus long-term persistence of their population.

However, separation of Peary caribou from mainland barren-ground caribou (R. t. groenlandicus or R. t. granti) at the subspecific level is not supported by mitochondrial DNA differences (Eger & Gunn, 1999). That is, Peary caribou do not form a monophyletic group - they have a polyphyletic origin. Therefore, establishing conservation units for caribou on the Canadian Arctic Islands would benefit most from a broad approach as referred to above where genetic classification forms only part of the basis for the conservation unit. The necessity for the use of genetic and phenotypic data along with ecological and behavioral separators will require collaboration and consensus between molecular and ecologically oriented biologists (cf. Crandall et al., 2000).

The classical taxonomy was based mostly on skull measurements and pelage differences (Manning, 1960; Banfield, 1961) and separated caribou on the QEI from caribou on Banks Island, and on northwestern Victoria Island by association, as R. t. pearyi vs. R. t. pearyi x groenlandicus. Microsatellite DNA analysis so far yields a clinal separation for caribou on the QEI from those caribou on the southern Arctic Islands, including Banks Island and northwestern Victoria Island (Zittlau et al., 1999; K. Zittlau & C. Strobeck, pers. comm., 2001).

The DNA findings reveal the diversity of caribou and although caribou on Banks Island are related to the caribou on the QEI, based both on the past classical taxonomy and recent DNA findings, the caribou should not be considered interchangeable between regions. This consideration should be applied to all of the geographic populations of caribou found across the southern Arctic Islands and on Boothia Peninsula. The complexity of the matter appears to be amplified in part by microsatellite DNA findings that indicate that Banks Island caribou are more closely related to an island-type caribou found on Boothia Peninsula than to Peary caribou on the QEI (K. Zittlau, pers comm. 2002). This point is then a major consideration in selecting donor animals in any translocations to boost or rebuild depleted populations. The Peary caribou's morphological and physiological adaptations and its behavioral repertoire mean that Peary caribou have greater fitness for the High Arctic and are distinct from all other forms of caribou.

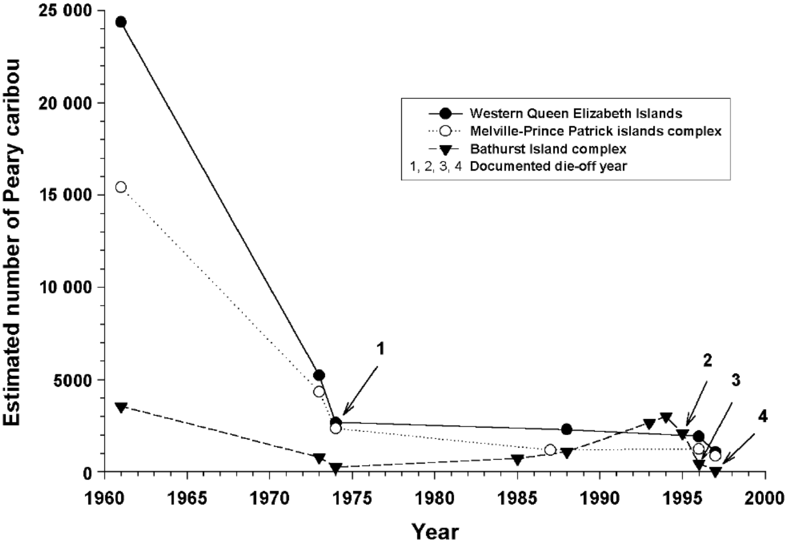

Fig. 2. Trends in the numbers of Peary caribou over 36 years from 1961 to 1997 at three spatial scales: Western Queen Elizabeth Islands; Melville-Prince Patrick islands complex; and Bathurst island complex; Canadian High Arctic.

Fluctuations in Numbers

Peary caribou on the QEI (ca. 411 000 km^2) were estimated at 25 845 when first aerially surveyed in summer 1961 (Tener, 1963: ca. 20% were calves). Most Peary caribou were on the WQEI (ca. 97 000 km^2), where 94% of the estimated caribou occurred on only 24% of the total island-landmass of the QEI (Fig. 2). Since 1961, there has been no comparable aerial survey of the EQEI to that conducted by Tener (1963). However, limited aerial surveys of some sections of Ellesmere Island all revealed few caribou and low mean densities (Riewe, 1973; Case & Ellsworth, 1991; Gauthier, 1996; R. Wissink, pers. comm., 2000).

By the mid 1970s, the overall number of Peary caribou on the WQEI had decreased to about 29% of the 1961 estimate (Fig. 2: Miller et al., 1977a). The following winter and spring (1973-74), the Peary caribou population declined 49% throughout the WQEI. The estimated number was reduced to about 12% of the 1961 estimate, with no calves observed by us in summer 1974. Several aerial surveys from 1985 to 1987 placed the estimated number of Peary caribou on the WQEI at only about 9% of the 1961 estimate (Miller, 1990b). The number of Peary caribou on the QEI as a whole was judged to be 3300-3600 or only about 13-14% of the 1961 estimate. From 1988 to 1996 only Bathurst Island and its neighboring islands were resurveyed and by 1994, the number of Peary caribou there recovered to about 85% of the 1961 estimate. The aerial survey in 1997 revealed that the number of Peary caribou on the WQEI then declined between 1994 and 1997 and in summer 1997 was at an all-time known low of only about 4% of the 1961 estimate (Miller, 1998; Gunn & Dragon, 2002). Currently, there is no reason to believe that more than several hundred to a thousand or so caribou exist on the EQEI. Therefore, at present, an estimate of 2000-2400 Peary caribou (only 8-9% of the 1961 estimate) for the entire QEI seems to be a reasonable 'best guess' (1100 to 1300, WQEI + 900 to 1100, EQEI).

At these low numbers, utilization of island and inter-island populations of Peary caribou by Inuit living on High Arctic Islands creates another important facet to the conservation of Peary caribou. This concern is particularly applicable to those caribou left in remnant populations such as those within the Bathurst Island complex (Figs. 2, 3). In summer 1997, Gunn & Dragon (2002) estimated 78 ± 25 (95% CL ≅ 29-127) Peary caribou left within the Bathurst Island complex. A caribou population within that 29-127 limits would require between 35 and 23 years at an average annual high rate of increase of 13% to reach about 2000 caribou to annually support a harvest of 100 1+ yr-old caribou or more animals (Fig. 3: 13% derived from the estimated finite rate of increase of $\lambda = 1.13$ from 1974 to 1994 for the Bathurst Island complex). Therefore, maintaining the maximum possible number of caribou in a population after a major die-off is all-important in minimizing the time required for that population to recover to a usable size.

Major Die-Offs

We know of four major die-offs and associated subsequent major to near total calf crop losses plus one

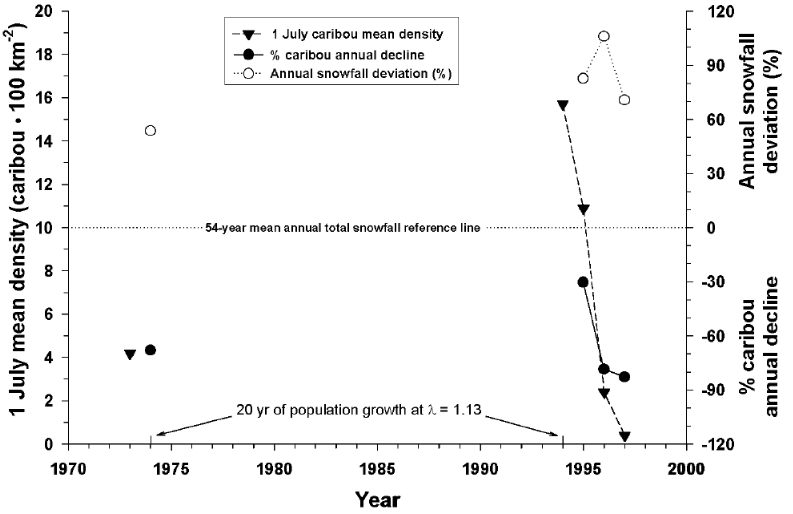

Fig. 3. Four major annual die-offs of Peary caribou, showing low mean density of caribou at start of die-off period, relative severity of total snowfall (1 Sep-21 Jun) expressed as the deviation from the 55-yr mean (in caribou-years, 1 Jul-30 Jun, 1947/48-2001/02) and the resultant percentage decline in the population during each die-off, Bathurst Island complex, western Queen Elizabeth Islands, Canadian High Arctic.

additional major calf crop reduction on, at least, the WQEI: 1973/74, 1989/90, 1994/95, 1995/96, and 1996/97 (Figs. 2-4: Parker et al., 1975; Miller et al., 1977a; Miller, 1992; 1998; Gunn & Dragon, 2002). All 5 of those winters and springs were characterized by significantly greater ($P<0.005$) than average total snowfall between 1 Sep-21 Jun of each year and ranked at the top of 55 caribou-years (1 Jul-30 Jun) for which weather records exist at Resolute Airport, Cornwallis Island (Fig. 4: Miller, 1998-1st, 1995/96; 2nd, 1994/95; 3rd, 1996/97; 4th, 1989/90; and 5th, 1973/74). It is more the extent and characteristics of the snow cover than snow depth per se which result from heavy snowfall and high winds that cause widespread prolonged and extreme relative unavailability of forage. This condition is compounded when associated with extensive icing that will ‘lock in’ the forage even further and prevent the animals from obtaining an adequate supply of food. However, so far, there has been a direct correlation between total snowfall and die-offs, when significantly heavier snowfall occurs both in early winter and overall throughout the 1 Sep-21 Jun period of that year (Fig. 4). Therefore, total snowfall is the best indicator that we have to date of the potential for an extremely severe ‘weather-year’ causing die-offs and calf crop failures. The timing, duration, types, and amounts of icing compound the impact of deep snow and tends to cloud the relative importance of the role of deep snow vs. icing in these drastic die-off years. Deep snow alone may severely stress Peary caribou and impact on their subsequent survival and reproduction. It is possible though that extensive and prolonged icing in association with deep snow is necessary or more likely to cause the major die-offs of Peary caribou (and muskoxen) on the QEI. For example, it is likely that relatively few 1+ yr-old caribou died during the deep snow winter of 1989/90 (Fig. 4) because the snow cover remained powdery in many areas throughout the winter until spring (Miller, 1992). Late winter inspection revealed only relatively small areas of hard packed snow cover and in spring many snow-free areas existed before ground fast ice formed on some remaining snow covered areas (Miller, 1992). Snow and ice conditions were still detrimental enough in winter and spring 1989/90 to cause a 40% reduction in potential calf production and/or early calf survival during June-July 1990. It also seems reasonable to predict that widespread and prolonged icing on, in and under the snow beginning in autumn, persisting through winter and being compounded in spring could create lethal conditions for Peary caribou even when in association with relatively shallow snow cover.

Our understanding of the relationship between weather and Peary caribou ecology is limited but has a basis in both on-site empirical observations and after the fact deductive reasoning. However, we need to amplify our understanding of how the various characteristics of snow or ice and particularly the many possible combinations of snow and ice impact Peary caribou. Advancing our understanding of what creates lethal conditions for Peary caribou (and muskoxen) will be through testing predictions about relationships, although this often poses obvious practical difficulties. However, we suggest that monitoring the Resolute weather records and comments by Inuit hunters could alert us to opportunities to test predictions about the effects of weather. This would demand that the responsible parties monitor the caribou when the weather data indicate a possibly lethal situation has taken place during the past autumn, winter and/or spring. For example, we offered a prediction in the preceding paragraph about the effect of icing and shallow snow cover. In Aug and Sep 2001, based on records from the Resolute Airport weather station, there were 26 days with freezing rain, associated with negative mean daily temperatures from 12 Aug through 30 Sep, and measurable snow that fell on 18 days and represented 37% of the total snowfall between 1 Aug 2001 and 21 Jun 2002. Then, in Apr 2002, Canadian Rangers traveling by snowmachine on Bathurst Island reported extensive icing (D. Stern, pers. comm. 2002). However, the total winter and spring snowfall (1 Sep 2001-21 Jun 2002) was below the lower 95% CL for the 55-yr mean at Resolute Airport. We suggest that this would have been a good opportunity to assess any 1+ yr-old caribou mortality at an extremely low mean density, and/or initial calf production and subsequent early calf survival, as well as caribou movements and distribution relative to the geographic extent of the icing. However, the opportunity was lost because no such effective monitoring program was in place.

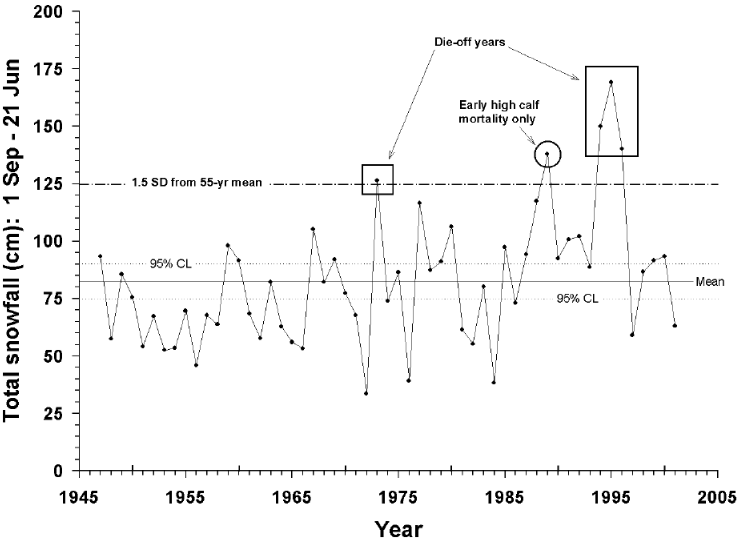

Fig. 4. Long-term (55-yr) trend in total snowfall between 1 Sep and 21 Jun of each caribou-year (1 Jul-30 Jun, 1947/48-2001/02) at Resolute Airport (74°43'N, 94°59'W), Cornwallis Island, Canadian High Arctic: showing highest total snowfalls associated with the four major die-off years (1973/74, 1994/95, 1995/96 and 1996/97) and the one year (1989/90).

The die-offs occurred when the caribou were at low mean overall densities (Fig. 3: Miller et al., 1977a; Miller, 1998; Gunn & Dragon, 2002). For example, within the Bathurst island complex the four annual major die-offs were initiated at mean densities averaging only 0.08 caribou x km^{-2} (Fig. 3). However, the number of Peary caribou within the Bathurst Island complex plummeted 97% in 3 years between 1994 and 1997 while the number of muskoxen fell precipitously by 89% (Miller, 1998; Gunn & Dragon, 2002). Earlier, two-thirds of the caribou population within the Bathurst Island complex was lost in only one winter and spring during the 1973/74 die-off (Fig. 3). Although we have only two points for major annual die-offs within the Melville-Prince Patrick islands complex, we know that a 46% decline began at only 0.07 caribou x km^{-2} in 1973/74. Then in 1996/97, the second documented major decline in the Melville-Prince Patrick islands complex was about 30% and occurred there at a starting mean density of only about 0.02 caribou x km^{-2}. All four Peary caribou die-off years involved similar high annual rates of deaths among muskoxen. Spatial and temporal synchrony of caribou and muskox die-offs supports snow/ice conditions as the causative factor.

Ecology

To obtain food in winter, caribou dig feeding craters in the snow by pawing down to the vegetation below with their broad hoofs. Wind removes the snow from exposed slopes and redeposits it as shallow but hard compacted cover and drifts in more sheltered and relatively well-vegetated sites. Freezing rain in autumn that results in ground-fast ice before snow cover accumulates, ice layering in the snow cover, crusting of the snow, and the formation of ground-fast ice in spring restrict forage availability (e.g., Miller et al., 1982; Miller, 1992, 1998). Forage restrictions lead to extreme, prolonged malnutrition and markedly reduced survival and low reproductive success (Parker et al., 1975; Miller et al., 1977a; Miller, 1998; Gunn & Dragon, 2002).

Forage selection by Peary caribou on the QEI is discussed by Parker & Ross (1976), Parker (1978), Thomas & Edmonds (1983, 1984), Miller (1995b, 1998) and Thomas et al. (1999). Lichens are relatively unimportant to those Peary caribou compared to lichen use by mainland caribou. Lichens on the QEI are relatively poorly represented in the plant biomass and they do not occur in extensive lichen mats as they do on the mainland. The general opinion is that the kinds of lichens eaten by caribou were probably never were well-represented or abundant on the QEI (D. C. Thomas, pers comm. 2002). Based on data from Thomas et al. (1999), Peary caribou forage on lichens year-round, but we conclude from the above data sources that their annual utilization of lichens appears to normally be <10% of the annual diet: or several-fold less than for barren-ground caribou (e.g., Thomas, 1998). The Peary caribou's annual use of lichens varies markedly among years on the QEI but is not known to ever, exceed the ca. 18% proportional representation of lichens in the total plant biomass (calculated from Table 12 of Thomas et al., 1999).

In late spring and early summer the caribou feed on vegetated coastal slopes and river valleys dominated in early summer by purple saxifrage (*Saxifraga oppositifolia*). Then, later in summer they follow the phenology ('greening') as plants flower and leaf-out on the higher elevations and interior sites on upland plains dominated by arctic poppy (*Papaver radicatum*). The last week or 10 days of Jun (spring) in the most favorable years, Jul (summer) and Aug (autumn) are the only periods of relative abundance and availability of high quality vegetation necessary to build up body reserves. Recovery from the nutritional stress experienced during the previous winter and the initiation of new body growth are particularly important for breeding animals to enter into a favorable reproductive state during the subsequent autumn or early winter rut (e.g., Thomas, 1982; Russell et al., 1993). Peary caribou rut in early winter in terms of their environmental setting.

In winter and spring Peary caribou seek out more exposed areas blown free of snow or with shallow snow cover, such as beach ridges, rock outcrops, and steep slopes along stream drainages (e.g., Parker, 1978; Thomas & Edmonds, 1983; Thomas et al., 1999). Depending on the year, Sep-Nov (early winter) or Dec-Feb (mid Winter), is the period of transition from high quality diet to low quality maintenance diet. In favorable years, animals do relatively well, while in unfavorable years, they fail to remain in good condition because of widespread forage unavailability due to snow/ice cover. In extreme years, the widespread relative forage unavailability often leads to subsequent high levels of winter and spring mortality and poor initial calf production during the next calving period or low levels of early survival of calves at or shortly after calving. Mar-May (late winter), and most of Jun (spring), usually are the periods of greatest range restriction and relative forage unavailability due to snow/ice cover at a time when the caribou are at the lowest ebb in their annual cycle of physical condition. Environmental stress in late winter is most critical when preceded by unfavorable snow/ice conditions in early and mid winter: often making the difference between high mortality among 1+ yr-old animals vs. mainly or only negatively influencing the new calf crop.

We have no evidence that the amount or quality of the absolute forage supply, predation, hunting pressure, competition with other grazers, contagious disease or heavy burdens of parasites, human disturbance, or ecosystem contamination made any significant contribution to the documented declines of Peary caribou on the WQEI in the 1970s or in the 1990s. The past and recent effect of predation by wolves on the size of Peary caribou populations cannot be determined. However, the stage could now be set for wolf predation to have serious impacts on at least some remnant caribou populations, unless the wolves die out quickly or abandon the low-density prey areas to seek new hunting grounds. Although disease and parasites are not known to have been important, warmer and wetter weather could lead to greater exposure to such agents. Other potential threats for the Peary caribou may include human disturbances from resource development and the contamination of arctic ecosystems.

Although Peary caribou are island dwellers, they are not necessarily restricted to a single island. Free movements among the QEI are possible, as those islands are locked in a sea of ice for 9 or 10 months of each year. Movement between or among some islands is possible on a year-round basis either by ice or open water crossings. Seasonal and annual range-use patterns of individual Peary caribou reflects the different alternatives available to them within their traditional range.

Distinct from seasonal and annual movements are irregular movements during periods of environmental stress-most commonly forage unavailability due to snow and ice conditions. Rarely, if ever, do we know the subsequent movements or the fate of environmentally-forced dispersing animals. For example, Peary caribou moved from Bathurst Island to Cornwallis and Little Cornwallis islands in the severe winter of 1995/96 (Miller, 1998). Many of them were killed by hunters (estimated at about 85 deaths). Whether the other migrant caribou on Cornwallis and Little Cornwallis islands died or returned to Bathurst Island is unknown but some likely died and some probably returned. There was no evidence that they stayed on Cornwallis Island or on Little Cornwallis Island.

Seasonal movements or annual migrations by

Peary caribou serve to maximize the use of the best ranges that are available to them on one or more islands (e.g., Miller, 1990a). Such repeated movements allow the animals to become familiar with the different sections of the range that they normally use on an annual basis. Many caribou on the QEI and on the southern tier of islands in the Canadian Arctic Archipelago make both intra- and inter-island seasonal migrations and, thus, function as 'inter-island populations' (Miller et al., 1977a, 1977b; Miller and Gunn, 1978, 1980; Miller et al., 1982; Miller, 1990a, 1990b). We know from aerial surveys and aerial searches, VHF radio telemetry, and satellite telemetry location-data that some Peary caribou live year-round on just one island-sometimes, even on small islands, ca. 20 km^2. Some of them make seasonal intra-island movements to different parts of the island, while others of them remain on relatively small sections of a large island throughout the entire year (e.g., Miller & Barry, this proceedings). Other Peary caribou migrate between summer and winter ranges on two or more islands by traveling over sea ice (Miller et al., 1977b). Some even make open water crossings by swimming between nearby islands (Miller, 1995a). Still others have more complex annual range-use patterns involving more than a dozen back and forth movements among five or six adjacent islands, each island only several kilometers from the next (Miller, 2002; F. L. Miller, unpubl. data).

Conservation Implications

The Canadian Government, as part of the international community concerned with global environmental issues, has accepted the maintenance of biodiversity as an ultimate conservation goal (Biodiversity Science Assessment Team, 1994). We believe, this entails conservation of each of the currently recognized geographical populations of caribou for maintenance of their existing biodiversity. Therefore, consideration must also be given to the need to conserve the caribou within each of the various areas on the Arctic Islands because of their probable different contributions to caribou diversity in Canada and the world and the desire of Inuit people to utilize those caribou populations.

The current state of knowledge supports that on the Canadian Arctic Archipelago there are at least four ecotypes of *Rangifer*. This consideration excludes the Baffin Island region and the islands in Foxe Basin and Hudson Bay where supposedly only the Canadian form of the barren-ground caribou (*R. t. groenlandicus*) is found. Those four ecotypes occur as six regional populations: i.e., populations delineated on a geographical basis by their known seasonal and annual distributions and by their known and perceived genetic and taxonomical relationships and termed 'geographic populations.' Although microsatellite DNA sampling which describes a finer scale of genetic variation than mitochondrial DNA is incomplete, the microsatellite DNA sampled for the western regional populations supports these divisions (Zittlau et al., 1999; K. Zittlau & C. Strobeck, pers. comm., 2001, 2002).

Peary caribou, the first ecotype, appear to occur as two regional groups: one on the WQEI, and the other on the EQEI. The second ecotype which is related to but distinct from Peary caribou are the caribou occurring as another regional group on Banks Island and northwestern Victoria Island. The third ecotype is the larger and distinct caribou of the Dolphin & Union Herd which occurs as a regional population on southern and eastern Victoria Island but winters on the adjacent coastal mainland. And the fourth ecotype, which occurs or occurred as at least two phenotypes, is the caribou occurring as a regional group in the Prince of Wales-Somerset-Russell islands-Boothia Peninsula complex. The ecology of this fourth group appears particularly complex because they use several calving areas on different islands and on Boothia Peninsula with intra- and inter-island seasonal migrations and migrations between islands and Boothia Peninsula. The situation is further complicated by barren-ground caribou (*R. t. groenlandicus*) and island-type caribou (taxonomically identified as *R. t. groenlandicus x pearyi*) on adjacent calving areas on northern Boothia Peninsula and some or all of those island-type caribou moving south of Boothia Isthmus to winter on the mainland (Gunn et al., 2000a). The presence of these island-type caribou on Boothia Peninsula has been documented by microsatellite DNA assay (K. Zittlau, pers. comm. 2002). In addition, at least, until the recent die-off of caribou within the Prince of Wales, Somerset and Russell islands complex (Gunn & Dragon, 1998), many of those caribou migrated to winter range on Boothia Peninsula and returned to the islands in late winter or spring (e.g., Miller & Gunn, 1978, 1980; Miller et al., 1982).

All of the caribou populations on both the WQEI and all of those, except the Dolphin & Union Herd, on the southern tier of Canadian Arctic Islands have experienced major reductions in size during the last part of the 20th century. This fact becomes especially important now as most of those remnant caribou populations are hunted with different Inuit settlements depending on them. Reconciling the needs of people and caribou conservation becomes difficult during caribou declines and periods of low numbers. However, using translocations to boost or quick-start caribou recoveries to help hunting opportunities should not be at the expense of diluting or altering the existing diversity of caribou and not, for example, mixing the regional populations through indiscriminate translocations. All translocation efforts should not proceed before the genetics of both the animals in the area being restocked and the donor animals (those used for the restocking) are worked out and found to be acceptably similar and ideally essentially the same. Caribou populations on the Canadian Arctic Archipelago have probably differentiated so fast from each other due to repeated 'bottlenecks' that finding genetically identical animals might be difficult, if not impossible (K. Zittlau, pers comm. 2002).

The unpredictable occurrence of weather extremes on the QEI limits growth of Peary caribou populations. Peary caribou appear to live in a 'non-equilibrium grazing system' as opposed to an 'equilibrium grazing system' (e.g., Caughley & Gunn, 1993; Behnke, 2000). In the non-equilibrium grazing system the number of caribou, regardless of their density, is driven by a sporadic, unpredictable, abiotic variable-the type, amount, and timing of annual precipitation (e.g., Caughley & Gunn, 1993; Behnke, 2000). In the specific case of Peary caribou-snow and ice-their extent, characteristics, and duration on the ground. The nature of the system means that the safe conservation strategy is to try to retain the maximum number of Peary caribou in the system after major and especially multi-year die-offs such as those in 1973-74 and 1994 to 1997. Inuit have already voluntarily limited their hunting in response to the die-offs of the early 1970s (Freeman, 1975; Ferguson, 1987). From 1989 to 1996, harvesting of caribou on Bathurst Island was allowed, but after the 1994-97 die-off, the Resolute Bay Hunters and Trappers Organization decided that there would be no organized community hunts for Bathurst Island caribou. However, individual hunters can still hunt caribou there. Inuit hunters from Grise Fiord halted caribou hunting on most of southern Ellesmere Island for 10 years, 1986-96 (Ferguson, 1987).

Peary caribou are living at the extreme edge of the species' range and wide population swings can be expected. For example, the caribou population within the Bathurst Island complex, south-central QEI, declined from an estimated 3600 to <300 between 1961 and 1974; then, took 20 years to increase to 3000 animals in 1994, then plummeted to less than <100 animals in just 3 years from 1994/95 to 1996/97 (Figs. 2-4: data sources Tener, 1963; Miller et al., 1977a; Miller, 1995b, 1998; Gunn & Dragon, 2002). If the 1994-97 die-off within the Bathurst Island complex or on the entire WQEI is simply, the pattern typical of range where highly variable weather drives fluctuations in numbers, then the conservation action is to work with Inuit hunters to allow caribou numbers time to recover to support sustainable annual harvests.

If, however, the exceptional winters were part of a longer-term trend with an anthropogenic cause, then the conservation context changes. The weather trends in the western and central Arctic are increasingly warmer temperatures and heavier snowfall, which are consistent with predictions for global warming (Maxwell, 1997; summary in Weller, 2000). Warmer and wetter autumns followed by higher frequency of freezing rain events and heavy winter snowfall (especially in early winter) and frequent or advanced thawing and freezing in late winter and spring will likely cause further reductions in Peary caribou numbers. We can expect brief periods of recovery during the more favorable winters and springs. If a trend toward more severe winters and springs or a greater frequency of recently realized severe winters and springs continues, however, then we can expect less pronounced recoveries and more frequent and deeper future declines. Even the possibility on some islands of island-extirpations of Peary caribou cannot be excluded. While there is uncertainty in predicting the outcome of the weather trends and changes in caribou numbers, there is risk to delaying conservation actions until trends are obvious. It is an asymmetry in the risks attached to decisions that is not that uncommon in conservation. If pessimistic forecasts are not borne out, then scientific credibility is reduced even if the actions resulting from the forecasts themselves do not cause any harm to the wildlife in trouble. On the other hand, actions taken earlier before a crisis in low numbers is further advanced-can be instrumental in averting a greater crisis and minimizing recovery time. It was this logic and extension of the precautionary principle that led in 1997, to the suggestion for captive breeding of Peary caribou but in the absence of local community support, the attempt was canceled. This reinforces the point that Peary caribou conservation has to include those people who share the Peary caribou ranges and conservation planning has to be built on local as well as scientific knowledge: a summary of views can be found in a workshop on Peary caribou conservation in Gunn et al. (1998).

Management and recovery of Peary caribou on the QEI and arctic-island caribou on the southern Canadian Arctic Islands and Boothia Peninsula have been reviewed by Gunn et al. (2000b). They (Gunn et al., 2000b:47) point out that "Management of endangered and threatened caribou populations on Canada's Arctic Islands requires implementation of recovery actions despite gaps in our knowledge and uncertainties in diagnoses of declines." No-one has control over the weather, which in its severest form appears to be the single driving force controlling Peary caribou numbers,. It is not feasible on a widespread, let alone range-wide, basis to use emergency or especially ongoing supplemental winter feeding as a tool for Peary caribou conservation (Miller & Reintjes, 1993). Therefore, the first step in a meaningful Peary caribou conservation program is to try to reduce losses from other sources. The obvious first action is to temporarily reduce the number of caribou killed by hunters. To promote this, a guarantee of an alternate source of replacement meat should be made (Gunn et al., 2000b). If the decline continues, the second or parallel step would be wolf control, ideally through non-lethal means and only on islands designated as having a priority for caribou conservation. Justification for taking preemptive actions without detailed knowledge of predation rates is presented in Miller (1998) and Gunn et al. (2000b). Concerned individuals should remember that the ultimate fate of the wolf on the Canadian Arctic Islands is dictated by the long-term success of the combined ungulate prey base-the caribou and the muskox. In turn, if competition with muskoxen causes caribou declines or prevents or seriously impedes recoveries, accelerated harvesting of muskoxen on those islands with a priority for caribou is a feasible option to implement.

The goal of the Canadian Recovery of Nationally Endangered Wildlife Strategy Plan is to prevent extinctions and to maintain and enhance caribou populations. The need for a cooperative approach to Peary caribou conservation is emphasized in national recovery planning. But we collectively also have to be aware that awaiting a more complete understanding of the trends in weather, Peary caribou numbers, and the accuracy of forecasts for global climate change could unnecessarily place the Peary caribou - an 'Endangered Species' - at added risk.

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Range size and seasonal movement for female woodland caribou in the boreal forest of northeastern Ontario

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Abstract: A preliminary examination was conducted of range size and distribution of female woodland caribou (Rangifer tarandus caribou) in northeastern Ontario. Annual and seasonal ranges were calculated using satellite telemetry data collected for 30 female caribou between 1998 and 2001. The mean annual home range size of collared females was 4026 km^2. Seasonal ranges varied in size depending on time of year ($P<0.05$). Calving and summer ranges were significantly smaller than autumn and late winter ranges. Early winter ranges were significantly larger than calving ranges and smaller than late winter ranges. Overall, range sizes of female woodland caribou in northeastern Ontario were larger than those reported for caribou in other Boreal Forest regions across Canada.

Key words: anti-predator behaviour, Rangifer tarandus caribou, utilization distribution, woodland caribou.

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Introduction

Knowledge of spatial behaviour is central to our understanding of the distribution and abundance of populations, as well as, factors limiting populations. Ungulates exhibit a diversity of movement patterns, ranging from short movements within a small home range to long distance migration between seasonal ranges. Analysis of spatial behaviour at the landscape scale commonly includes delineating annual home ranges, seasonal ranges, migratory behaviour, and home range fidelity (White & Garrott, 1990). Factors influencing animal movement include reproduction and other physiological cycles, as well as, predation and habitat structure.

Burt (1943: 351) defined home range as "that area traversed by the individual in its' normal activities of food gathering, mating, and caring for young". Therefore, reproductive status, forage, and habitat requirements all influence home range size. Other factors found to influence range size in large ungulates include population abundance, ambient temperature, biting insects, snow depth, and availability of cover (Edge et al., 1985; Downes et al., 1986; Sweanor & Sandegren, 1989; Kilpatrick et al., 2001). According to Irwin & Peek (1983), social relationships and population density played a secondary role to food availability in the range size of elk in Montana. Predation and human-induced disturbances such as hunting are also known to be influential (Kilpatrick & Lima, 1999). Hastings (1990) indicated the importance of spatial factors in understanding predator prey interactions. Range size and the tendency of an animal to return to the same range during consecutive years (fidelity) may reflect the pattern and scale at which factors limiting survival (e.g., predation, forage, shelter) are influential (Rettie & Messier, 2001; Johnson et al., 2002).

White & Garrott (1990: 121) defined migration as "a regular, round-trip movement of individuals between two or more areas or seasonal ranges." The occurrence of migratory behaviour within a herd may be influenced by seasonal changes in food avail-

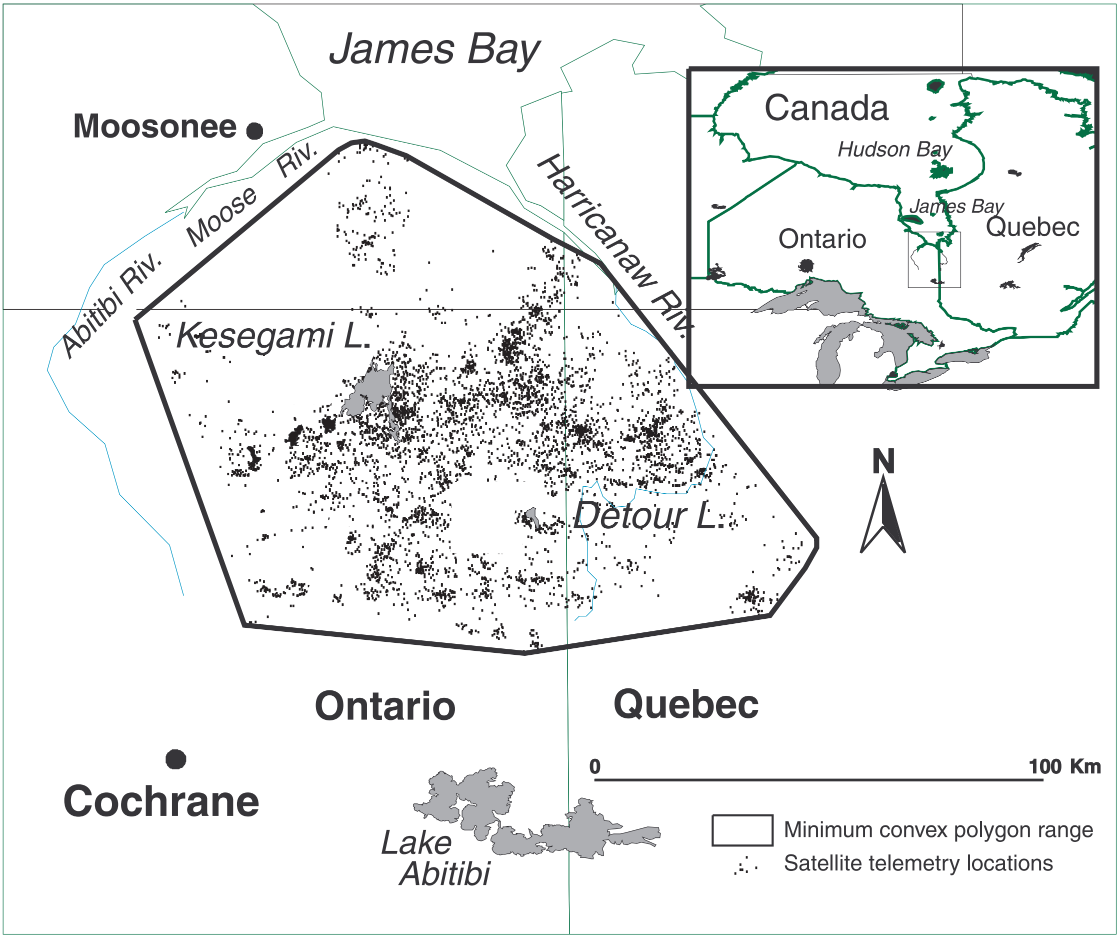

Fig. 1. Collared female woodland caribou distribution south of James Bay, Ontario, Canada, 1998-2001.

ability and the avoidance of predators during calving, rutting, and winter periods (Fryxell et al., 1988; Alcock, 1993). Gasaway et al. (1983) found that predation, severe winters, and harvest by man were additive in their impact on moose and caribou survival in Alaska. Huggard (1993) found that wolf predation on elk increased from 1 animal every 5.4 days with no snow, to 1 every 1.1 days, when snow depth reached 60 cm. Many studies have suggested that wolf predation may limit caribou populations in the boreal forest ecosystem (Edmonds, 1988; Written et al., 1992; Rettie & Messier, 1998).

The forest dwelling woodland caribou (Rangifer tarandus caribou) has declined across North America (Mallory & Hillis, 1998) and is officially listed as "threatened" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2002). As human disturbances, notably forestry activities, have expanded northward, woodland caribou have become extirpated from most of the southern boreal forest of Ontario, and the present southern limit of their known distribution is just north of Cochrane (Fig. 1). In January 1997, Ontario Ministry of Natural Resources (OMNR) personnel observed approximately 200 animals in a 20 km^2 area adjacent to Detour Lake (Fig. 1). This observation revealed a need for information on the habitat requirements and population status of woodland caribou in the region in order to develop effective forest management strategies. The initial step in this study was to obtain basic descriptive information on the ranging behaviour of these animals.

An additional issue was whether management practices utilized elsewhere in Ontario were relevant for woodland caribou in northeastern Ontario. This would partly depend on regional differences in forest communities and differences in spatial behaviour and home range distributions. Woodland caribou inhabiting boreal forest throughout the year are relatively sedentary and have a high degree of overlap in ranges between successive seasons (Darby &

Pruitt, 1984; Mallory & Hillis, 1998; Rettie & Messier, 2001).

The primary objectives of this study were to examine home range size and seasonal distribution of female woodland caribou in the boreal forest of northeastern Ontario. We hypothesized that: (1) seasonal ranges of female woodland caribou in northeastern Ontario were of similar size throughout the year and (2) female woodland caribou migrate between seasonal ranges. Annual and seasonal home ranges are compared to ranges reported elsewhere in Canada. Seasonal differences in range size and distribution are discussed in relation to theories on reproduction and predator avoidance.

Methods

Study area

The study area of approximately 65 000 km^2 was bounded by James Bay in the north, Lake Abitibi in the south, the Abitibi River to the west, and the Harricanaw River in the east (Fig. 1). Climate in the region is modified continental with compression effects from the cold influence of Hudson Bay and the warmer Great Lakes to the south (Carleton & Maycock, 1978; Legasy et al., 1995). Mean daily temperatures for January and July are -18.2 °C and 16.7 °C, respectively. Total annual precipitation averages 920.1 mm, with a total annual snowfall averaging 316.2 cm (Anon., 1998).

The study site included the southern section of the James Bay lowlands, which is characterized by paleozoic rocks covered by glacial and marine quaternary deposits (Carleton & Maycock, 1978). Little relief occurs in the region, except in areas associated with the Moose River drainage. The area includes the clay belt running across Ontario and Quebec, characterized by a relatively flat plain of lacustrine clay and silt, with high to moderate depths of lime clay more than 9 m deep (Taylor et al., 2000). Peat soils are also common and few lakes exist within the region. The larger Kesagami Lake (171 km^2) occurs near the center of the study site and many smaller kettle lakes were created by ice shed from the receding glacier (Taylor et al., 2000). Rivers and streams in the area are typically clay banked and drain northward into James Bay.

Forest communities in the region are predominantly black spruce stands and treed muskeg. Important tree species include black spruce, balsam fir (Abies balsamea), white spruce (P. glauca), jack pine, and white birch (Betula papyrifera). Common ground and shrub layer species include black spruce, balsam fir, beaked hazel (Corylus cornuta), speckled alder (Alnus incana), labrador tea (Ledum groenlandicum), leatherleaf (Chamaedaphne calyculata), bog laural (Kalmia polifolia), sheep laural (Kalmia angustifolia), creeping snowberry (Gaultheria hispidula), small cranberry (Vaccinium oxycoccos), Sphagnum spp., Schreber's moss (Pleurozium schreberi), reindeer lichen (Cladina rangiferina), coral lichen (Cladina stellaris), cloudberry (Rubus chamaemorus), and blueberry (Vaccinium spp.). Fens with open ponds or dense shrub cover and tamarack (Larix laricina) tree cover occurred most extensively in the north end of the region near James Bay. Mixed deciduous stands were most frequent in the southern end of the area near Lake Abitibi. Common species included trembling aspen (Populus tremuloides), balsam fir, mountain maple (Acer spicatum), speckled alder, honeysuckle (Lonicera spp., Diervilla lonicera), wild sarsaparilla (Aralia nudicaulis), violet (Viola spp.), and Canada mayflower (Maianthemum canadense).

Capture and telemetry data

Female caribou were captured and immobilized by herding animals to a net using a helicopter and ground crew. Thirty animals were captured in March 1998 and March 1999 and outfitted with radio-collars equipped with both satellite and very high frequency (VHF) transmitters (model ST-14, Telonics Inc.).

Animal locations were obtained from satellite radio-collar transmitters every 2 days (13 Mar-6 Jul and 15 Oct-15 Jan) or every 7 days (16 Jan-13 Mar and 7 Jul-15 Oct). Locations of inferior quality were removed from the data set based on signal quality class and the number of signals received during the satellite overpass. A geographic information system (ArcInfo v. 3.5, ArcView v. 3.2, ESRI Inc.) was used to project location coordinates from decimal degrees to Universal Transverse Mercator (UTM) units and to calculate home range estimates (Hooge & Eichenlaub, 1997).

Range size and distribution

Five seasonal periods were defined based on calving dates and the movement patterns exhibited by individual animals: calving (May–Jun); summer (Jul–mid-Sep); autumn (mid-Sep–Nov); early winter (Dec–mid-Feb); and late winter (mid-Feb–Apr). Annual home ranges were calculated for female caribou employing the minimum convex polygon method (Mohr, 1947). The minimum convex polygon method was chosen for ease of comparison with other studies. The fixed kernel method (Worton, 1989) was used to calculate seasonal home ranges. According to Seaman & Powell (1996), the fixed kernel estimate is less prone to overestimate the area of utilization and has lower error associated with the

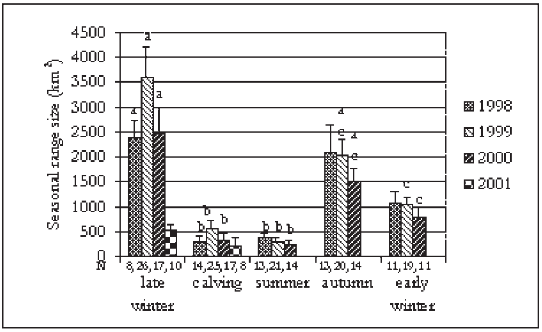

Fig. 2. Seasonal range sizes (km²) of female woodland caribou in northeastern Ontario, Canada between 1998 and 2001. Bars indicate mean value plus 1 SE. Within each year, categories with different letters above the error bar are significantly different (ANOVA of log transformed data with post-hoc Tamhane confidence intervals, α = 0.05). No statistical comparisons were made between years.

surface estimate. Annual home ranges (95% minimum convex polygon method) were calculated for animals for which we had locations from all seasons. Seasonal home ranges were calculated using the fixed kernel method and a 95% probability utilization distribution of seasonal data for each animal (Worton, 1989). Seasonal core activity areas were calculated with the fixed kernel method using a 30% probability distribution. A one -way analysis of variance (ANOVA) with post-hoc Tamhane confidence intervals was used to test for differences among seasonal home range sizes. Log transformations were employed to correct for heteroscedasticity in range sizes. Tests were considered to be significantly different at an α of 0.05. Statistical analyses were done with SPSS for Windows version 9 (SPSS Inc., 1998).

For this study, migration was defined as the seasonal movement of animals to separate summer and winter ranges. Migration was assessed by examining the distribution of seasonal ranges of each animal. The presence or absence of overlap in core activity areas for early winter and summer ranges was noted.

Results

Between late winter 1998 and early winter 2001, 5728 telemetry locations were obtained for 30 female caribou fitted with satellite collars and collared animals were monitored for periods ranging from 81 to 1162 days. Twenty-five percent of the collared animals were monitored for more than 828 days, fifty percent were monitored for more than 605 days, while seventy-five percent were monitored for more than 363 days. Of eleven collared animals that died during the study period, seven were attributed to predation.

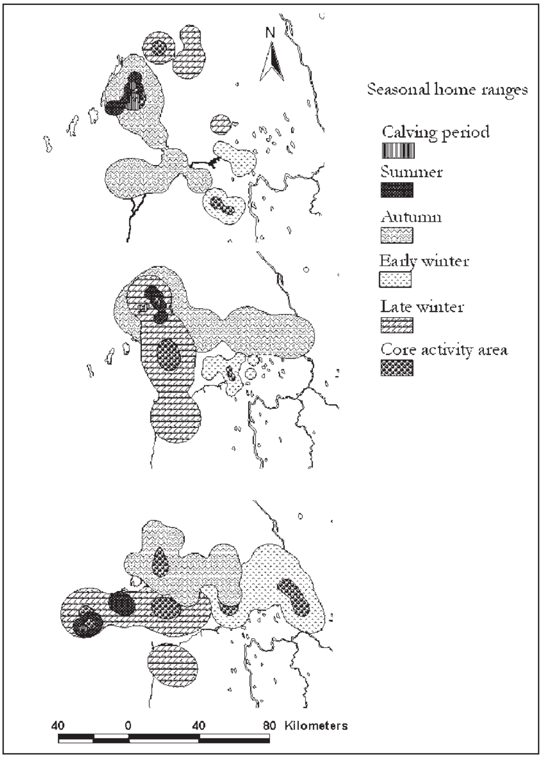

Fig. 3. Seasonal ranges of three adult female woodland caribou in northeastern Ontario, Canada. Fixed kernel estimates are shown for 95% seasonal home ranges and 30% core activity areas.

During 1998, the mean annual home range size of adult females measured 3664 km² (n=13, SE±537 km²) and individual home range size varied between 1135 km² and 8798 km² (Table 1). In 1999, the mean annual home range size was 4790 km² (n=20, SE±451 km²) and individual home ranges varied between 1199 km² and 9582 km². In 2000, the mean annual home range size was 3212 km² (n=13, SE±453 km²) and individual home ranges varied between 593 km² and 5985 km². Pooling the data for 1998 to 2000 produced a mean annual home range of 4026 km² (n=46, SE±292 km²).

Significant differences were found in the size of seasonal ranges for most years (1998: F=6.29, n=50, P=0.001; 1999: F=24.79, n=110, P<0.001; 2000: F=20.83, n=72, P<0.001). In 2001, data were only obtained for the late winter and calving period. No seasonal difference in range size was found for this year (2001: F=2.93, n=17, P=0.106). In general, late winter and autumn ranges were significantly larger than calving and summer ranges (Fig. 2).

Table 1. Preliminary estimates of annual home range size (km^2) and seasonal movement (km) of female woodland caribou in northeastern Ontario, Canada. Ranges were calculated using the minimum convex polygon method for comparison with other studies. Each year was considered to commence in late winter of the year stated and continue to early winter of the following year.

Year	n	Min	Max	Mean	Std. Error	Distance between summer and winter ranges (km)
1998	13	1088	7266	3664	537	53
1999	20	1199	9582	4790	451	34
2000	13	593	5985	3212	453	38

Early winter ranges were significantly larger than calving and summer ranges, but smaller than late winter ranges.

Preliminary evidence suggests that female caribou migrate between summer and winter ranges. Observations of seasonal range distributions indicated that individuals underwent large-scale, distinct movements between early winter and calving ranges. No overlap was observed in the core activity areas for early winter and summer ranges. Fig. 3 illustrates a typical seasonal range distribution of a collared woodland caribou female in northeastern Ontario. Movement was greater during autumn and late winter, as reflected in range sizes (Fig. 3), when animals were traveling to and from summer and early winter ranges. The mean distance between the arithmetic centers of summer and late winter ranges was 53.4 (n=10, SE±13.1 km) in 1998, 33.7 (n=17, SE±5.3 km) in 1999, and 37.9 (n=10, SE±8.9 km) in 2000.

Discussion

Annual home ranges of female woodland caribou in northeastern Ontario were larger than those reported in the literature for other parts of Canada. Mean range sizes of caribou in central Saskatchewan ranged between 208 and 1240 km^2 (Rettie & Messier, 2001). In northwestern Ontario, median annual home range size was 322 km^2 (Racey et al., 1997). Centre to center distance between winter and summer ranges were similar to observations in northwestern Ontario, west central Manitoba, and Alberta (Edmonds, 1988; Racey et al., 1997; Metsaranta, 2002). Seasonal ranges, particularly during the autumn and late winter, were also considerably larger than those reported elsewhere (Darby & Pruitt, 1984; Edmonds, 1988; Rettie & Messier, 2001). However, it is possible that the larger seasonal ranges reported here resulted from using a kernel estimator, which will overestimate range size when sample size is small (Seaman & Powell, 1996). This was expected to be a problem for the shorter calving and summer seasons. Even so, the significant differences found in seasonal range sizes suggest that the kernel estimator was adequate in delineating utilization distributions, in spite of the limitations of small sample size.

The lack of difference in the size of late winter and calving ranges in 2001 suggests year may be a factor influencing range size. Further work will require identifying the importance of annual changes in environmental factors, such as snow, which may influence animal movement patterns.

Similar to other studies of woodland caribou, migration between communal winter ranges by aggregations of animals was not observed (Darby & Pruitt Jr.,1984; Edmonds, 1988; Rettie & Messier, 2001). However, females exhibited large-scale seasonal movement, evident from the large autumn and winter ranges. Examination of autumn locations of collared animals suggested movement in November, following the rut, accounted for most of the range size. Differences in range size among these animals and caribou in other regions suggest that limiting factors may differ in affecting local range use and movement. Rettie & Messier (1998) suggested that predation was the primary limiting factor affecting woodland caribou behaviour in Saskatchewan.

According to Lima & Dill (1990), predation risk is one of the most important factors influencing animal decision-making. This would include choices as to the timing and location of feeding, mating, and caring for young. Fryxell et al. (1988) discussed the importance of seasonal migration in ungulates, as a predator avoidance strategy. Predator avoidance may affect the occurrence and timing of migration, the home range size and location, as well as, habitat selection. Even so, many biotic and abiotic factors interact to influence an animals' spatial behaviour. The relative importance and interaction of variables such as land-cover type, energetic costs of movement, and predation risk may vary in relation to one another and the spatial scale at which animal movements are examined (Brashares & Arcese, 2002; Johnson et al., 2002).

Woodland caribou are known to select isolated areas during calving as an anti-predator strategy

(Bergerud et al., 1984; Bergerud, 1985; Cumming & Beange, 1987) and the relatively large autumn and late winter ranges in our study may reflect movement to areas with fewer predators or greater escape habitat. The use of small calving and summer ranges, compared to other ranges may reflect the relative immobility of calves at this time and the need for adequate cover. Although food availability and quality may also influence home range size, Barten et al. (2001) found that females with young used sites with fewer predators at the cost of less abundant forage. Wilson (2000) found that the abundance of lichens was one of the most important indicators of late winter habitat use by woodland caribou in northeastern Ontario. However, no information is currently available as to summer feeding habits or predator abundance in the region. Future work in this study will require assessing the landscape and habitat characteristics of calving and other seasonal ranges. Seasonal differences in mortality of collared animals will also be examined in relation to spatial behaviour and habitat selection.

The large-scale movement of caribou in northeastern Ontario to relatively small calving and summer ranges suggests predator avoidance may operate at different spatial and temporal scales, depending on the time of year. Ferguson et al. (1998) examined fractal measures of female caribou movements and suggested that female caribou with calves reduce movement rates and pathway complexity to minimize predation. Seasonal migration between ranges would operate at a relatively course spatial scale and involve greater movement rates along linear pathways.

Our findings demonstrate that home ranges of female woodland caribou varied in size depending upon season. Calving and summer ranges were significantly smaller than autumn and late winter ranges. The large variation in seasonal ranges of woodland caribou are indicative of differences in movement rates at different times of year. Further analyses of woodland caribou movement patterns, reproduction, habitat features, and seasonal mortality will be conducted to determine the effect of these factors on annual and seasonal range size.

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Mapping caribou habitat north of the 51st parallel in Québec using Landsat imagery

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Abstract: A methodology using Landsat Thematic Mapper (TM) images and vegetation typology, based on lichens as the principal component of caribou winter diet, was developed to map caribou habitat over a large and diversified area of Northern Québec. This approach includes field validation by aerial surveys (helicopter), classification of vegetation types, image enhancement, visual interpretation and computer assisted mapping. Measurements from more than 1500 field sites collected over six field campaigns from 1989 to 1996 represented the data analysed in this study. As the study progressed, 14 vegetation classes were defined and retained for analyses. Vegetation classes denoting important caribou habitat included six classes of upland lichen communities (Lichen, Lichen-Shrub, Shrub-Lichen, Lichen-Graminoid-Shrub, Lichen-Woodland, Lichen-Shrub-Woodland). Two classes (Burnt-over area, Regenerating burnt-over area) are related to forest fire, and as they develop towards lichen communities, will become important for caribou. The last six classes are retained to depict remaining vegetation cover types. A total of 37 Landsat TM scenes were geocoded and enhanced using two methods: the Taylor method and the false colour composite method (bands combination and stretching). Visual interpretation was chosen as the most efficient and reliable method to map vegetation types related to caribou habitat. The 43 maps produced at the scale of 1:250 000 and the synthesis map (1:2 000 000) provide a regional perspective of caribou habitat over 1200 000 km^2 covering the entire range of the George river herd. The numerical nature of the data allows rapid spatial analysis and map updating.

Key words: forest fire, lichen, northern Québec, *Rangifer tarandus*, remote sensing, vegetation, visual interpretation.

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Introduction

From estimates in the order of 50 000 animals in the 1950s, the total number of caribou (*Rangifer tarandus*) in Québec/Labrador possibly approached 1 000 000 animals in the mid 90s. In the past two decades the sizes and dynamics of the Québec/Labrador caribou herds have attracted attention on several fronts including: population management, native and recreational harvest, low flying jet aircraft, hydro-electric developments, airport safety and finally a concern for habitat deterioration caused by the animals themselves. In order to address some of these management issues, a baseline set of mapped information was needed to serve as a unifying tool for the various interests in the area. Satellite imagery was chosen as a time-saving and cost-effective means for synoptic habitat mapping for very large areas. Habitat mapping has been derived from optical satellite imagery mostly in the 80s and early 90s. The inherent assumption is that wildlife habitat is related to vegetation cover and ecological characteristics visible on satellite images.

In the early 1980s, several studies evaluated the potential of Landsat MSS imagery in wildlife habitat mapping for birds and mammals (Epp, 1985). Habitats were mapped for white-tailed deer (*Odocoileus virginianus*) (Dixon et al., 1982), moose (*Alces alces*) (Laperrière et al., 1980; Dixon et al.; 1984; Bowles, 1985) and caribou (Thompson & Klassen, 1979; Polson & Campbell, 1987). Habitat

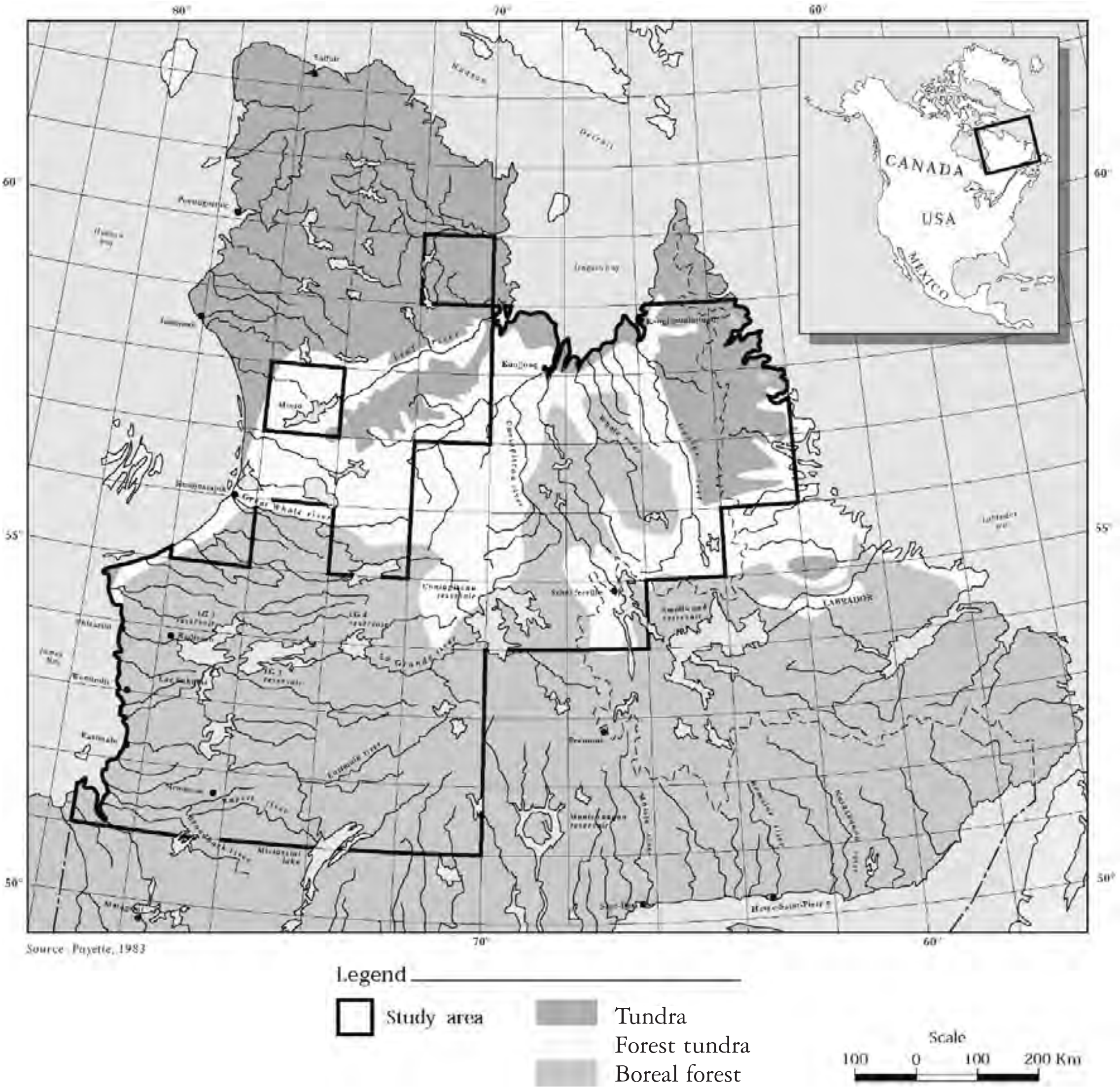

Fig. 1. Study area in northern Québec, Canada.

potential for wildlife in the Boreal Forest was also assessed by mapping vegetation types using MSS data (Grondin et al., 1983; Henderson, 1984; Talbot & Markom, 1986). The coarse resolution (80 m x 80 m) and the limited number of spectral bands (four visible and near infrared bands) of the MSS sensor limit its applications to general purposes: to provide a regional view, to delineate broad vegetation patterns or to be used as a first stratificator for field studies. In those studies, confusion between classes was frequent and the sensor was not adapted for systems with high vegetation heterogeneity. Visual interpretation seems to allow a more precise recognition of vegetation types (Grondin et al., 1983).

The increased spatial resolution (30 m x 30 m) of the Landsat TM sensor, in operation in the mid 80s, combined with additional spectral information (six visible and infrared bands) offered new possibilities in thematic mapping and map scale precision. Numerous studies, using Thematic Mapper data to map wildlife habitat in large remote areas, have been reported for caribou in Norway (Tømmervik & Lauknes, 1987), for moose in Ontario and Newfoundland (Oosenbrug et al., 1988; Ellis et al., 1990), for white-tailed deer in Michigan and southern Québec (Sirois & Bonn, 1984; Ormsby & Lunetta, 1987), for wood bison (*Bison bison athabascae*) and muskox (*Ovibos moschatus*) in the Northwest Territories (Matthews, 1991; Ferguson, 1991) and waterfowl in western Canada and the United States

(Jacobson, 1991). The extent of mapped areas in these studies varies from 200 to 10 000 km², with an average of 3300 km². The waterfowl habitat inventory stands apart with its 900 000 km² in the prairie region (Jacobson, 1991). In these studies, the number of vegetation or habitat classes always varies between 7 to 15.

The objectives of the study were threefold: 1) to develop an operational methodology to map caribou habitat north of the 51st parallel in Québec using Landsat TM imagery, 2) to develop a simple classification of vegetation types, accounting for the wide biogeographic variability, while linking it to lichens and 3) to produce digital maps of caribou winter habitat. A fundamental underlying principle was that these maps would be easy to update over time with a minimal commitment of resources. Final maps sought were to serve as a basic management tool to assist the decision-making process of different interests groups in northern Québec in relation to northern development and caribou population management.

In a project of this scope, many constraints challenge the cartographer. The remoteness of northern Québec, along with the vast areas to survey (over 1 200 000 km² north of the 51st parallel) were major difficulties. The long distance movements of herds from calving to wintering grounds covered a wide biogeographical variation (three biomes) difficult to classify in a reasonable number of vegetation classes. The predominance of terrestrial lichens in the caribou winter diet (Gauthier et al., 1989; Crête et al., 1990), of graminoids (mostly Cyperaceae) in spring, and of dwarf birch leaves (Betula glandulosa) and other shrubs in summer (Crête & Doucet, 1998) had to be integrated in the definition of vegetation classes because of the the critical importance of the calving grounds. Moreover, disturbance by forest fires that affects lichen regeneration, and lichens abundance which can influence caribou winter distribution (Couturier & St-Martin, 1990) add a temporal dimension to mapping. Finally, the method had to deal with mosaics of habitat types, which were difficult to map without multiplying the number of vegetation classes.

Study area and data sets

Study area

The study aimed to cover the entire annual range of the George river caribou herd from wintering habitats in the James Bay region northeastwards to the calving grounds of the George river Plateau covering more than one million km². The study area also overlaps with the wintering range of the Leaf river caribou herd. Extending from 51st to 60th parallels between James Bay and the Labrador Sea, the actual mapped area covers 536 000 km² and exhibits a wide range of biophysical characteristics.

The study area extends over three biomes (Payette, 1983; Fig. 1). The Boreal Forest covers about 61% of the mapped area, the Forest Tundra 26%, and the Shrub Tundra 13%. Black spruce (Picea mariana (Mill.) BSP.) is by far the dominant tree-species throughout the area. Tree cover is continuous in the Boreal Forest (except in peatlands) and is decreasing while lichens cover increases progressing north in the forest tundra, where lichen-heath-dwarf birch (Betula glandulosa Michx.) communities cover extensive areas. In the true tundra biome, the communities without trees are dominated by arctic floristic elements.

The long-term repeated influence of natural fires, in conjunction with climate, is responsible for this vegetation zonation (Payette et al., 1989). Forest fires remain the most important disturbance controlling vegetation diversity and lichens composition (Morneau & Payette, 1989; Arseneault et al., 1997). The natural fire rotation period dictates the spread of lichens regeneration, community composition, biomass and spatial extension (Morneau & Payette, 1989). The fire rotation period is estimated at 100 years in the Boreal Forest, 180 years in the southern Forest Tundra and about 1460 years in the northern Forest Tundra (Payette et al., 1989).

Satellite imagery data

To cover the study area, 37 Landsat TM scenes were needed, ranging from 1985 to 1994 to produce a single mosaic. We tried to use images from the latter part of the growing season because the spectral discrimination of vegetation, at this time of the year, is at its best. Among the six visible and infrared bands of the TM sensor (TM1 blue band, TM2 green band, TM3 red band, TM4 near infrared band, TM5 and TM7 middle infrared bands), only three bands (TM3, TM4 and TM5) were selected because they enable to distinguish and discriminate several vegetation types.

Topographic map data

Forty-three numerical topographic maps at the scale of 1:250 000 (National Topographic System of Canada) were used as base map. Topographic map at the scale of 1:50 000 (paper copy) were used for the geometric correction and as a guide for wetland delimitation. Finally, to produce a synthesis vegetation map for the entire study area, we used a numerical base map at the scale of 1:2 000 000.

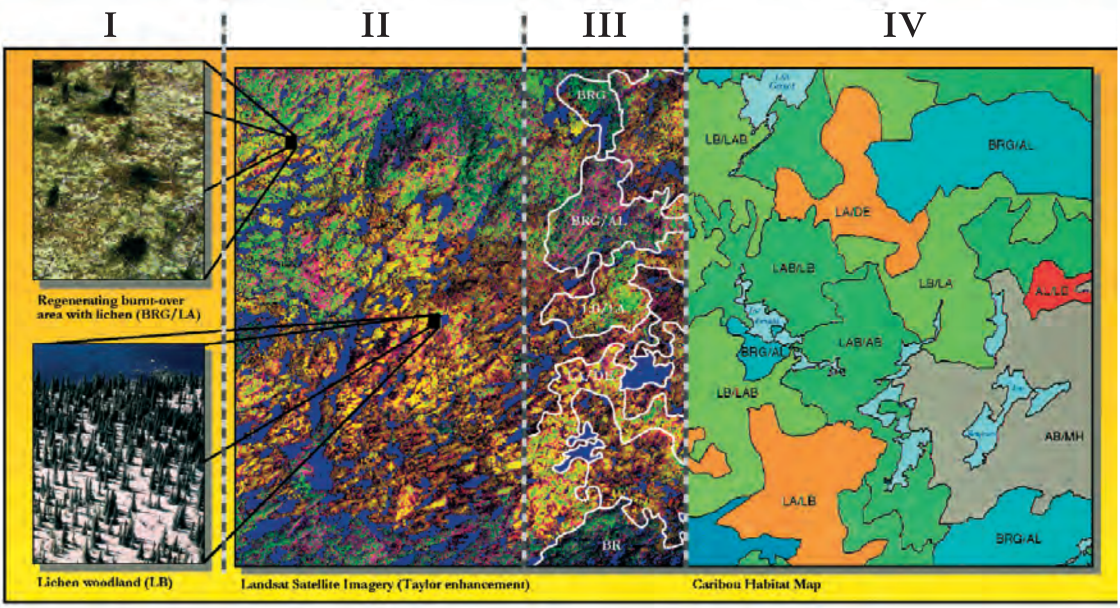

Fig. 2. Caribou habitat mapping method: I) Field survey of pre-selected control points; II) Landsat image with a Taylor enhancement to highlight lichens; III) Visual interpretation, delimitation of polygons and assignment of an attribute; IV) Map edition.

Method

The overall method of digital mapping including field survey, visual interpretation of the geocoded and enhanced images, polygons delimitation, assignment of a label and production of a thematic map, is illustrated in Fig. 2.

Field surveys

Reference data were gathered during summer and autumn. The objectives of the field surveys were to 1) analyze the colours and texture represented on the preliminary image enhancement 2) refine the image enhancement 3) understand the landscape from the visual interpretation 4) obtain data on specific classes, and 5) describe vegetation classes.

The field surveys were conducted by helicopter to verify predetermined control points located on Landsat subscene photographic prints at the scale of 1:100 000. Selection and number of control points enabled to cover the variability of each colour on each image, and the patterns of colours or landscape types. Ground control points were also sampled to have a more precise description or a better understanding of the vegetation cover, in particular lichen abundance and type. To obtain precise geographic coordinates, a Global Positioning System on board the helicopter was used during field survey in 1994 and afterwards. For each control point, panoramic (oblique) and vertical colour slides were taken for visual reference during the interpretation process.

Digital image processing

Before enhancement, each satellite image was geometrically corrected and geocoded to the Universal Transverse Mercator cartographic projection system with a 25 meters re-sampling spatial resolution. The geocoded images were merged to produced mosaics corresponding to the 1:250 000 topographic maps. To minimise the radiometric variability between images acquired at different dates, they were calibrated on the most recent image.

The enhancement process produces an image with optimum colour contrasts that facilitate visual interpretation. Two enhancement methods were employed, the Taylor enhancement method (Beaubien, 1984) and the false colour composite method (bands combination and stretching). The Taylor method consists in the production of three component channels, by using original bands, and interpreted them as intensity, red-green and blue-yellow.

Vegetation classification

After reviewing the literature on caribou and habitat mapping, vegetation cover, especially lichens, was selected as the main variable reflecting caribou habitat quality for map production. We then proceeded with the definition of 9 classes, knowing that number of classes would probably evolved over time. This

Table 1. Vegetation classification.

Sites	Preliminary classes	Final classes	Symbol[1]	Vegetation and spectral characteristics
WELL-DRAINED WITH LICHEN	Lichen with <10-15% of tree or shrub cover	1. Lichen	**LI**	True dominance of the lichen stratum with very sparse shrub layer. Spectral dominance of the lichen stratum.
	Lichen with >15% of shrub cover	2. Lichen-Shrub	**LA**	Lichen stratum with spectrally significant shrub layer. No trees.
	Lichen with >25% of shrub cover	3. Shrub-Lichen	**AL**	Abundant shrub layer with presence of lichen. Spectral dominance of shrubs.
	Lichen, sedges-grasses and low shrubs in various proportions	4. Lichen-Graminoid-Shrub	**LAH**	Lichen stratum with abundant dwarf shrubs and the presence of sedges and grasses.
	Lichen with 15-25% of tree cover	5. Lichen-Woodland	**LB**	Lichen-covered floor with open coniferous tree layer. Sparse layer of shrubs. Combination of spectral response of conifers and lichens.
	Trees with shrubs and lichen (approx. 30% of trees, shrubs and lichen cover)	6. Lichen-Shrub-Woodland	**LAB**	Lichen, shrub and tree layers in similar proportions giving a mixed spectral response. Shrub layer usually more abundant than trees.
DISTURBED	Recent burnt-over area (<30 years-old on average)	7. Burnt-over area	**BR**	Stage 1 of post-fire succession: spectral dominance of bare ground, dead trees with pioneer species of lichen. Sharp boundaries.
	Regenerating lichens (*Cladina mitis*) and shrubs	8. Regenerating burnt-over area	**BRG**	Stage 2 of post-fire succession: combined reflectance of little bare ground and pioneer lichens with regenerating lichens and shrubs. Mosaic of colors with clear boundaries.
POORLY-DRAINED, WITHOUT LICHEN	Spruce-moss forest	9. Shrub-Woodland	**AB**	Coniferous forest, more or less open, with abundant shrub layer and feather mosses. May include treed bog. Combination of spectral response of conifers and shrubs (and mosses) with dominance of one or the other.
	Wetland (including bog and fen)	10. Wetland	**MH**	Include all types of wetlands from herbaceous fens to open bogs. Variable spectral and spatial response on the image. Mapped with the help of topographic maps (1 : 50 000) and color composite type of enhancement.
OTHERS WITHOUT LICHEN	Shrubs (or deciduous trees)	11. Shrub	**AR**	True dominance of deciduous plants (trees or shrubs).
	Dwarf shrubs with sedges and grasses in variable proportions	12. Graminoid-Shrub	**HA**	Combined presence of dwarf shrubs and of sedges and grasses in variable proportions.
	Moss with dwarf shrubs	13. Moss-dominated tundra	**M**	Moss-dominated strata with dwarf shrubs.
	Bare area	14. Bare area: outcrops/granular deposits	**DE**	Without vegetation cover or with poor vegetation cover masked by spectral dominance of rocks.

[1] derived after the French denomination. For example: LA = Lichenaie Arbustive.

preliminary classification provided a broad overview of vegetation types over a large area, with refined divisions and more precise definitions of lichen classes. The final classification of 14 classes (Table 1) was determined by successive refinements over the first three years of the project. As the surface area mapped increased, knowledge of the vegetation evolved. With a better understanding of the images and the enhancement process, new classes were added and the definitions of existing ones refined.

Visual interpretation and cartography

The interpretation process consisted in the visual recognition of vegetation classes based on colour tints, texture and context observed on the enhanced images (false colour and Taylor compositions) displayed at the scale of 1:70 000 approximately on the monitor (Thibault et al., 1990). Ancillary data (topographic maps, thematic maps of physical units, biomes or fire dating) and field survey results provided the context information clarifying the interpretation.

The interpretation usually consists of successive refinements. First, broad vegetation units were outlined. These units were then subdivided while isolating the lichen component. If necessary, the lichen-rich areas were subdivided once more, to reflect structural variations in the lichen cover as defined by the classification (e.g. Lichen-Shrub or Shrub-Lichen, Lichen Woodland with openings of Lichen-Shrub). Remaining areas without lichen were then subdivided to reflect landscape reality and yield significant polygons without excessive intra-variability.

For a homogeneous group of colours forming a specific vegetation type (for example Lichen Woodland), a single attribute was given. More complex areas, with many vegetation cover types, received a complex attribute with a dominant and a sub (indicated with /) or co-dominant (indicated with -) vegetation class (Shrub Woodland co-dominant Lichen Woodland).

The 1:250 000 scale was chosen for map production because of the need to cover large areas with limited number of homogeneous regions or polygons, each larger than 5 km^2.

GIS integration and map production

The polygon boundaries and attributes were integrated in a GIS software and a colour thematic map was produced. The colour of each polygon was assigned by the dominant class. Statistics of the classes, spatial coverage with or without sub-dominant, were generated for each 1:250 000 map, or for a target region.

Results

Method development

This study allowed the development of an operational method for mapping caribou habitat. Visual interpretation of enhanced images that uses field knowledge by the interpreter was chosen over other methods of per-pixel automatic classification. Two different types of enhancement were needed to visually interpret correctly all the vegetation cover types defined in the classification. To extract lichen cover types, the Taylor enhancement method was used. This method requires a field survey and a good knowledge of the spectral reflectance for the vegetation cover types observed within the study area. The Taylor method displays three band combinations produced with the original TM3, TM4 and TM5 bands in different colour axes (first axis is dark to bright, second axis is red to green and third axis is blue to yellow). White lichens (Cladina mitis, Cladina stellaris) possess very high reflectance values in each of the three band combinations. The first band combination displays lichens in bright colour, the second one displays shrubs in red, lichens and bare areas in green. The third one displays burnt and bare areas in blue and lichens in yellow. This enhancement method allows the production of a contrast image facilitating visual interpretation and distinction between lichen cover types. A second enhancement was made for a better discrimination of the remaining cover types (free of lichens) that are sources of confusion in the Taylor enhancement. It consists in displaying TM4, TM5 and TM3 spectral bands in red, green and blue respectively and to apply linear stretching to all bands. This false colour composite helps to visualise general patterns and broad vegetation classes (e.g. wetlands, burns, lichen dominated areas, coniferous forest dominated areas) and allows a better discrimination of specific classes: wetlands, deciduous cover types, bare hilltops and anthropical elements.

Vegetation classification

The final classification (Table 1), that takes into account the possibilities of images in terms of visual distinctiveness, is based on the physionomic structure of vegetation. Classes (or cover types) are defined using a binomial denomination based on the two spectrally dominant strata: coniferous trees, deciduous shrubs (or trees), graminoids (grasses or sedges) and lichens or mosses. A trinomial denomination is possible (e.g. Lichen-Shrub-Woodland) when the overall reflectance of a vegetation type is a mixture of 3 different strata. A single designation is also possible (e.g. Lichen) when the reflectance is strongly dominated by one stratum.

The final classification of 14 classes (Table 1) includes six classes of upland sites with lichens, two fire-related classes with pioneer lichens and with regenerating lichens and six classes for other land cover types, including one class representing spring habitat (Graminoid-Shrub). The detailed description of vegetation classes is presented below.

1) Lichen: The lichen class corresponds to a very open mature lichen woodland with tree cover not exceeding 10-15% dominated by Cladina stellaris with sparse layer of shrubs. Its occurrence, in the Boreal Forest, is restricted mainly to sandy deposits along rivers and often associated with Lichen-Woodland (LI/LB). In the Tundra biome, this class occurs on well-drained sites, often associated with granular deposits (LI/DE). Lichens, with arctic taxa such as Alectoria, Cetraria or Cornicularia dominate the ground cover with sparse or intermixed dwarf shrubs, such as Ledum decumbens, Salix uva-ursi, Arctostaphylos alpina, etc. It may include more exposed arctic land with lichens and graminoids (such as Deschampsia cespitosa, Carex bigelowii, Luzula confusa, Hierochloa alpina), almost without shrubs. Associated with the bare areas class, it covers significant areas in the Minto lake region.

2) Lichen-Shrub: The heath community without trees is characterized by a continuous lichen floor covering sprinkled with low ericaceous shrubs, including dwarf birch and willows and possibly sparse stunted spruces. In the Boreal Forest, the Lichen-Shrub class occurs mainly as a sub-dominant class in regenerating burnt-over areas (BRG/LA) and indicates an advanced stage of regeneration where the lichen stratum dominates in patches. It is limited to exposed summits of lichen heath and bedrock (LA/DE). In the northern part of the Forest Tundra biome, the Lichen-Shrub class is ubiquitous, in association with granular deposits (LA/DE, DE/LA), with strips of Shrub-Woodland (LA/AB), with increased presence of shrubs (LA/AL; AL/LA) or with Lichen-Woodland, generally in young regenerated areas (LA/LB, LB/LA). In the Tundra biome, this class is similar to the preceding Lichen class but with an important coverage of low arctic shrubs. Boulders or rocks represent about 15% of ground cover. With a higher coverage of rock, LA is in mosaic with DE. The sparse lichen heath community is not visible on the image when the rocks cover reaches 30% or less of the ground cover.

3) Shrub-Lichen: It corresponds to a variant of the Lichen-Shrub class, where shrubs have a greater importance. Spatial coverage of the shrub stratum exceeds that of the lichen stratum. This class rarely occurs as the dominant and with no significant spatial extent. It is often associated with the post-fire regeneration mosaics in the Boreal Forest biome (BRG/AL, AL/LAB or else).

4) Lichen-Graminoid-Shrub: It is characterized by the presence of lichens, sedges-grasses or herbs and low shrubs in different cover percentages and various spatial arrangement in response to the variations in the micro-topography and in the moisture regime. This class was retained to depict complex vegetation types where periglacial processes are very active, usually in mesic to humid sites. It includes dry, earth hummocks, cryoturbated surfaces with polygons, and moist depression areas or furrows. It corresponds approximately to the "hummocky tundra" of Ferguson (1991). This class includes also mosaics of intermixed Lichen/Shrub with sedges-dominated arctic fens. When the mosses and graminoid components are more important in poorly-drained sites, the Lichen-Graminoid-Shrub class is associated with the Wetland class (LAH/MH, MH/LAH, LAH-MH). When the dwarf shrubs are predominant, the Lichen-Graminoid-Shrub class is combined with the Shrub class in the attribute of the mapped polygons (LAH/AR, AR/LAH).

5) Lichen-Woodland: It represents the mature and open black spruce lichen forest, occurring between 50 to 100 years after fire on well-drained sites. A few ericaceous shrubs, usually Vaccinium spp., occur in the dwarf shrub layer. The forest floor is characterized by a thick carpet of lichens (Cladina stellaris, Cladina rangiferina, Cladina mitis). These stands contain the highest values of lichen biomass (Arseneault et al., 1997). This class may also include open jack pine lichen stands. This is the typical and dominant forest type of the southern part of the Forest Tundra biome and the dominant class over the entire mapped area.

6) Lichen-Shrub-Woodland: This class represents a closer form of Lichen-Woodland where the mature coniferous stratum is more dense (around 30% of ground cover) and where the shrub layer takes expansion over the lichen stratum. It appears usually in mosaic with closed coniferous moss forest (Shrub-Woodland). It also represents

a post-fire regenerating stage with young shrubby spruces and important shrub cover occurring before the mature lichen woodland (stage 3).

7) Burnt-over area: The burnt-over area is characterized by the dark burned ground, bare rocks, the presence of dead trees and a regeneration by ericaceous (Vaccinium spp., Ledum groenlandicum, etc.), deciduous (Salix spp., Alnus) shrubs and dark species of lichen.

8) Regenerating burnt-over area: This class corresponds typically to a Shrub-Lichen structure of vegetation, where the yellowish Cladina mitis is the dominant species. It consists generally of a mosaic of regeneration types including bare ground, shrub-dominated areas, young jack pine stands, lichen-dominated parts with or without young black spruce regeneration. The overall mosaic still stands easily apart from mature portions of the territory.

9) Shrub-Woodland: It is typically a mature black spruce forest with mosses and ericaceous shrubs. The density of the tree cover varies depending on latitude and soil conditions. Ericaceous species typically dominate the understory, often with an abundance of Ledum groenlandicum. Alnus rugosa may provide tall shrub cover. Continuous ground cover by Sphagnum and feathermoss is characteristic of this class. The Shrub-Woodland occurs mainly on poorly drained sites in association with wetlands, on moist to wet lowland or lower slope sites and in mountainous areas. This class comprises mature jack pine or jack pine – black spruce stands. Some wetland black spruce stands with stunted trees and sphagnum-dominated on wet, organic sites (treed bogs) are also included. Prostrate forms of black spruce stands (krummholz) with an abundant shrub layer is represented by the Shrub-Woodland class. This class is more abundant in the southern part of the Boreal Forest region and occurs sporadically as a sub-dominant towards its northern limit.

10) Wetland: This class include all types of wetlands from herbaceous fens to shrub-Sphagnum bogs or associations of the two types, palsa bogs occurring in the Forest Tundra biome, and coastal marshes. Forested portions of bogs with significant covering of black spruce could be confused with the Shrub-Woodland class. In the Tundra, the wetland class corresponds to arctic fen, a wet sedge meadow with mosses and water. It should be noted that, if these arctic fens do not cover large enough areas, they may be included in the Graminoid-Shrub class. Wetlands occupy extensive areas on the marine deposits of the James Bay lowlands. Usually, it occurs mainly as a subdominant class.

11) Shrub: The shrub class is characterized by the dominance of deciduous species, mainly shrubs. It consists typically of slopes dominated by white birch (Boreal Forest), dwarf birch, alders and willows, with Ledum groenlandicum. The shrub class may be used to note shrubby openings in the coniferous forest or to specify the dominance of shrubs in a post-fire regenerating area. Riparian thickets of alders and willows are also part of this class. In the Tundra, it is often associated with the Bare Area class and represents the dwarf shrub tundra without lichen or appears as linear entities corresponding to rivers or slopes.

12) Graminoid-Shrub: This class brings together mesic to humid vegetation types characterized by the importance of the herbaceous and/or shrub stratum. It was first created to depict the "green valleys" standing out the rocky plateaux of the George River region and representing a significant habitat for caribou in summer (Crête et al., 1990). It includes also cryoturbate areas without lichens where variations in the microtopography lead to a mixed presence of shrubs and herbs and mosaics of sedge meadows (fens) and shrub-dominated rocky tundra.

13) Moss-dominated Tundra: It corresponds to a tundra community where the moss stratum is dominated by Rhacomitrium lanuginosum, with dwarf shrubs such as Ledum decumbens, Diapensia lapponica, Loiseleuria procumbens, and Salix uva-ursi. This class is confined to the vegetation of the plateaux surrounding the George River and is usually combined with the Bare Area class.

14) Bare Area (outcrops and granular deposits): This class is defined by the spectral dominance of the "bare" component. It includes all kinds of substrates devoid of vegetation, such as rock outcrops, blocks, sand, gravel, anthropic features (quarry, mine), etc. Interspersed vegetation may be present up to 50-60% of spatial cover, but it is completely masked by the strong spectral dominance of rock.

Map production

An area of 536 000 km^2 was mapped from 37 enhanced Landsat TM images, representing 43 caribou habitat maps at a scale of 1:250 000. Between 120 and 300 thematic polygons were delineated and identified for each 1:250 000 map. Maps were generally composed of three to four dominating classes, accounting for more than 80% of spatial cover. Maps located within the limit of 2 biomes, or with high physical variability are more diversified and 6 to 7 dominating classes are needed to map these regions. Occurrence and spatial covering of each class is highly variable. Three classes (Lichen-Shrub-Graminoid, Graminoid-Shrub, Moss-dominated Tundra) were used exclusively for mapping complex areas (mosaics of cover types) specific to the Tundra biome.

A synthesis colour vegetation map of northern Québec at a scale of 1:2 000 000 was also derived from the 1:250 000 maps. A simplified classification of seven classes was first elaborated, by merging similar classes (two lichen classes, one post-fire class, and four other classes). The minimal area of a polygon was fixed at 10 km^2. New and larger polygons were delineated by merging the existing polygons of similar dominance to adapt them to the smaller scale. The synthesis map provides a rapid overview of broad vegetation types relevant for caribou in northern Québec.

Discussion and conclusion

The development of a suitable vegetation classification representative of caribou habitat was the major concern. Exploration of the possibilities of image enhancements together with field assessment of vegetation cover types leads to the development of a classification of 14 vegetation classes, six of them related to lichen. Vegetation classes are superimposed against the backdrop of the three biomes, and bring out the important features of caribou habitat. The high number of classes was necessary to cover the variability of the vegetation cover throughout the entire range of caribou in northern Québec. The classification is a physiognomic one, based on vegetation structure. Unlike aerial photographs, the coarse resolution of Landsat data does not allow the recognition of species, thus classes cannot be defined by their floristic composition. However, the numerous field surveys allowed grafting onto the structural classes the description of a typical floristic composition by biomes and the association with biophysical characteristics. The database, consisting of 1164 sampling sites with associated colour slides, is a valuable source of data for more in-depth exploring of the maps.

The basic premise of the method developed was the use of visually-based image interpretation to derive caribou habitat maps. This classical approach, even subjective and time-consuming, was more accurate than computer-assisted classification to assess complex vegetation cover types over large areas with high biophysical variability. Visual interpretation on a paper colour map was used in other studies to allow for a preliminary analysis of very broad vegetation cover types and the selection of a sub-area for detailed investigation (Matthews, 1991). However, most habitat mapping studies with satellite imagery are based on a pixel-by-pixel automatic classification. These computer-assisted methods are using the spectral signature of vegetation types for the classification step. Often, as for caribou habitat, the identification unit is not the individual pixel but more a group of pixels forming an entire vegetation type, with no sharp spectral limits. Visual image interpretation relies on criteria of tone, brightness, shape, texture, pattern, size, shadow, height and context. As predicted by Ryerson (1989), these criteria are still difficult to quantify and entirely automatic methods (artificial intelligence) to integrate them are not yet developed. To map caribou habitat, visual interpretation provided a very accurate recognition of vegetation classes. It proved to be the best method to outline large units consisting of vegetation complexes.

The success of habitat mapping using satellite imagery is also linked to the spectral distinctiveness of the vegetation cover relevant for the species studied. The effective discrimination of wet graminoid communities permits a successful mapping of muskox habitat (Ferguson, 1991). The non-discrimination of tolerant vs. intolerant deciduous stands, an important characteristic of winter habitat for white-tailed deer (Sirois & Bonn, 1984), or the difficulty to distinguish balsam fir (Abies balsamea (L.) Mill.) from black spruce (Picea mariana (Mill.) BSP.) in coniferous stands for moose habitat (Oosenbrug *et* al., 1988), limits the application of satellite data to the regional level. On the other hand, the high spectral reflectance of lichens (white colour) in the visible electromagnetic spectrum makes it highly discernible on Landsat TM imagery. The six lichen classes, where lichens occur in various combination with other strata (herb, shrub or tree), were easily enhanced, identified by visual interpretation and mapped. A high degree of confidence is associated with them.

Burnt areas are among the more outstanding features when looking at images of the boreal region. Sharp limits, large areas and uniformity of colour in recent burns, contribute to their easy mapping. These characteristics offer a good potential for an automated update of recent burnt-over areas. Interpretation should be necessary however to map the evolution of older burns (Class: Regenerating

Burnt-over Area) and their progressive replacement by a mosaic of lichen classes.

The use of GIS technology for database integration provides a powerful tool for data management (sorting, modelling, etc.), statistical analysis for any targeted region, easy map updating and spatial analysis. Overlaying other data sources on caribou habitat map, like telemetric data on caribou movements, will offer new types of analysis and insights for caribou management.

Because of the long distance migrations, caribou management requires the knowledge of habitat characteristics in a very large area. The information needed for wildlife biologists to formulate conservation strategies or to direct future research is current habitat availability and changes in land cover types over time. The maps produced in this study provide a good source of reliable information about lichens, vegetation and fire regeneration. Future development is oriented toward the systematic update of maps, every 10 years for example, to monitor changes related to fire disturbance.

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Preliminary assessment of habitat characteristics of woodland caribou calving areas in the Claybelt region of Québec and Ontario, Canada

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Abstract: Woodland caribou (Rangifer tarandus caribou) require a diversity of forested habitats over large areas and may thus be particularly affected by the large-scale changes in the composition and age-class distribution of forest landscapes induced by the northern expansion of forest management. In this study we examine habitat characteristics associated to the use of calving areas by woodland caribou females and calves at different spatial scales. Thirty females were captured and collared with Argos satellite transmitters that allowed to locate 14 calving areas. Field surveys were conducted at each of these areas to measure the landscape composition of forest cover types and local vegetation characteristics that are used for both forage conditions and protection cover. At the scale of the calving area, univariate comparisons of the amount of forest cover types between sites with and without calves showed that the presence of calves was associated to mature black spruce forest with a high percent cover of terrestrial lichens. Within calving grounds, univariate comparisons showed that vegetation features like ericaceans and terrestrial lichens, that are important food resources for lactating females, were more abundant in calving areas where females were seen with a calf in mid-July than in areas where females were seen alone. The protection of the vegetation cover against predators was however similar between calving areas with or without a calf. Logistic regression results also indicated that vegetation characteristics associated to forage conditions were positively associated to calf presence on calving grounds. Our results suggest that foraging conditions should be given more attention in analyses on habitat requirements of woodland caribou.

Key words: food availability, habitat requirement, logistic regression, multi-resources analysis, multi-scale analysis, protection cover.

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Introduction

A number of studies have already shown the impacts of forest management and other human activities on populations of woodland caribou (Cumming, 1992; Chubbs et al., 1993; Cumming & Beange, 1993; Smith et al., 2000). Forest management can have direct or indirect negative effects on caribou populations by displacing them (Darby & Duquette, 1986), by changing predator-prey dynamics (Bergerud & Elliot, 1986; James & Stuart-Smith, 2000) or, like fire, by affecting food availability (Klein, 1982; Darby & Duquette, 1986; Pruitt & Schaeffer, 1991). Since the late 1800s and the early 1900s , the historical range of woodland caribou has decreased (Bergerud, 1974; Racey & Armstrong, 2000; Courtois et al., 2001). Even though many hypotheses were made to explain the possible causes of this range restriction, it is hard to point out one unique factor (Racey & Armstrong, 2000). But still, low productivity of females (Bergerud, 1980), high rates of mortality of newborns within the first six weeks (Bergerud, 1974; Bergerud, 1980), and susceptibili-

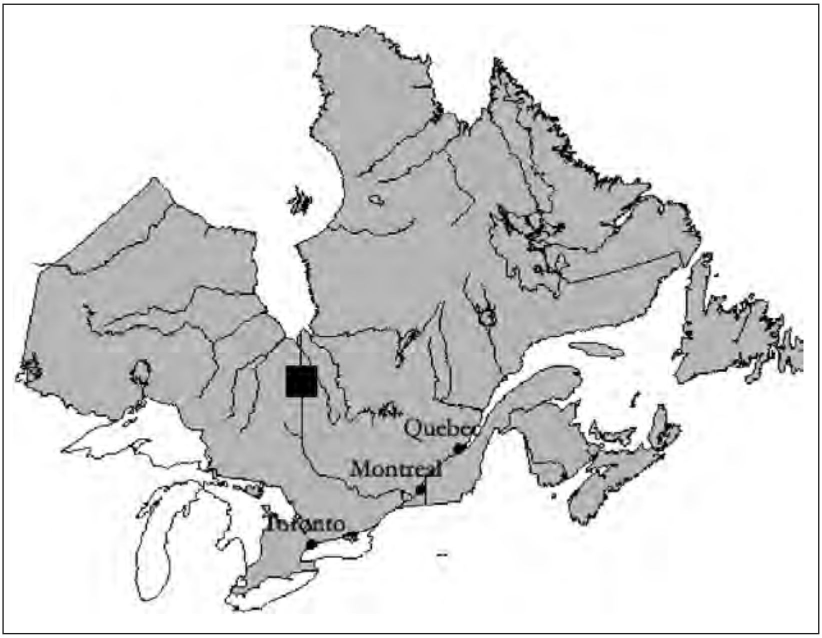

Fig. 1. Location of the study area within the Claybelt of Québec and Ontario.

ty of caribou toward disturbances (Chubbs et al., 1993; Cumming & Beange, 1993; Nellemann & Cameron, 1996; Dyer et al., 2001) make them a fragile species. Late winter and calving seasons are two critical mortality periods for woodland caribou (Bergerud, 1980). Wilson (2000) has recently shown the importance of forage conditions, particularly terrestrial lichens, in late winter habitat selection by woodland caribou. Information regarding forage conditions and protection cover used by female woodland caribou in calving areas is limited. Some studies have established relationships between food quality at the end of the gestation period and survival of calves (Rognmo et al., 1983; Post & Klein, 1999). At the landscape scale, during the calving period and in the summer, females of woodland caribou are associated with the abundance of old growth forests surrounded by wetlands (Hillis et al., 1998) or to islands in lakes (Bergerud, 1980). This combination of habitats should provide them with food (Paré, 1987) and protection against predators (Bergerud & Page, 1987).

In this study we characterised calving areas used by woodland caribou in the Claybelt region of Québec and Ontario. More specifically, we evaluated if sites where females were seen with their calf had different habitat features than those where females were alone. We hypothesise that the presence of offspring during spring and summer is related to both food resources and protective cover provided by habitat characteristics. Hence, we tested two predictions: (1) calving areas with females seen with their calf have a greater forage biomass than calving areas where females were seen alone, and (2) the protection cover in the understory of calving areas where females were seen with a calf is greater than in calving areas where females were seen alone.

Methods

The study area is located in the northern Claybelt region between 49°15' and 50°53'N and from 81°14' to 78°36'W (Fig. 1). It is part of the black spruce-moss bioclimatic subzone (Saucier et al., 1998). The landscape is dominated by black spruce (Picea mariana [Mill.] B.S.P.) with an understory of mosses and Sphagnum spp. These forests have frequent wetlands and other non-commercially productive forests. Jack pine (Pinus banksiana Lamb.) forests with dense terrestrial lichen cover are also present. Topography for this region is essentially uniform and flat (Vincent & Hardy, 1977).

In the late winter of 1998 and 1999, capture and marking of individuals from the studied population was done. For two years, a total of 30 females were collared with Argos satellites platforms (Telonics Inc.) equipped with a mortality sensor. At the same time, blood samples were taken from adult females and laboratory analyses were conducted to verify for gestation status with the help of PSPB tests (Russell et al., 1998). The tests were positive for all samples from captured females (unpubl. data). Because the tests were conducted in late winter and foetal resorption is considered to be low (Bergerud, 1980), each positive test was assumed to lead to a birth. We also made the assumption that each year the gestation rate was similar, based on the small variation in pregnancy rates observed in North America (Bergerud, 1980; Courtois et al., 2002).

In mid-July 2000, aerial surveys were conducted to estimate the survival rate of calves. At that time, 16 collars were still functional, 14 were found and all these females were located near their calving areas. For the purpose of this study, the term "calving

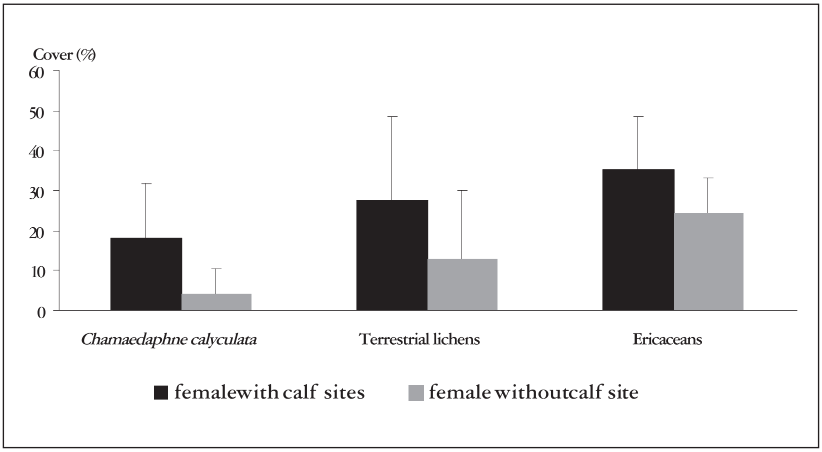

Fig. 2. Differences in mean percent cover (%) of leather leaf (*Chamaedaphne calyculata*) (P=0.034), terrestrial lichens (P=0.159) and other ericaceans (P=0.224) for the female with calf sites (n=7) and female without calf sites (n=7).

areas" represents areas utilised by females during the calving period, i.e., from mid-May to mid-June.

For each collared female, we generated minimum convex polygon home ranges that allowed the delineation of calving areas. These areas covered between 3 to 5 km^2 (Lantin, unpubl. data). By flying over the females, we were able to determine if the female was followed by a calf or not, looking both at the presence of calf at heel and female behaviour (tendency to stay near a specific place or to look back in the same direction). When no calf was seen with the female or no indication of its presence was observed at the time of the survey, the calf was assumed dead. Based on this criterion, 7 out of 14 females were followed by a calf in mid-July.

When flying over the calving area, the landscape composition of calving grounds was visually evaluated to determine the relative proportions of each habitat type: (1) wetlands, (2) closed canopy spruce forests with mosses, (3) medium to dense forests with mosses, (4) open spruce forests with mosses, (5) dense spruce forests with terrestrial lichens, (6) medium-to-dense forests with terrestrial lichens and (7) clear-cuts. This visual evaluation covered an area of approximately 5 km^2 (1.2 km radius) i.e., the entire calving ground.

Quantitative evaluation of vegetation was conducted within the portion of each calving area that comprised the highest concentration of locations. This ensured that the transects and sample plots were representative of the area used by the female during the calving and summer periods even though vegetation characteristics were measured in a single transect. Vegetation at the ground level was characterised for the 14 calving areas associated with female sight records. The sampling protocol used was adapted from a transect sampling procedure developed by the Société de la faune et des parcs du Québec from another study on woodland caribou in eastern Québec (Courtois, 1997).

One transect was located at each site. Vegetation measurements were taken at five rectangular plots (2 m X 10 m) equally spaced along the 130 m transect. Within each plot, vegetation measurements including the percent cover of (1) moss, (2) terrestrial lichens, (3) *Sphagnum* spp., (4) herbs (graminoïds and Carex sp.), (5) ericaceans, (6) bare ground, with fine woody material were made in a 1 m radius circular plot located within each 2 m X 10 m rectangular plot. The volume of terrestrial lichens was estimated using the method by Arseneault et al. (1997) that combines measures of height of the lichen mat and percent cover within the circular plots. Woody plants as food for ungulates were measured by counts of the number of coniferous and deciduous stems with twigs available to browse in the 2 by 10 m plots (i.e. twigs more then 5 cm length located between 30 cm and 3 m from the ground) (Shafer, 1963). Abundance of epiphytic lichens was measured on the five nearest trees from the end of the 2 m X 10 m plot by a visual estimation index between 1 and 5 (where 1 is the less abundant and 5 if the most). A visual estimate of canopy closure was made at every meter on a 10 m chain (Vales & Bunnell, 1988; Potvin et al., 1999). Measures of lateral cover obstruction were taken on a 200 cm by 30 cm board at 15 m from the beginning of the sampling plots at 0° and 270° (Nudds, 1977). Finally, the abundance of large downed woody debris (>10 cm DBH) was counted along a 10 m transect that crossed each 2 m X 10 m plot. Presence of lichens was recorded on each downed woody debris. Presence of lichens on downed woody debris was an indication of the time since the tree fell down. Hence, dead wood was categorised into old downed woody debris with lichens (ODWD) and recent downed woody debris without lichens (RDWD).

Statistical analyses were conducted on presence/absence of a living calf in each calving area. At the scale of the entire calving area, the composition and

Table 1. Results of Mann-Whitney U-test at α=0.1 for differences in mean percent of forest cover types in the calving area [mean (standard deviation)] between sites with and without calves.

Types of forests	female with calf	female without calf	P
Wetlands	47.86 (29.84)	26.43 (20.15)	0.178
Closed canopy spruce forest (>60%) with mosses	5.71 (15.12)	16.43 (18.87)	0.157
Medium to closed canopy spruce (31–60%) forest with mosses	20.00 (30.41)	29.29 (19.88)	0.323
Open spruce forest with mosses (<30%)	7.14 (18.90)	17.14 (29.84)	0.476
Dense spruce forests with terrestrial lichens	10.71 (14.56)	0.00 (0.00)	**0.062**
Medium to dense forest with terrestrial lichens	8.57 (17.01)	7.14 (18.90)	0.657
Clear-cuts	0.00 (0.00)	3.57 (6.27)	0.142

amount of forest cover types were measured and Mann-Whitney U tests (Zar, 1999) were applied to test for differences in the landscape composition of calving grounds with and without a calf. Within calving areas, the transect became the sampling unit, and vegetation variables mean values over the 5 plots within each transect where used in all analyses. Differences in vegetation characteristics between sites with and without calves were assessed using Mann-Whitney U-tests (Zar, 1999). Given the small sample size in this study, P values where considered to be statistically significant at both α=0.05 and α=0.1 levels. Significance levels of 0.1 have been used in other studies involving small samples of observations of woodland caribou (Mahoney & Schaeffer, 2002). Finally, logistic regression with a stepwise procedure was used to identify the combination of vegetation characteristics that best predicted calf presence on females calving areas.

Results

At the scale of the entire calving area, the composition and relative proportions of forest cover types did not differ between areas used by females with a calf and areas occupied by females without a calf for a P value of 0.05. However, at the P=0.1 level, the importance of mature black spruce forests with a dense cover of terrestrial lichens was significantly associated to calf presence in calving areas (Table 1).

When analyses were conducted at the transect scale at the P=0.05, only the cover of leather leaf (*Chamaedaphne calyculata* (L.) Moench.) was significantly different between female with calf sites and female without calf sites (Prob>|Z|=0.0398) (Fig. 2). Percent cover of terrestrial lichens and other ericaceans, were also more abundant in transects where females were seen with a calf, although this difference was not statistically significant at the P<0.05 level (Fig. 2). At a level where P=0.1, the percent cover of litter, the volume of terrestrial lichens, the abundance of ODWD with lichens, RDWD without lichens, percent conifer in the canopy and total canopy cover were all significant for differentiating the two groups of sites (Table 2). There were no significant differences for all the other variables at both P=0.05 and P=0.1 (Table 2).

A logistic regression analysis of calf presence in transects produced the following equation:

Logit $\text{calf}_{(\text{absent, present})}$ =3.3066+0.0546 • % cover of herbs+0.0472 • % cover of leather leaf-0.0741 • nb Larch-0.0557 • nb RDWD-0.0460 • nb shrubs. (χ^2=4.3004; P=0.0381)

Again, results from the logistic regression indicated that calves were seen in sites where leather leaf was more abundant. The presence of herbs was also associated with the presence of calves. Larch (*Larix laricina* (Du Roi) K.Koch), and RDWD without lichens and shrubs (mostly from the genus *Salix* spp.) in the sites were negatively associated with calf presence.

Discussion

Food resources may play an important role in the survival of calves in their first weeks of life (Skogland, 1985; Cameron et al., 1993; Post & Klein, 1999). Skogland (1985) argued that calf survival from reindeer populations could be influenced by nutritional conditions of females at the end of the gestation period and at the beginning of lactation. Our results show that calves presence is associated to several habitat features that are used as forage conditions by lactating females both at the scale of the calving area and within calving areas. Ericaceans, terrestrial lichens and herbs are part of caribou's spring and summer diet and may represent up to 60% of their diet (Simkin, 1965; Bergerud, 1970; Gaare & Skogland, 1975; Darby, 1979; Thompson & McCourt, 1981). These vegetation variables were

Table 2. Results of Mann-Whitney U-test, at α=0.05 (bold with*) and α=0.1 (bold), for mean values (standard deviation) of vegetation characteristics between sites with and without calves

Sites´ characteristics	female without calf	female with calf	P
Mosses cover (%)	60.86 (30.05)	58.86 (21.26)	0.654
Terrestrial lichens (cm^3)	2.45 (3.54)	6.77 (6.61)	**0.084**
Lichen cover (%)	12.86 (6.42)	27.43 (7.91)	0.159
Herbs (graminoïds and Carex spp.) cover (%)	0.29 (0.49)	1.57 (1.81)	0.154
Larch density (nb trees/ha)	0.2 (0.12)	0.00 (0.00)	0.318
Ledum groenlandicum cover (%)	10.57 (7.48)	9.29 (5.56)	0.698
Chamaedaphne calyculata cover (%)	4.29 (6.07)	18.29 (13.43)	**0.034***
Vaccinum spp. cover (%)	8.14 (11.91)	4.00 (4.58)	0.132
Kalmia angustifolia cover (%)	1.57 (0.98)	3.57 (2.82)	0.172
Bareground cover (%)	13.00 (10.20)	3.00 (3.96)	**0.077**
Arboreal lichens (nb. Thalli)	23.90 (14.99)	28.40 (18.36)	0.749
Open canopy (%)	52.3 (20.5)	71.4 (1.92)	**0.096**
Coniferous canopy (%)	47.1 (19.8)	28.6 (19.2)	**0.096**
Lateral visibility 0-50 cm (%)	22.86 (29.75)	10.29 (10.61)	0.440
Lateral visibility 50-100 cm (%)	52.57 (23.63)	46.86 (28.00)	0.797
Lateral visibility 100-150 cm (%)	68.86 (18.36)	66.29 (21.21)	0.798
Lateral visibility 150-200 cm (%)	67.43 (20.71)	69.43 (21.22)	0.370
ODWD with lichens (nb. of logs/plot)	0.17 (3.21)	0.46 (0.32)	**0.082**
RDWD without lichens	3.46 (3.21)	0.89 (0.54)	**0.053**

more abundant in sites with calves than in sites without calves using either univariate comparisons or logistic regression. Moreover, at the scale of the calving area, the only forest cover type that was associated to calves presence was spruce forests with terrestrial lichens, another indication of the possible importance of foraging conditions in woodland caribou habitat use during the calving period. One limitation in our results is whether or not lone females remain in the same area where their calf may have died. However, when we analysed our caribou locations during the calving period, the variation in locations was similar between the 14 females suggesting that females without a calf did not disperse over a long distance from the calving area (Lantin, unpubl. data).

The logistic regression model showed that calf presence was associated with availability of leather leaf and herbs. The leather leaf, as other ericaceans, is a plant species that is generally associated with higher biomass of terrestrial lichens (Kershaw & Rouse, 1971). It is found in relatively mesic peatland areas instead of bogs. Even though terrestrial lichen percent cover was less in sites without a calf it did not come out as a significant variable in the logistic regression analysis. The small size of our sample set (n=14) may be in part responsible for this lack of statistical significance with lichens abundance and we recognise that further research with a larger sample set and more sampling intensity should be conducted to adequately test if lichens abundance is biologically a significant variable in habitat use by caribou during the calving period.

The absence of calves in areas with Larch is not surprising given that, in our study area, this tree species is normally found on organic soils that are poorly drained and on which the process of paludification takes place (Girardin et al., 2001; Giroux et al., 2001). The build-up of thick moss and organic layers (Paré & Bergeron, 1995) do not provide good substrate conditions for terrestrial lichens because of the abundance of *Sphagnum* spp. that are effective competitors for ground lichens (Johnson, 1981; Boudreault et al., 2002). Well-drained sites, as the ones with C. calyculata, thus offer more abundant food resources to female caribou.

The results from the logistic regression also show a negative association between the abundance and volume of logs and shrubs, and the presence of calves. At first glance, structural heterogeneity of the understory characterised by more shrubs and downed deadwood should provide some protection cover against predators. On the other hand, chances to escape for a newborn caribou could be reduced by the presence of logs and downed woody debris and dense shrub cover. Accumulation of deadwood could generate obstacles on the ground that may cause deadly injuries (Baskin, 1983) and that may increase the time needed to securely escape from predators. Finally, visual obstruction variables (also known as lateral visibility), a set of habitat features that provide a key information on the protection cover of forest stands against predators, did not show statistically significant differences. Percent cover values of lateral visibility were indeed highly similar between sites with and without calves (Table 2).

Several studies suggested that predation is a key factor in woodland caribou population dynamics (e.g. Bergerud, 1974; Bergerud & Elliot, 1986; Seip, 1992; Rettie & Messier, 2000). Barten et al. (2001) hypothesised that calving site selection of caribou females is driven first by predator avoidance factors, resulting in a trade-off between these factors and forage conditions. Rettie & Messier (2000) suggested that habitat selection by woodland caribou follows a hierarchy of spatial scales where predator avoidance is linked with habitat selection at a landscape level whereas available forage habitat is associated to stand level habitat selection. Our study was not designed (used vs. unused random sites) to evaluate habitat selection of calving sites by female woodland caribou, nor to evaluate which habitat factors, between foraging conditions and protection cover, had the upper hand in such selection. Nevertheless, calving sites with the presence of a calf were associated more often with foraging condition variables than with protection cover against predator variables. That calf presence shows stronger associations with vegetation features characterising forage conditions at the local scale of calving sites may thus not be a surprise if the Rettie & Messier (2000) model of a hierarchical habitat selection process is indeed occurring for this species.

Whereas the literature on woodland caribou range reduction still emphasizes predation as a driving factor (Bergerud & Elliot, 1986; Bergerud & Page, 1987; Cumming, 1992; James & Stuart-Smith, 2000; Courtois et al., 2002), the effect of habitat suitability of forest cover types with regards to forage conditions has received less attention. This is probably because the availability of forage over the landscape has not traditionally been considered as a limiting factor (Bergerud, 1974). However, Dyer et al. (2001) have showed that the total habitat avoided by caribou greatly exceeds the physical footprint of industrial development (roads, wells, seismic lines) in Alberta. Even though this avoidance does not lead to a net loss of habitat, they conclude that infrastructures associated to industrial development seriously reduce availability of habitat for woodland caribou and that this may have consequences on their demographic response. A net loss of functional habitat for caribou because of a loss of forage may, however, occur with increased timber harvesting in the boreal forest combined with the persistence of natural disturbances such as large forest fires. Short timber rotation length in managed forests has been identified as one of the most important long-term effect of forest management on boreal forest ecosystems and their wildlife (Spies et al., 1994; Wallin et al., 1994, Thompson et al., 1995, Drapeau et al., 2000). Increases in the proportion of early-successional habitats and decreases in late seral habitats could influence forage conditions of woodland caribou over the landscape given that these forest cover types are used for winter forage. Reduced availability of lichen and other food resources following fire may also affect forage conditions for caribou at large scales (Klein, 1982; Morneau & Payette, 1989). Hence, cumulative effects of disturbances (human and natural) and the loss of late seral forest cover types may reduce forage conditions of woodland caribou and eventually affect its demography.

Conclusion

Although, this investigation provides indirect and correlative data on the association of forage conditions with calf occurrence for a small sample set of calving areas, it nevertheless indicates that more attention should be paid to forage conditions in habitat use studies of woodland caribou. Predation may have been an important cause of mortality for several of our calves, variables associated to protection cover were not, however, as important as variables describing available forage when comparing calving areas with and without calves. Further studies on the variation in abundance and quality of forage should be conducted across forest cover types and throughout seasons to better assess habitat suitability for woodland caribou in forested environments. Such baseline data could then be incorporated into landscape level models assessing the effects of disturbances (natural and anthropogenic) that woodland caribou face under different development scenarios in the commercial boreal forest.

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Vegetation characteristics of forest stands used by woodland caribou and those disturbed by fire or logging in Manitoba

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Abstract: This study examined woodland caribou (Rangifer tarandus caribou) in an area known as the Kississing-Naosap caribou range in west central Manitoba. The vegetation characteristics of areas used by caribou and areas disturbed by fire or logging were measured in order to develop a model to estimate habitat quality from parameters collected during standard resource inventories. There was evidence that habitat index values calculated using a visual score-sheet index could be used as the basis to relate parameters commonly collected during resource inventories to habitat suitability. Use of this model to select long and short-term leave areas during forest management planning could potentially mitigate some of the negative impacts of forest harvesting. Abundance of arboreal lichen and wind-fallen trees were important predictor variables in the suitability model, but their inclusion did not explain more variance in habitat suitability than models that did not include them. Extreme post-fire deadfall abundance may play a role in predator-prey dynamics by creating habitat that is equally unsuitable for all ungulates, and thus keeping both moose and caribou densities low.

Key words: arboreal lichen, deadfall, disturbance, environmental impacts, forest management, habitat suitability, mitigation, predator-prey.

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Introduction

Woodland caribou (Rangifer tarandus caribou) are believed to be the late-successional forest ungulate in the boreal forest biome of North America. Numerous researchers have investigated the microhabitat characteristics of areas used by woodland caribou in boreal forest ecosystems over an entire year, as well as during specific seasonal periods, and across various disturbance regimes (e.g. Schaeffer & Pruitt, 1991; Racey et al., 1996; Rettie et al., 1997; Antoniak & Cumming, 1998; Martinez, 1998; Hirai, 1998; Wilson, 2000).

Studies have generally emphasized the importance of the abundance of arboreal and terrestrial lichen as a primary factor associated with microhabitat used by caribou during winter (Antoniak & Cumming, 1998; Martinez, 1998; Wilson, 2001). Snow conditions have also been considered important during winter, particularly factors contributing to lower levels of snow accumulation (Schaeffer & Pruitt, 1991; Wilson, 2000). The proximity of escape habitat in the form of water or open bogs and wetlands is thought to be important during the calving and post-calving periods in the spring and summer (Bergerud, 1985; Cumming & Beange, 1987; Bergerud et al., 1990). Spring and summer habitat characteristics also reflect changes in diet from terrestrial and arboreal lichens in winter to emergent herbs, grasses, and deciduous shrubs during the snow-free period (Bergerud, 1972; Darby & Pruitt, 1984). Characteristics of habitats used during the breeding season (fall rut) are less known, although it is thought that sparsely treed and open upland areas or open muskeg swamplands are the primary habitat types used (Fuller & Keith, 1981; Cumming, 1992). Two other factors are thought to be important at all times of year. Deadfall can be a barrier to movement, potentially making habitat unsuitable for caribou,

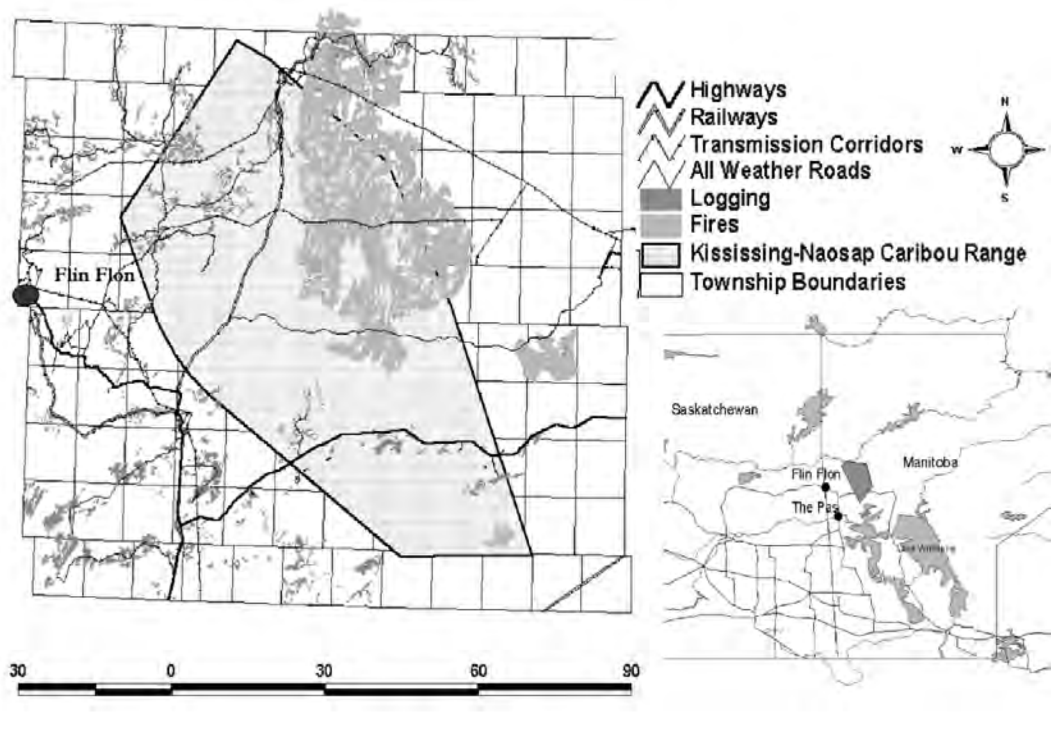

Fig. 1. Location of the Kississing-Naosap caribou range in west central Manitoba. The study area intersects the boundary of the Boreal Shield and Boreal Plains ecozones.

other ungulates, or predators depending upon its abundance. Shrub density can affect the ability of caribou to see and escape from predators, and can also change the suitability of the habitat to favour other ungulate species (e.g. moose, Van Dyke et al., 1995; Courtois et al., 1998).

Natural and human habitat disturbance can cause a number of changes in microhabitat characteristics. Natural disturbance (fire) is thought to reduce the abundance of lichens and increase accumulations of snow and deadfall, which reduce residual forage availability (Klein, 1982; Schaeffer & Pruitt, 1991). Human disturbance (logging) is thought to alter the structure of floral communities to favour deciduous early successional forest species (Carleton & MacClennan, 1994). These habitat types are generally thought to be unsuitable for caribou, as arboreal and terrestrial lichen forage species abundance is lower and the density of competing ungulates and predators is higher (Rettie & Messier, 2000). The tendency for caribou to segregate themselves spatially from other ungulates (particularly moose) in spring and summer is well known (Bergerud et al., 1984; Bergerud, 1985; Poole et al., 1999). This ability is potentially compromised by habitat disturbance (Smith et al., 2000).

It is believed that woodland caribou habitat selection varies with spatial scale in response to variations in impact of limiting factors at different spatial scales (Bergerud et al., 1990; Rettie & Messier, 2000). Johnson (1980) describes four scales or orders of habitat selection extending from the selection of geographic ranges (first order) down to the selection of components within a daily area (fourth order). Models of habitat suitability for caribou exist at various orders in this hierarchy. The majority are based on the general format for habitat suitability models (United States Fish and Wildlife Service, 1981), where a number of habitat variables are weighted in a mathematical relationship to give a defined habitat area a suitability score that ranges from 0 to 1. Such models are generally developed as decision support tools for resource management agencies. The source data are generally derived from forest resource inventory databases, as these are the standard vegetation databases used for forest management planning. Examples of such models have been developed in Manitoba (Palidwor & Schindler, 1995), British Columbia (Apps & Kinley, 1998), and Ontario (Antoniak & Cumming, 1998).

Most habitat suitability models apply at the level of the forest stand, and relate to the third order of habitat selection – the characteristics of habitats within an individual's home range (Johnson, 1980). A potentially useful model of habitat suitability that uses a visual score sheet assessment technique and relates to the third and fourth (the microhabitat characteristics within forest stands) order scales was previously developed in this study area (Storey & Storey, 1980). This method has been proposed in the past as a tool to evaluate forests in Manitoba for their suitability for woodland caribou, but has not been widely implemented (Hristienko, 1985). This visual score sheet method assesses seven habitat index components (stand type; tree size class and canopy closure; cover; food plant diversity; food plant percent ground cover; deadfall; and area diversity) on a scale of 1 to 10. These components are then weighted to derive an aggregate habitat index ranging from 1 to 10 for that area. The visual assessment is based on how closely a site's characteristics for each of the habitat index components resembles ideal conditions, which in this case was defined as ideal winter habitat conditions (Storey & Storey, 1980).

Study area

This investigation was conducted in west central Manitoba and studied woodland caribou in the Kississing-Naosap range (approx. 4500 km^2), located northeast of the towns of Flin Flon and The Pas (Fig. 1). Though precise range definitions have changed, a population estimate for the general area of the Kississing-Naosap range in 1992 varied from 150 to 300 individuals (Johnson, 1993). An aerial survey of the general area conducted in the winters of 1993 and 1994 observed between 90 and 164 animals (Cross & Smith, 1995). Though it could be debated, the data available indicate that the population in this region remained fairly stable or declined slightly throughout the last fifteen years.

The Kississing-Naosap range intersects the boundary of the Churchill River upland and the mid-boreal lowland eco-regions of the boreal shield and boreal plains eco-zones. The boreal shield landscape consists of rolling uplands and lowlands with many bedrock outcrops. This contrasts with the boreal plains landscape, which is topographically level to gently rolling, 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 snowy winters. Mean daily temperatures in the study area range from +17.7 °C in July to -21.4 °C in January. Mean annual rainfall and snowfall range from 323.3 mm and 170.2 cm in The Pas to 345.3 mm and 143.9 cm in Flin Flon. Snowfall accumulation is typically present from mid-November to early April, with maximum mean depths of 40 cm to 45 cm occurring in January and February.

Logging began in the area in the early 1970s (Anon., 1996). The Kississing-Naosap caribou range is within the provincial Forest Management License Area No. 2 and is currently actively managed by Tolko Industries, Ltd. under a Forest Management Plan approved until 2009 (Anon., 1996). Fires are a natural component of ecosystems in the area, although they are currently actively suppressed. The most significant recent burn was the Webb Lake fire in 1989, which burned approximately 125 000 hectares in the central portion of the study area and a significant portion (approx. 25%) of the range of the Kississing-Naosap caribou (Anon., 1996). Caribou in the Kississing-Naosap range are also affected by highway and rail transportation corridors, road development associated with forestry operations, hydro transmission line construction, and various recreational activities. Because of the potential cumulative impacts of all of these disturbances and the potential for an increase in development pressure in the near future, the Kississing-Naosap range is being considered for designation as a high-risk range under a provincial woodland caribou conservation policy.

Study objectives

To mitigate the potential impacts of logging on woodland caribou, natural resource development agencies have proposed a number of management techniques. In the Kississing-Naosap range in west-central Manitoba, Canada, managers have established short and long term leave areas and undisturbed travel corridors that allow access to known calving sites and other important habitats (Anon., 1999). Qualitative information on the presence of caribou sign is sometimes collected as part of pre-harvest forest investigation surveys and operational timber cruises for forest management (Anon., 1996). However, quantitative relationships between parameters collected during these surveys and microhabitat suitability for woodland caribou have not been established in the area.

In order to establish such relationships, microhabitat characteristics thought to be important to woodland caribou were investigated in undisturbed areas used by this subspecies and in areas disturbed by fire or logging. Quantitative ecological and Forest Resource Inventory (FRI) parameters were related to habitat index scores calculated from the visual score sheet method previously developed in the study area (Storey & Storey, 1980). A visual arboreal lichen abundance index to quantify the relative biomass of arboreal lichen at the sites sampled was also developed. The assumption that the visual score sheet index could distinguish habitats during different calendar seasons and disturbance regimes was tested. It was also hypothesized that a small number of easily measured quantitative FRI and ecological variables could be related to the visual index and predict habitat suitability for woodland caribou at the micro-site level.

Material and methods

Data collection

Sampling areas were located in undisturbed seasonal ranges known to be used by individual animals, as well as human disturbed (logged) sites, and naturally disturbed (burned) sites. Seasonal ranges (100% MCP) were defined from radio-telemetry locations collected from February 1996 to January 2000 as part of a concurrent study of range use and habitat selection. Six home ranges in each of the four calendar seasons (spring, summer, fall, and winter) were selected for use as sampling areas. These were chosen using a random number generator. The first six radio transmitter frequencies to be generated were selected. Fourteen disturbed sites of varying ages and disturbance types were also sampled. A random number generator was used to select ten by ten kilometre township squares as sampling areas for transects located at disturbed sites.

Line transects, a minimum of 500 m in length with plots located at 50 m intervals, were conducted within each sampling area. Transect start points within individual sampling areas were randomly selected using GIS, but limited to areas within 500 m of roads or lakes in order to provide access. Transect bearings were selected to intersect at least one location where the animal was known to have been present. When transportation resources were not available to access a randomly selected home range during the data collection period, an alternate site was selected. A similar procedure was used to select the starting point for transects located at logged and fire disturbed sites. Data collection occurred between July 29th and August 4th, 1999 and June 5th and July 26th, 2000. A total of 38 areas were sampled, consisting of 393 individual sample plots.

Data collected at each sample plot included scores for each habitat index component, Forest Resource Inventory (FRI) characteristics (species composition, age, height, canopy closure, diameter), and ecological characteristics (shrub/herb species composition), including stand attributes thought to be important to caribou (deadfall density, visual density, and arboreal lichen abundance).

Data were collected hierarchically, using a number of nested plot sizes. Habitat index components were calculated by observing the characteristics of a 50 m x 50 m plot. The seven habitat index components (stand type; tree size class and canopy closure; cover; food plant diversity; food plant percent ground cover; deadfall; and area diversity) were each assessed on a scale of 1-10 (Storey & Storey, 1980). The individual habitat index components were also weighted and averaged (Storey & Storey, 1980) to give an aggregated habitat index score ranging from 1-10 for each plot. A brief description of how the habitat index components were scored is provided in the appendix.

Forest Resource Inventory and ecological characteristics were observed in a 10 m x 10 m plot located at the centre of the 50 m x 50 m visual index plot. Tree species composition, density, and diameter distribution at each plot was measured using the point-centred quarter method (Cottam & Curtis, 1956). Height and age were measured from a single representative tree selected at each plot. Heights were measured using a Suunto clinometer. Cores were extracted using an increment borer and collected for aging with the aid of a dissecting microscope. Crown closure was estimated visually to the nearest ten percent.

Shrub species composition was recorded from the same 10 m x 10 m plot as the FRI characteristics, while herb species composition was recorded on a randomly selected 2 m x 2 m plot within the 10 m x 10 m plot. Shrub and herb species composition was determined by visually estimating the percent cover (Daubenmire, 1959). Cover percentages were recorded to the nearest five percent. Shrubs were considered to be any woody plants between 1 and 5m in height and less than 10cm in diameter. Herbs included all non-woody plant species and woody shrubs less than 1m in height. Deadfall amounts were determined by counting the number of fallen trees greater than 0.5 m from the ground along the 50 m line walked between each plot. Visibility was quantified by measuring the distance at which an individual walking along the transect between plots was no longer visible to an observer located at the previous plot.

Arboreal lichen abundance was assessed using a four level abundance index ranging from zero to three. To quantify this index, arboreal lichens were collected from sites throughout the study area. Nine sites representing each of the levels of abundance, with the exception of sites given an index value of 0,

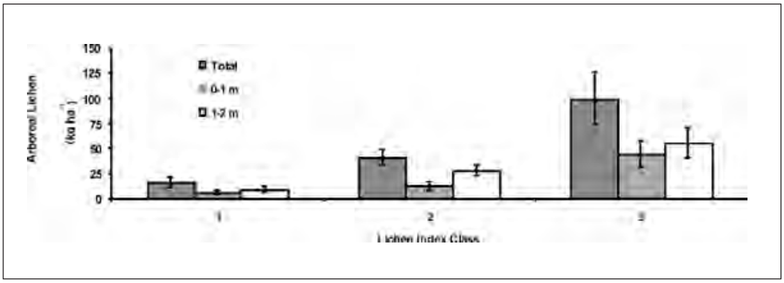

Fig. 2. Mean (SE) arboreal lichen biomass in each arboreal lichen abundance index class at heights of 0-1 m, 1-2 m, and total available height (0-2 m).

were sampled using a modification of the procedure first described by Van Daele & Johnson (1980). Lichens were collected from heights of 0-1 m and 1-2 m at each sample site, as maximum snow accumulation in this study area averaged less then 50 cm (Anon., 1998). For sampling purposes, each of the sample heights were divided into quarters. One quarter was then randomly selected and all arboreal lichens were stripped and collected. Samples were air dried for 48 h and oven-dried at 70 °C for one hour and measured to the nearest 0.01 g. This was then multiplied by four times the tree density at the plot to determine arboreal lichen abundance in kg ha-1 in each height stratum.

Data analysis

The hypothesis that the total amount of arboreal lichen in each abundance index class did not differ was tested using a one-way analysis of variance and a Tukey's HSD multiple range test. Lichen biomass values were log-transformed to correct for skewness and stabilize variance. One-way analysis of variance and Tukey's HSD multiple range tests were used to explore the hypothesis that each of the individual visual index components, as well as the final habitat index did not differ among seasons and disturbance regimes. Where variance homogeneity assumptions were not met, the ANOVA results were confirmed with non-parametric (Kruskal-Wallis) tests.

Relationships between the habitat index score and measured habitat variables were modeled using stepwise multiple linear regression. Two regression models were developed. The first used standard FRI data as predictors (Model 1). The second used a combination of FRI data and ecological data as predictors (Model 2). Plant species percent cover estimates were reduced to presence/ absence data to simplify the data requirements for applying the models. Only plants present in a minimum of 15% of plots were used to eliminate skewness.

Approximately half of the 393 plots sampled were randomly selected to develop the regression models. To examine the internal reliability of the regression models, the regression predicted habitat values were correlated with measured habitat values at the sites not used to develop the regression model. The predicted habitat values were also regressed onto the measured habitat values. A one standard error of the estimate prediction interval was then applied to the measured/predicted relationship starting from the lowest possible habitat value that the regression models (1 or 2) could estimate in order to determine three statistical habitat quality categories.

All statistical analyses were done with SPSS 9.0 for Windows and results were considered statistically significant with $P<0.05$.

Results

Arboreal lichen abundance index

Significant differences in the relative biomass of arboreal lichen were found among the four abundance index classes (Fig. 2). This was true for total lichen biomass ($F(2,24)=9.93$, $P<0.01$), lichen biomass from 0-1 m above ground ($F(2,24)=8.36$, $P<0.01$), and lichen biomass from 1-2 metres above ground ($F(2,24)=7.31$, $P<0.01$). Post-hoc testing (Tukey, $P<0.05$) showed that, in all cases, lichen biomass in each index class differed significantly from the others. Mean total lichen biomass was 15.7, 41.1, and 100.1 kg ha^{-1} for abundance classes one, two, and three respectively (Fig. 2). Since the abundance index classes as defined reflected true differences in lichen biomass, this variable was considered in the rest of the analysis.

Habitat index component values

Each of the components in the habitat index was analyzed individually. Means and standard deviations for the habitat index components by season and disturbance type are listed in Table 1. In each case, there were significant differences ($F(5,387)=9.81$ to 58.82 , $P<0.01$) between seasonal use areas and disturbance regimes. Using post-hoc testing (Tukey $P<0.05$), it was found that used sites scored higher than disturbed sites in most cases, although there were some exceptions (Table 1). Burned sites were more likely than logged sites to not be different from used sites. An exception to this was deadfall, where burned sites scored much lower (indicating higher deadfall accumulation) than any of the used sites or logged sites, which did not differ significantly from each other.

For each habitat index component, sites used in the winter were found in the highest value subset, with the exception of food plant diversity, where it scored less than fall sites. Both fall and winter sites had significantly higher food diversity than spring and summer sites. Summer sites also had significantly lower food plant ground cover than all the other seasons, but did not differ significantly from burned sites for this parameter (Table 1). Besides these variables, there was homogeneity in the habitat index component scores among seasons. All sites tended to be either closed or open stands of mature softwoods or mixed softwoods with more than 75% food plant ground cover and some (rather than no) deadfall, usually within 100 m of at least one or more other distinct habitat types.

Aggregate habitat index values

After analyzing each of the seven components individually, the individual scores were weighted to determine an aggregate habitat index score ranging from 0 to 10 for each plot. Significant differences were again noted between season and disturbance classes (F(5,390)=86.2, P<0.01) (Fig. 3). Post-hoc testing (Tukey, P<0.05) found that within seasonal use areas, winter sites scored significantly higher than summer sites, neither of which differed from spring or fall sites. All used sites as a group scored significantly higher than disturbed sites of either type. Within disturbed sites, burned areas scored significantly higher than logged areas (Fig. 3). At used sites, mean habitat index scores were 8.0, 7.5, 7.2, and 7.5 for winter, spring, summer, and fall areas respectively. At disturbed sites, mean habitat index scores were 5.7 and 5.0 for burned and logged areas, respectively.

Regression models to predict aggregated habitat index values

Habitat index scores were related to FRI variables only (Model 1, Table 2) and a both FRI and ecological variables (Model 2, Table 3) using multiple linear regression to create a statistically significant relationship (F(4,193)=67.79 and 78.20 for Models 1 and 2, respectively, P<0.01). Presence of spruce trees, age, and mean tree diameter were positive predictors, while the presence of trembling aspen trees was a negative predictor for Model 1 (Table 2). Presence of spruce trees and arboreal lichen index were positive predictors, while presence of trembling aspen shrubs and deadfall density were negative predictors for Model 2 (Table 3). Both models explained approximately 60% of the variance in habitat index

Table 1. Comparison of habitat index components scores among sampling categories. Scores are presented as means ranging from 0-10, and (standard errors). Letters represent homogenous subsets calculated using Tukey's HSD post-hoc testing. Subset A represents the highest scoring subset, B the second highest, etc.

Sampling category	Habitat index component						
	Stand type	Tree size class and crown closure	Cover	Food plant diversity	Food plant ground cover	Deadfall	Area diversity
Spring (n=63)	9.8 (0.12) A	7.5 (0.21) A	7.4 (0.23) A	5.1 (0.23) C	8.1 (0.27) A, B	9.0 (0.21) A	6.0 (0.26) A, B
Summer (n=68)	9.3 (0.22) A	7.7 (0.22) A	6.7 (0.28) A, B	5.2 (0.23) C	7.1 (0.25) B, C	9.5 (0.19) A	6.0 (0.28) A, B
Fall (n=60)	9.7 (0.18) A	6.9 (0.27) A	6.9 (0.32) A, B	7.1 (0.19) A	8.8 (0.18) A	8.9 (0.13) A	5.3 (0.26) B, C
Winter (n=60)	9.9 (0.10) A	7.7 (0.23) A	7.5 (0.26) A	6.0 (0.20) B	9.0 (0.21) A	9.5 (0.12) A	6.8 (0.23) A
Burned (n=52)	7.9 (0.38) B	3.7 (0.35) B	6.1 (0.25) B	4.6 (0.29) C, D	6.3 (0.39) C, D	7.3 (0.51) B	5.0 (0.29) B, C
Logged (n=90)	6.6 (0.31) C	4.2 (0.20) B	4.6 (0.25) C	3.9 (0.11) D	5.3 (0.24) D	8.8 (0.18) A	4.2 (0.26) C

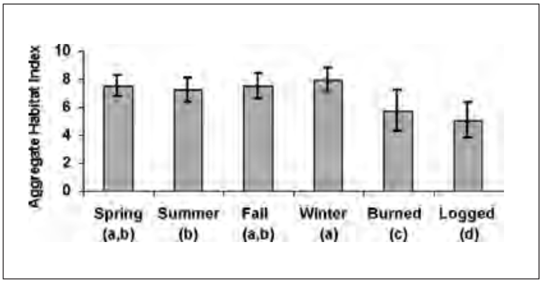

Fig. 3. Comparison of the aggregate habitat index scores among sampling categories. Scores are presented as means (+/- 1 s). Letters represent homogeneous subsets calculated using Tukey's HSD post-hoc testing. Subset A represents the highest ranking subset and D the lowest ranking subset.

scores ($r^2=0.58$ and 0.62, $P<0.01$, for Models 1 and 2, respectively).

Measured habitat index scores were significantly correlated with the regression model predicted habitat index scores for plots not used to calculate the models ($r^2=0.58$ and 0.51, $P<0.05$ for Models 1 and 2, respectively. A regression relationship between measured scores and model predicted scores was developed by regressing predicted habitat index values onto measured habitat index values (Table 4). A prediction interval of +/- one standard error of the estimate was then applied to the relationship between actual and predicted values to calculate three statistical habitat quality categories for both models (Table 4). The bottom limit for the low quality habitat category was set to the lowest possible predicted value from the Model 1 and Model 2 relationships (4.6 and 5.0 for Models 1 and 2 respectively (Table 2 and 3)). Using the Model 1 and Model 2 equations to predict habitat index values, any sites scoring more than 8.7 for Model 1 or 8.4 for Model 2 represent high quality woodland caribou habitat.

Discussion

The aggregated habitat index was successful in distinguishing between seasonal habitat preferences,

Table 2. Regression model (Model 1) for predicting the aggregated habitat index score from Forest Resource Inventory parameters only.

Variable	Regression coeffecient (a)	Multiple R^2 (b)	% change in R^2 (b)
(1)Presence of Spruce (0,1)	1.13	0.48	--
(2)Age (Years)	0.009	0.53	+10.4%
(3)Mean diameter (cm dbhob)	0.006	0.57	+7.5%
(4)Presence of Trembling Aspen (0,1)	-0.47	0.58	+1.8%
Constant	4.96	--	--

(a) Refers to final model with all four variables included.
(b) Refer to interim stepwise models, with the first, first and second, first, second, and third, first, second, third, and fourth variables included respectively.

Table 3. Regression model (Model 2) for predicting the aggregated habitat index score from a combination of Forest Resource Inventory and ecological parameters.

Variable	Regression coeffecient (a)	Multiple R^2 (b)	% change in R^2 (b)
(1)Presence of Spruce (0,1)	1.54	0.51	--
(2)Presence of Trembling Aspen shrubs (0,1)	-0.78	0.57	+11.8%
(3)Arboreal lichen index (0,1,2,3)	0.34	0.61	+7.0%
(4)Deadfall density (stems m^{-1})	-0.02	0.62	+1.6%
Constant	5.72	--	--

(a) Refers to final model with all four variables included.
(b) Refer to interim stepwise models, with the first, first and second, first, second, and third, first, second, third, and fourth variables included respectively.

Table 4. Regression relationships between actual and predicted values for Models 1 (FRI parameters only) and 2 (FRI and ecological parameters in combination), and the statistical habitat quality classes calculated from these relationships based on +/- standard error of the estimate prediction intervals. The bottom limits of the low quality category are based on the smallest possible value that either the Model 1 or 2 relationships could predict.

Habitat Quality	Model 1 - FRI parameters Predicted Value = 0.57 (Actual Value) + 2.76 SE Estimate = 0.71	Model 2 - FRI and Ecological parameters Predicted Value = 0.59 (Actual Value) + 2.72 SE Estimate = 0.86
Low	4.6 to 7.3	5.0 to 6.7
Medium	7.3 to 8.7	6.7 to 8.4
High	8.7 to 10.0	8.4 to 10.0

particularly winter and summer areas. The relationship was not as clear for spring and fall areas, which did not differ from either winter or summer use areas. Migrations between winter and summer ranges are a factor influencing where animals are located during the spring and fall, resulting in the sampling of areas that animals may have only been temporarily associated with. A closer look at the spatial distribution of study animals revealed that, in many cases, areas sampled as spring or fall use areas were often used at other times of the year, usually summer or winter. It is also possible that there are no differences in the vegetation characteristics of habitat used by this species in the spring and fall relative to other times of the year. Both of these possibilities suggest that summer and winter are the only two times of year that woodland caribou select habitats with specific characteristics at the micro-site scale in this area. At larger spatial scales, such a conclusion is supported by habitat and movement studies elsewhere in Canada that have shown a bimodal pattern of range use, with distinct summer and winter use areas (Edmonds, 1988). However, such a pattern is not constant, with some populations showing much overlap between seasonal ranges (Ouellet et al., 1996; Stuart-Smith et al., 1997).

Considering all factors, the visual score sheet worked as it was intended. Numerically the trend was appropriate. Within use areas it generated the highest scores for winter sites and the lowest scores for summer sites, with intermediate scores for spring and fall (Fig. 3). Scores for disturbed areas were lower than for all used areas. Statistically, it was able to generate significantly different aggregate habitat index scores for the two seasons (summer and winter) that caribou seem to recognize in this area. It was also able to generate significantly different aggregate scores for used areas and areas disturbed by fire or logging.

Habitat index prediction relationships

The results support the conclusion that the habitat index could successfully be related to both standard FRI data and FRI data in combination with ecological data, to distinguish three habitat quality classes. In each case, approximately 60% of the variance in habitat value could be explained using the quantitative data set under consideration. Although the addition of ecological data created a different model than the FRI data alone, it did not explain any more variance and created similar habitat quality categories. This analysis provides evidence that the relative abundance of arboreal lichen and deadfall density are important ecological parameters influencing micro-habitat suitability for woodland caribou. However, it does not necessarily support the need to measure these parameters during pre-harvest forest assessments or during FRI data collection since they did not help to create a better assessment of habitat suitability in this case.

With the exception of arboreal lichen, no other individual forage plant could be considered a predictor of habitat suitability. This is not surprising considering the variety and seasonal fluctuation in the forage plants that woodland caribou are known to consume (Bergerud, 1972). Generally, arboreal lichen is most important as a forage plant during winter (Bergerud, 1972). Mean scores for the arboreal index in this study were 1.4 (s=0.9, n=60) for winter sites, 1.3 (s=0.9, n=191) for other seasons, and 0.2 (s=0.5, n=141) for disturbed sites (J. Metsaranta, unpubl. data). Thus, in this study area, arboreal lichens appear to be equally abundant at sites used during all seasons, and much less abundant at disturbed sites.

Many studies have postulated the importance of arboreal or terrestrial lichen in determining habitat suitability for woodland caribou. However, few studies have considered deadfall density. The only habitat index component that did not differ between used sites and logged sites was the abundance of deadfall (Table 1). Measured deadfall density at burned sites was 17.3 stems m^{-1} (s=16.5, n=50), while measured deadfall density at all other sites was

5.2 stems m-^{1} (s=6.4 n=325) (J. Metsaranta, unpubl. data). Schaeffer & Pruitt (1991) also examined the influence of deadfall on woodland caribou, and found that deadfall densities were much higher in burned areas than in corresponding unburned areas that continued to be used by caribou. They found continued use of unburned or crown burned residual stands and unburned lowlands during summer, with an apparent lack of use only in winter (Schaeffer & Pruitt, 1991). Similarly, in this study, a number of animals continued to use unburned residual portions and unburned islands in lakes within the extensive area burned by the Webb Lake fire in 1989.

Previous telemetry studies in the Reed Lake area southeast of this fire documented traditional caribou use of the burned area prior to 1989, but generally during summer only (Shoesmith & Storey, 1977; Benoit, 1996). Although data for determining if the current level of use is less than before the fire is lacking, the results would still suggest that a certain level of habitat suitability remains within the burned area since it has not been completely abandoned. Previous studies have suggested that the reduction in caribou habitat suitability following fire occurs as a result of lichen combustion or increased snow accumulation reducing residual forage availability (Klein, 1982; Schaeffer & Pruitt, 1991). The results of this study suggest that deadfall accumulation may also be an important factor, with the degree of impediment to travel imposed by the accumulation of deadfall possibly limiting the use of burned uplands at all times of year.

Lichens begin to re-establish in both logged and burned areas anywhere from 10 to 50 years after disturbance, with regeneration potentially occurring sooner after logging than after fire (Harris, 1996; Webb, 1998). Although disturbance by fire may have short-term detrimental effects on caribou, the long-term effects tend to be positive in terms of forage productivity (Klein, 1982; Schaeffer & Pruitt, 1991). However, in the interim period, the post-fire accumulation of deadfall might concurrently discourage use of this habitat by all ungulates, by creating areas that are virtually impassable to travel.

The literature has generally emphasized the positive impacts of fire on moose habitat by its tendency to create more abundant forage for this species (e.g. Schwarz & Franzmann, 1989; Loranger et al., 1991). However, it is also acknowledged that this may not universally be the case, depending on such factors as fire intensity and pre-fire moose density (e.g. Peek, 1974; Gasaway et al., 1989). Some have suggested that moose appear to avoid blowdown areas, where presumably deadfall densities would be high (Cumming, 1980). If this was in fact true, and continued to be the case during the 15 to 40 year post-fire period when moose populations are thought to be highest (Schwarz & Franzmann, 1989), then changes in the composition of the faunal community (i.e. increases in moose populations, and as a consequence increases in wolf populations (e.g. Bergerud & Elliot, 1986; Seip, 1992)) that potentially have a negative effect on woodland caribou might not occur.

The proposed mechanism for preventing this faunal shift is the post-fire accumulation of deadfall that could occur under certain fire intensity and vegetation combinations. Such circumstances may create habitat that, for a certain period of time, is equally unsuitable for both woodland caribou and moose. In the 12 years after the Webb Like fire in 1989, two surveys of moose populations in this area have been conducted (Cross, 1991; Cross, 2000). An initial survey in 1990 predicted that moose density in this burned area should increase. However, a second survey in 2000 concluded that these increases had not yet occurred, and that areas where deadfall accumulations were high were nearly devoid of moose activity (Cross, 2000).

Conclusions

The analysis provides evidence for the efficacy of the visual score sheet method (Storey & Storey, 1980) for assessing microhabitat suitability for woodland caribou. It also shows that habitat index values calculated using the visual score-sheet index could be used as the basis to relate FRI and ecological parameters to microhabitat suitability. Any of the three methods presented here (i.e. the score sheet method or Model 1 and Model 2) could be used to select forest stands for inclusion into short and long-term leave areas and travel corridors with more confidence that they contain habitat that will be suitable for use by woodland caribou. This would potentially, at least at the microhabitat scale, mitigate some of the negative impacts that forestry and other development has had on this species.

However, it is known that different selective pressures act at different spatial scales to limit woodland caribou populations (Bergerud et al., 1990; Rettie & Messier, 2000). It is also known that there are no simple solutions to natural resource management problems, and that unless an ecosystem approach is applied, actions can have unwanted and unpredicted consequences (Thompson & Welsh, 1993). Management actions to conserve woodland caribou populations need to consider all the factors that potentially act to limit this species (Cumming, 1992). Ecologically, it is known that these act at both small and large spatial scales. Applying the models presented here could conserve habitat characteristics needed by woodland caribou at small spatial scales. However, a further investigation quantifying the pattern and arrangement of suitable habitat types at a larger spatial scale would further increase the confidence in the ability to mitigate the impacts of development on this species.

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Appendix

Habitat index component scores

The following is a description of the factors that were assessed at a site when assigning values to each of the seven habitat index components that comprised the aggregated habitat index. A full description of each of the habitat index components and how they are weighted to determine an aggregate score can be found in Storey & Storey (1980).

I – Stand Type:
- Newly Cleared Land - 1
- Pioneer Shrubs - 4
- Hardwoods (>70%) - 6
- Mixed Hardwoods (50-70%) - 7
- Mixed Softwoods (50-70%) - 10
- Softwoods (>70%) - 10
- Overmature forest (>50% softwoods) – 6

II – Tree Size Class/Canopy Closure:
- Semi-open mature - 10
- Semi-open mixed - 9
- Closed or open mature - 8
- Closed or open mixed - 7
- Semi-open or open poles - 5
- Closed poles - 4
- Regeneration - 2
- No trees present – 1

III – Cover (includes tree trunks and branches between 0.5 and 2.0 metres height):
- 0% - 1
- 25% - 5
- 50% - 10
- 75% - 8
- 100% - 5

IV – Food Plant Diversity (only species in significant amounts):
- No food species present - 1
- Only herbs - 3
- Mosses, lichens and herbs - 6
- Deciduous shrubs, mosses, lichens, and herbs - 8
- Evergreen shrubs, deciduous shrubs, mosses, lichens, and herbs - 10

V – Food Plant % Ground Cover:
- 0% - 1
- 25% - 4
- 75% - 8
- 100% - 10

VI – Deadfall:
- Impossible to walk - 1
- Difficult to walk - 3
- Some deadfall, but no problem walking - 10
- No deadfall - 8

VII - Area Diversity:
- Homogeneous, far from different stand type - 1
- Within 100 m of 1 different stand type - 5
- Within 100 m of 2 different stand types - 8
- Within 100 m of >2 different stand types - 10

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Single-island home range use by four female Peary caribou, Bathurst Island, Canadian High Arctic, 1993-94

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Abstract: Spatial and temporal use of seasonal, and collectively, annual ranges by four female Peary caribou (Rangifer tarandus pearyi) was investigated using satellite telemetry. Knowledge of how caribou use space allows a better understanding of their demands on those ranges and enhances evaluation of associated environmental stressors. The study took place during an environmentally favorable caribou-year with high reproduction and calf survival and low (none detected) 1+ yr-old mortality, 1 August 1993 to 31 July 1994, Bathurst Island, south-central Queen Elizabeth Islands, Canadian High Arctic. All four females exhibited a pattern of single-island seasonal, and collectively, annual range use. Estimates of the maximum area encompassed by each individual during the course of the annual-cycle varied from 1735 to 2844 km^2 (mean±SE=2284±250 km^2). Although, there was 46% spatial overlap among individual ranges, temporal isolation resulted in the four individuals maintaining seasonal ranges distinctly separate from each other. This collective area encompassed 4970 km^2 and equaled about 31% and 18% of Bathurst Island and the Bathurst Island complex, respectively. Individual wintering areas formed a relatively small portion of each individual's annual range (mean±SE=71±17 km^2): 24 km^2, 158 days of occupation, <1% of the annual area; 70 km^2, 187 days, 4%; 95 km^2, 200 days, 4%; and 94 km^2, 172 days, 6%. Seasonal movements were greatest during pre-rut and pre-calving.

Key words: displacement vs. travel, distributions, Rangifer tarandus pearyi, movements, satellite telemetry locations.

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Introduction

Collection of detailed information on seasonal and annual movements and distributions of Peary caribou (Rangifer tarandus pearyi) has been limited by the high costs to carry out studies that require considerable aerial support. Year-round monitoring has been prevented, even with the use of conventional Very High Frequency (VHF) radio telemetry, by winter unavailability of suitable survey aircraft; stormy weather, fog, and white-outs; along with the long 'Polar night' from November into February.

The Peary caribou was listed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) as 'Threatened' in 1979 (Gunn et al., 1981) and then as 'Endangered' in 1991 (Miller, 1990b). In 1989, the Canadian Wildlife Service selected the south-central Queen Elizabeth Islands, centered on Bathurst Island (Fig. 1), to continue ecological studies of the relationship between Peary caribou and their environment, particularly the stresses of unfavorable winter and spring snow and ice conditions. The area is important because the Inuit of Resolute Bay (74°41'N, 94°50'W) on Cornwallis Island have resumed hunting caribou on Bathurst Island in the 1990s (Fig. 1). The caribou on Bathurst and its satellite islands are the most accessible to those hunters. Also, based on past performance this population of Peary caribou appears to have, during climatically favorable periods, the potential to support the desired level of annual harvest.

For the reasons listed above, satellite telemetry permits a much fuller investigation of the spatial and temporal aspects of seasonal and year-round range

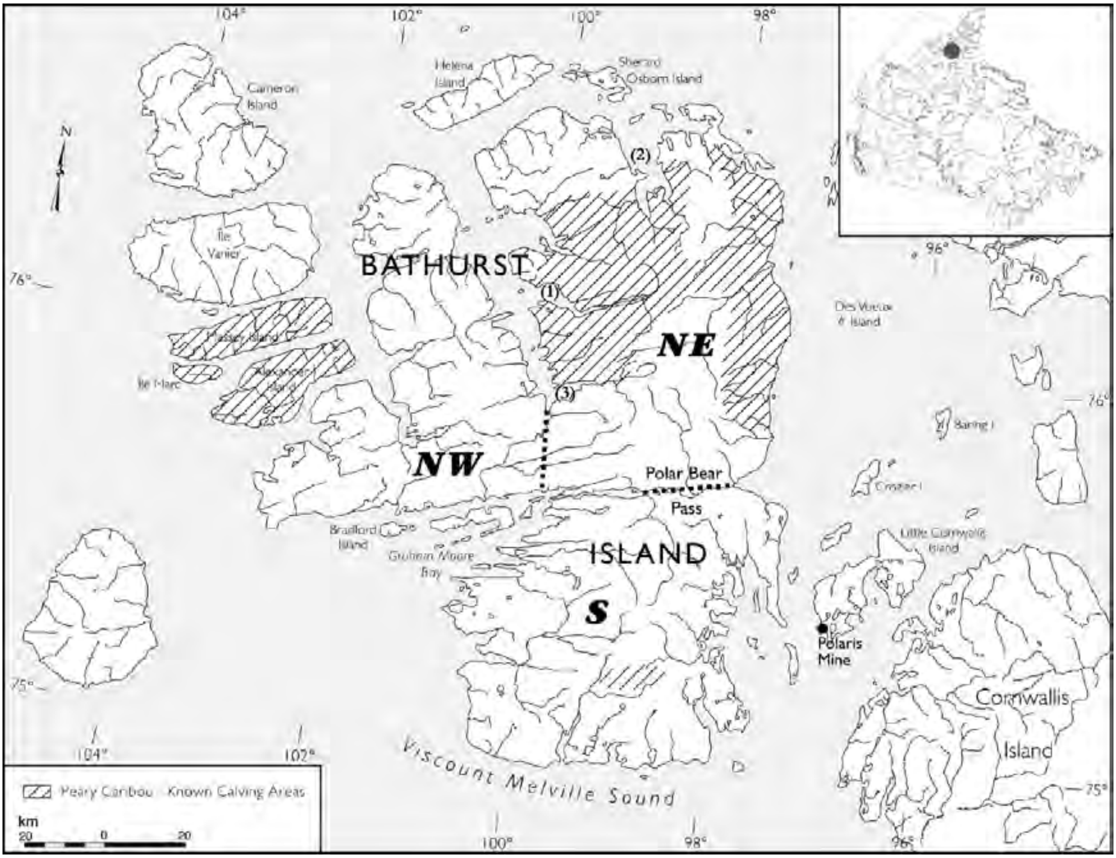

Fig. 1. Bathurst Island complex, south-central Queen Elizabeth Islands, Canadian High Arctic: Bathurst Island divided into 3 survey strata, northwest (NW), northeast (NE), and southern (S); and all known calving areas within the Bathurst Island complex shown (from Miller, 2002): (1) Stewart Bay area; (2) Young Inlet area; and (3) Dundee Bight area on Bathurst Island, plus Alexander and Massey islands to the west of Bathurst Island.

use than previously possible, even with VHF radio telemetry. The use of satellite telemetry neck-collars on Peary caribou was initiated in July 1993. The following is an analysis of seasonal, and collectively, annual range use by four female Peary caribou equipped with telemetry neck-collars on Bathurst Island, Canadian High Arctic, between 1 August 1993 and 31 July 1994. The findings are based on satellite location-data points obtained from Service Argos Inc. The sample size of animals is minute but the previous total lack of such detailed information for Peary caribou warrants documentation of these findings. This is particularly true because of the Peary caribou's 'Endangered' status and because these findings considerably advance our understanding of the ecology of Peary caribou. This work is a first step in gaining insight into how Peary caribou use seasonal range on a relatively large island (Bathurst Island, 16 042 km^2) during an environmentally favorable annual-cycle.

Material and methods

Study area and animals

Our study area is the 'Bathurst Island complex' - a grouping of 30 south-central Queen Elizabeth Islands in the Canadian High Arctic (Miller, 1998). The entire Bathurst Island complex is about 28 000 km^2. The islands are mostly low-lying and mainly below 150 m above mean sea level (amsl) in elevation, with typical high arctic tundra vegetation. The general climate, geology, topography, and vegetation have been described (see Miller, 1998 for references).

Bathurst Island itself was divided into three strata: Northeast (NE), 6630 km^2; Northwest (NW), 4068 km^2; and South (S), 5344 km^2 (Fig. 1). The major area of interest in this study is NE Bathurst Island. Although Bathurst Island is mainly low-lying, the terrain is broken and many sites lie between 150 and 300 m amsl, with a maximum elevation of 412 m amsl on northern NW Bathurst Island. The configuration of the island results in a proportionately long coastline with numerous drainages feeding freshwater into the sea. Many of these drainages along the west coast of NE Bathurst Island have steep embankments, rising to intermediate elevations >150 m amsl. The rough right-angle orientation of these drainages to the prevailing northerly winds and the rapidly increasing hours of daily sun during late winter promote the earlier removal of snow on those sites both by wind action and sublimation. The resulting mosaic of patches of snow-free ground and shallow snow-covered areas provide the most favorable late winter and spring ranges for Peary caribou.

Prior to our study, the Peary caribou on Bathurst Island suffered a 68% single-year major decline in winter and spring 1973-74 (Miller et al., 1977a; Miller, 1998; Miller & Gunn, this proceedings). Then, from some time after summer 1974, the caribou population on Bathurst Island and within the entire Bathurst Island complex experienced an overall continual period of growth to summer 1994, averaging about 13% • yr^{-1} (Miller, 1998; Miller & Gunn, this proceedings). By summer 1993 the inter-island population of Peary caribou within the Bathurst Island complex appeared to be of a healthy size, well represented by the various sex and age classes, and highly productive (Miller, 1995b). This favorable condition continued throughout autumn, winter, spring, and summer 1993-94: we counted 2400 Peary caribou by low-level helicopter survey and estimated about 2700 caribou within the Bathurst Island complex (Miller, 1995b). Nearly 95% (2273) of those caribou were seen on Bathurst Island and 79% (1790) of them were on NE Bathurst Island. Among the 12 survey search zones established on Bathurst Island, caribou were over-represented relative to the available landmass in each zone only on the interior of NE Bathurst Island (Miller, 1995b).

The potential for increasing abundance was high based on the population's sex and age composition within the Bathurst Island complex (Miller, 1995b). The sex ratio for the 1256 1-yr-old or older caribou (1+ yr-old) counted among those 1790 caribou on NE Bathurst Island was 39 males : 61 females (or 64 males : 100 females). Calves represented 30% of all caribou counted on NE Bathurst Island (the supposed theoretical maximum realized rate of annual increase, Bergerud, 1978). Nearly all (97%) of the breeding cows still had a calf at heel, and there was, on average, one bull for every three breeding cows.

Procedures

Peary caribou were captured using an aerial net-gun (Barrett et al., 1982). A Bell 206L (Jet Long Ranger) turbo-helicopter on high skid gear was used as the pursuit aircraft. Each telemetry neck-collar housed a satellite Platform Transmitter Terminal (PTT) package and a conventional VHF radio package (Telonics, Electronics Consultants, 932 E. Impala Avenue, Mesa, Arizona, U.S.A.). Details of the capture equipment and the telemetry packages; capture, handling, and release procedures; and results of the capture efforts are reported in Miller (1995b; 1997).

Location-data points were received monthly from Service Argos Inc., Landover, Maryland, U.S.A. Only location-data points with a Service Argos Quality Class (QC) rating of QC-1, -2, or -3 were used to determine a single location-data point for each duty-day. For the purpose of mapping the seasonal caribou movements, the location-data point with the highest QC rating (3, <150 m; 2, <350 m; and 1, <1000 m) was selected on each duty-day. When more than one location-data point of the same QC rating occurred on the same duty-day, they were averaged to obtain a single composite location-data point. Location-data points of QC-0 (>1000 m) were examined but were found unreliable.

The duty-cycle for the PTTs varied among four seasons: first a 5-day interval from 22 July 1993 until 30 September 1993 (12 h on, 108 h off); followed by a 2-day interval from 30 September to 15 November 1993 (12 h on, 36 h off); next a 5-day interval from 15 November 1993 until 14 May 1994; and then a 2-day interval from 14 May to 23 July 1994. The duty-cycle was then automatically reset to a new four-season cycle. Thus, between 1 August 1993 and 31 July 1994, the PTTs could potentially provide location-data points on 108 days.

To estimate the maximum area encompassed by each individual caribou during the course of their annual-cycle we connected the perimeter points of their satellite location data. We separated each individual's range use into temporal periods based on the known annual life-history cycle of caribou (e.g., Bergerud, 1978). Consecutive location-data points within these temporal periods were either linear directional movements or multi-directional traverses within a confined area. We grouped these consecutive location-data points by their respective style into temporal periods by visual inspection. We designated those discernible periods as either an 'Area Period' or 'Movement Period' (see Table 2). We then described each individual's annual use with schematic illustrations that clarify their spatial and temporal aspects (see Figs. 2-5). A Movement Period can best be described as an extended duration of range use along a continual path of travel, as opposed to an Area Period which has breadth and has all observations confined to a more specific section of range.

Table 1. Approximation of annual size of areas encompassed by perimeter locations and associated relevant land statistics for four female Peary caribou, Bathurst Island, Canadian High Arctic: based on connection of satellite perimeter location-data points obtained during an environmentally favorable year, 1 August 1993 to 31 July 1994.

Animal I.D.[a]	Maximum latitudinal axis (km)	Maximum longitudinal axis (km)	Size of annual home range (km^2)	% of total area of Bathurst Island occupied[b]	% of total area of Bathurst Island complex[b]
93-02F	81	57	2844	17.7	10.3
93-03F	59	57	1735	10.8	6.3
93-04F	47	58	2017	12.6	7.3
93-05F	89	47	2542	15.8	9.2
(Mean±SE)	(69±9.7)	(55±2.6)	(2284±250)	(14.2±1.6)	(8.3±0.9)

[a] Satellite-collared animal I.D., F equals female.

[b] Bathurst Island equals 16 042 km^2 and Bathurst Island complex equals 27 592 km^2.

We make a distinction among 'movement', 'travel', and 'displacement': movement or travel is the actual path traveled by a caribou and is the asymptotic limit of discrete location-data points as the time interval between them becomes shorter. This actual path is always unknown with satellite location-data - only continuous location data would provide this. The distance the animal actually moves or travels can at best only be approximated by the displacement between consecutive points. The terms 'movement' and 'travel' are thus misleading in their application to actual 'rates of movement', 'movement distance', 'rates of travel', and 'travel distance'. Whereas, 'displacement' is directly measurable using these data and best defines the actual point to point measurement and its ecological limitations should be clear. Thus, we use displacement as our unit of measure and we define 'displacement' as the difference between the initial position and any later position, measured as a horizontal plane vector. For example, two observations at a 5-day interval yields a 100 km south to north displacement during migration. However, the animal may have traveled 50 km NW from its origin, then 100 km due east, and finally 90 km again NW. Thus, it actually traveled 240 km to realize a 100-km displacement. Therefore, any measure of movement or travel distance and or rates, in this example, would be 58 percent in error. In addition, we still would not know whether that movement, travel, or displacement was accomplished in 3 or 4 days rather than 5 days, as determined by the 5-day sampling interval.

We examined variation in short-term rates of displacement by seven time interval classes (0.01-0.2, 0.2-0.4, 0.4-0.6, 0.6-0.8, 0.8-1.0, 1.0-2.0, and 2.0-8.0 h) location data. We restricted our analyses to only those rates of travel that were physically possible for a caribou to sustain (set at <16 km • h^{-1}). The majority (62%) of the spurious values that we omitted came from the lowest time interval class, 0.01-0.2 h. More importantly, the frequency of occurrence of spurious values was many times greater in this shortest time interval class than in other classes.

Results

Satellite location data

Adequate sets of location-data points in QC-1, -2, and -3 were obtained for four females during the study year (Tables 1-3, Figs. 1-7, females 93-02, 93-03, 93-04, 93-05). The limited number and fragmentary distribution of location-data points obtained in QC-1, -2, and -3 for the fifth PTT-collared animal (female, 93-01) did not allow any analysis or production of a map of her seasonal range and movements or her annual distribution. However, the limited QC-1 to QC-3 location-data points obtained from her suggested that she too had remained on NE Bathurst Island throughout the study period.

Range use

Other than by coastlines, neither the size nor the configuration of the area encompassed by each female appeared to be influenced by the size or configuration of NE Bathurst Island. None of the four females used any of the remaining 11 072 km^2 on Bathurst Island during the August 1993 to July 1994 study period: 1783 km^2 on the NE; 3945 km^2 on the NW; and 5344 km^2 on the S. All location-data points indicate that the females captured on NE Bathurst Island in late July 1993 remained there through July 1994 (Figs. 2-5). Estimates of the areas

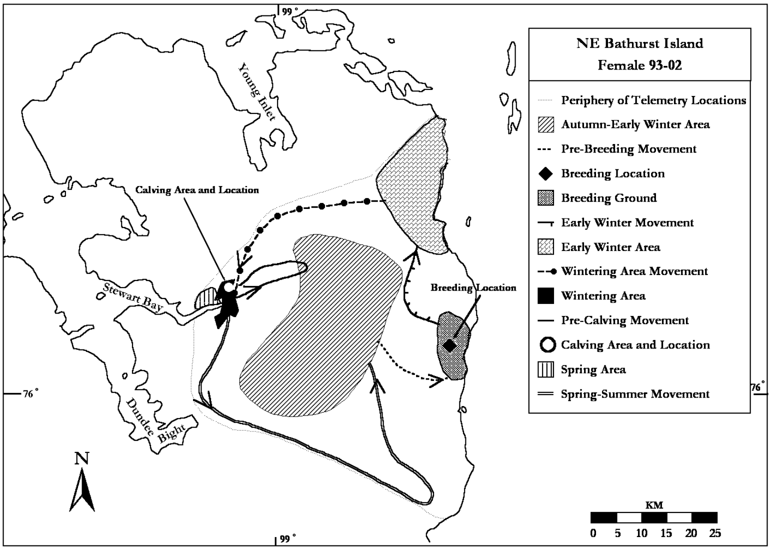

Fig. 2. Schema of seasonal range occupation and major directional movements of female Peary caribou 93-02 during the annual-cycle of the study period, Bathurst Island, Canadian High Arctic, 1 August 1993 to 31 July 1994: extrapolated from satellite location-data points.

encompassed by each individual averaged 2284 ± 250 km^2 SE and varied from 1735 to 2844 km^2 (Table 1).

The collective land area encompassed by these four females was 4970 km^2: essentially all (98%) of it was on NE Bathurst Island and represents 73% of the NE Stratum (Figs. 1-5). Less than 3% (123 km^2) of the collective area extended into NW Bathurst Island (Figs. 1, 4). Female 93-04 was the only one of the four that occupied it. Thus, the four females collectively ranged over only 18% of the entire Bathurst Island complex and only 31% of Bathurst Island.

All individuals occupied the smallest ranges during most of the winter on a monthly and seasonal basis (Table 2; Figs. 2-5). Female 93-02 confined herself to only 24 km^2, female 93-04 to 70 km^2, female 93-05 to 94 km^2, and female 93-03 to 95 km^2.

Shifts in monthly ranges were relatively large in September, October, and November during Pre-Breeding, Breeding, and Early-Winter periods

Table 2. Discernible periods recognized for four PTT-collared female Peary caribou, Bathurst Island, Canadian High Arctic, 1 August 1993 to 31 July 1994.

Discernible periods in a caribou-year	Female 93-02	Female 93-03	Female 93-04	Female 93-05
Autumn Movement		1 Aug-26 Aug		
Autumn-Early Winter Area	1 Aug-10 Oct	26 Aug-14 Oct	1 Aug-2 Oct	1 Aug-25 Sep
Pre-Breeding Movement	10 Oct-16 Oct	14 Oct-18 Oct	2 Oct-14 Oct	25 Sep-16 Oct
Breeding Location	18 Oct	18 Oct	18 Oct	18 Oct
Breeding Ground	16 Oct-20 Oct	18 Oct-24 Oct	14 Oct-18 Oct	16 Oct-20 Oct
Early Winter Movement	20 Oct-25 Oct			
Early Winter Area	25 Oct-20 Nov			
Wintering Area Movement	20 Nov-15 Dec	24 Oct-26 Oct	18 Oct-30 Oct	20 Oct-25 Nov
Wintering Area	15 Dec-22 May	26 Oct-14 May	30 Oct-4 May	25 Nov-16 May
Pre-Calving Area		14 May-28 May	18 May-1 Jun	
Pre-Calving Movement	22 May-1 Jun	28 May-1 Jun	4 May-18 May	16 May-30 May
Calving Location	3 Jun	4 Jun	3 Jun	3 Jun
Calving Area	1 Jun-5 Jun	1 Jun-5 Jun	1 Jun-9 Jun	
Calving-Spring Area				30 May-17 Jun
Spring Movement		5 Jun-13 Jun		17 Jun-19 Jun
Spring Area	5 Jun-19 Jun			
Late Spring-Early Summer Area				19 Jun-3 Jul
Spring-Summer Movement	19 Jun-13 Jul		9 Jun-23 Jul	
Summer Movement				3 Jul-17 Jul
Summer Area	13 Jul-31 Jul			17 Jul-31 Jul

(Table 2; Figs. 2-5). Subsequently, shifts in range size of similar magnitudes then occurred during the Pre-Calving Period in May at the end of late winter and in the beginning of June, just before spring calving (Figs. 2-5). At the time, accessibility to an adequate quantity of forage was assured by the widespread relative abundance of summer-time forage throughout the region. However, the relatively large size of each caribou's summer range most likely resulted from its tracking of the plant phenology in order to maximize and prolong its intake of the highest quality forage as new stands became available on different parts of its range (e.g., Miller, 1995b; 1998).

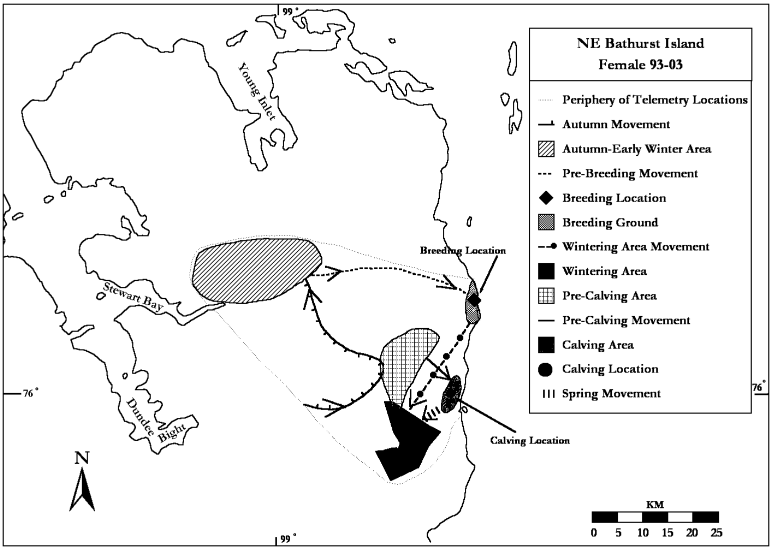

Fig. 3. Schema of seasonal range occupation and major directional movements of female Peary caribou 93-03 during the annual-cycle of the study period, Bathurst Island, Canadian High Arctic, 1 August 1993 to 31 July 1994: extrapolated from satellite location-data points.

Individual Ranges

We were able to collectively discern 20 periods among the four PTT-collared female Peary caribou during the annual-cycle of the study period (Table 2; Figs. 2-5). However, each individual female exhibited only 11 to 14 of those detectable breaks in their respective pattern of range use (Table 2). Only eight of the discernible divisions were shared by all four females (Table 2).

Only one female (93-02) made a detectable Autumn Movement, which lasted 26 days. Time spent by all four females on their respective Autumn-Early Winter Area varied from 49 to 71 days (mean±SD=59.8±9.4 days). Then, Pre-Breeding Movement lasted for 4 to 21 days (mean±SD=10.8±7.6 days) before each female arrived on her respective Breeding Ground, where they spent only 4 to 6 days (mean±SD=4.5±1.0 days). Only one female (93-02) made a 5-day Early Winter Movement from the Breeding Ground to an Early Winter Area, where she spent 26 days, before making her Wintering Area Movement. The other three females each made a Wintering Area Movement directly from their respective Breeding Ground to their respective Wintering Area. Wintering Area Movement varied from only 2 days to 36 days (mean±SD=18.8±14.8 days). Each female then spent nearly half or slightly

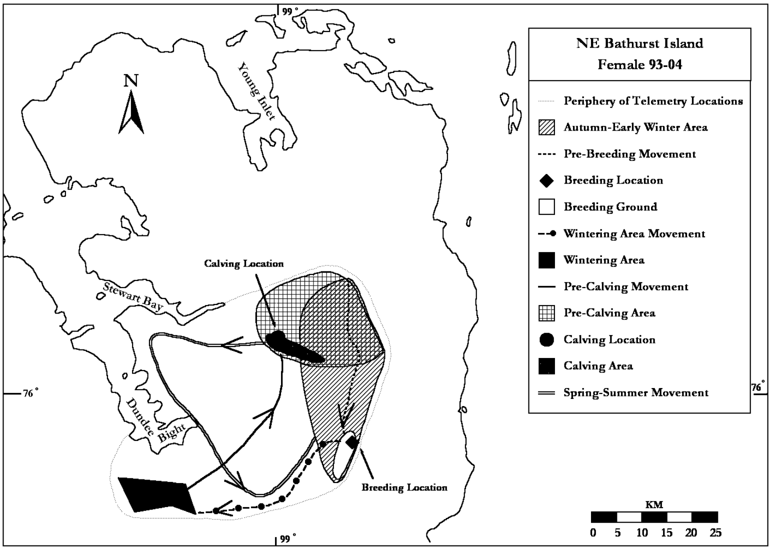

Fig. 4. Schema of seasonal range occupation and major directional movements of female Peary caribou 93-04 during the annual-cycle of the study period, Bathurst Island, Canadian High Arctic, 1 August 1993 to 31 July 1994: extrapolated from satellite location-data points.

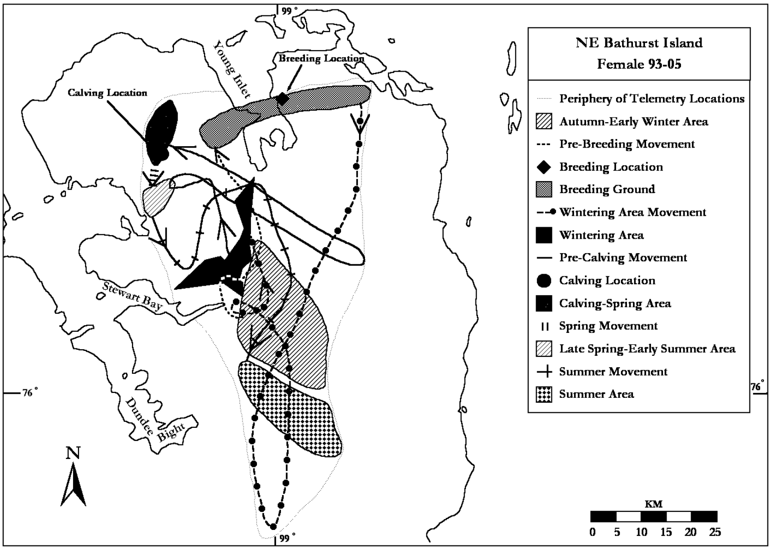

Fig. 5. Schema of seasonal range occupation and major directional movements of female Peary caribou 93-05 during the annual-cycle of the study period, Bathurst Island, Canadian High Arctic, 1 August 1993 to 31 July 1994: extrapolated from satellite location-data points.

more than half of the annual-cycle on her respective Wintering Area (mean±SD=179.3±18.2 days): duration, 158-200 days (Figs. 2-5). Two of the females (93-03, 93-04) occupied a Pre-Calving Area for 14 and 13 days, respectively, before making their Pre-Calving Movement. The Pre-Calving Movement varied from 4 to 14 days (mean±SD=10.3±4.8 days) among the four females. Three of the females (93-02, 93-03, 93-04) then spent 5, 4, and 8 days, respectively, on their Calving Area. The fourth female (93-05), however, occupied a Calving-Spring Area, where she spent 18 days (4 days before calving and 14 days post-calving). A detectable Spring Movement was made by only two females (93-04, 93-05), 8 and 2 days, respectively. Only one Spring Area was recorded, 93-02, 14 days (no satisfactory location-data points were obtained for 93-03 between 13 June and 29 July 1994 but the 29 July location placed her in the same general area as her 13 July location). One female (93-05) held a Late Spring-Summer Area for 14 days. Two of the four females (93-02, 93-04) made an extensive Spring-Summer Movement of 24 and 44 days duration, respectively. One female (93-05) made a Summer Movement that lasted 14 days. Lastly, two females (93-02, 93-05) occupied a Summer Area for 18 and 14 days, respectively (the number of satellite location-data points were not satisfactory enough to evaluate the Summer Area for 93-03). Female 93-04 remained in a movement phase from 9 June until at least 23 July 1994, but whether she settled on an area during the last week of July or kept moving is unknown.

Table 3. Measures of variation in long-term rates of displacement for four female Peary caribou, Bathurst Island, Canadian High Arctic, 1 August 1993 to 31 July 1994: presented by individual female and by movement period.

Animal I.D.	Movement period	Duration of movement period (days)	Displacement distance (km)	Minimum distance traveled (km)	Ratio: displacement vs. Minimum distance	Displacement as % of minimum distance
93-02	Wintering Area	25	45.6	59.6	1:1.3	76.5
	Pre-Calving	10	4.0	34.0	1:8.5	11.8
	Spring-Summer	24	34.8	120.4	1:3.5	28.2
93-03	Autumn	26	28.2	54.8	1:1.9	51.4
93-04	Pre-Breeding	12	35.2	38.0	1:1.1	92.6
	Wintering Area	12	34.8	38.3	1:1.1	90.9
	Pre-Calving	14	33.1	38.2	1:1.2	86.6
	Spring-Summer	44	22.4	90.4	1:4.0	24.8
93-05	Pre-Breeding	21	31.7	50.3	1:1.6	63.0
	Wintering Area	36	36.0	171.2	1:4.8	21.0
	Pre-Calving	14	29.2	133.1	1:4.6	21.9
	Summer	14	40.5	87.7	1:2.2	46.2

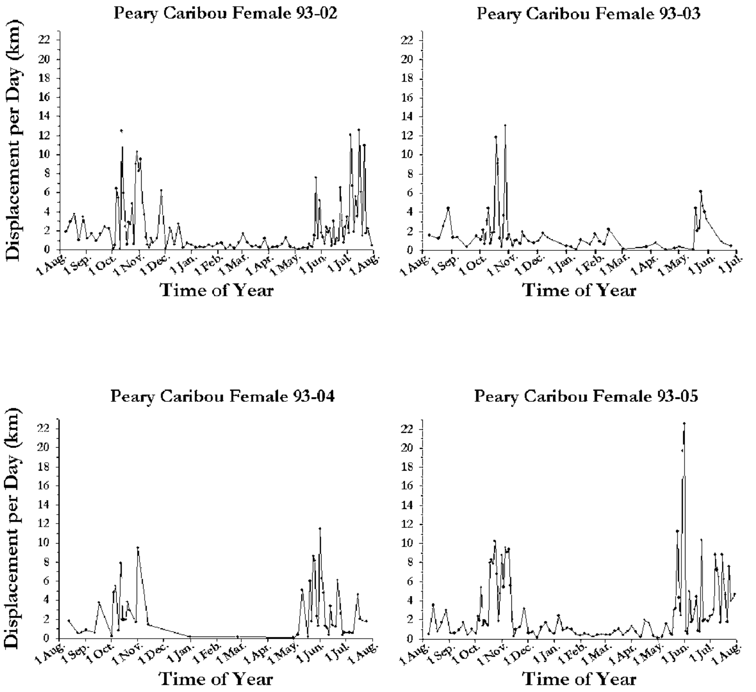

Fig. 6. Average daily displacements (km) for four PTT-collared female Peary caribou, Bathurst Island, Canadian High Arctic, 1 August 1993 to 31 July 1994: extrapolated from satellite location-data points.

Potential social affinities

Spatial overlap only among the four caribou was 46% of their overall range (Figs. 2-5). This is an ecologically limited statistic as it does not account for the all-important temporal overlap that occurred, which was much less. Although spatial overlap of individual ranges during the annual-cycle of the study period was appreciable, no evidence of any social affinities between or among any of the four females was obtained. Close association of the females was restricted temporally (Figs. 2-5). The temporal potential for socialization among all four females occurred only in August. Thus, although two to four females occurred on the same general section of range at the same time, all distances separating them at those times did not support close association between or among any of them (Table 3). Analysis of separation distances for 357 paired same-date observations did not indicate that any of the four females belonged to the same persistent social grouping or even to the same temporary social aggregation during any period of the 1993-94 annual-cycle.

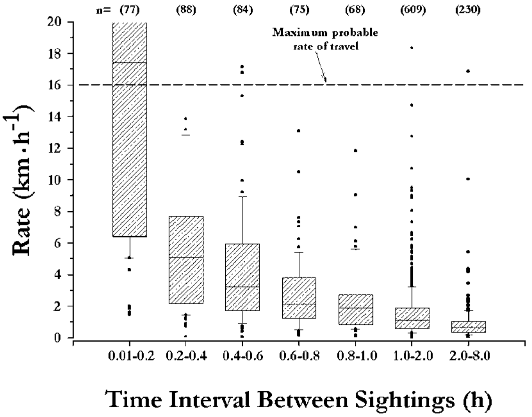

Fig. 7. Standard Box Plot (10th, 25th, 50th, 75th and 90th percentiles, and outliers) illustrating variation in short-term rates of displacement by time interval classes for four female Peary caribou, Bathurst Island, Canadian High Arctic, 1 August 1993 to 31 July 1994.

Displacement vs. minimum distance traveled

The distances moved by Peary caribou in this study, their associated rates of displacement and the assumed rates of travel were not outstanding for caribou (Table 3; Fig. 6). About 52% of the consecutively paired samples obtained in the 0.01-0.2 h time interval were not used because their application would have yielded rates of displacement or travel that are physically impossible for caribou to sustain over hours (Fig. 7). The remaining usable samples in the 0.01-0.2 h class still produced the highest average rate of displacement. From this class the average rate of displacement fell by 52% between 0.2-1.0 h and declined a further 64% between 1.0-8.0 h. For the 48-h and the 120-h class, the average rate of displacement fell another 15% and then plummeted nearly 94% more at 240 to 1056 h (Table 3).

About half of the rates of displacement obtained during the ultra-short 0.01-0.2 h time interval appear to be markedly inflated by the influence of the compressed time interval and the possible maximum error associated with location-data points. At maximum possible error, based on information provided by Service Argos Inc., this error varied between 2000 m for QC-1 to QC-1 comparisons and 700 m for QC-2 to QC-2 comparisons.

Displacement distances, the direct line displacement from the beginning point to the end point, for large time-scale movements (Table 3: 240-1056 h; n=12) averaged 59% less than the summed distance the animals displaced along consecutive sample points to the same end. Based on the summation of points in this shorter time scale, on average, the caribou traveled at least 2.4 times as far as going directly from start point to end point. This represents a significant error in using the start point to end point distance over even several hours let alone over several days or more to obtain distance traveled or a rate of travel. Among the 12 Movement periods this ratio varied between 1:8.5 and 1:1.1. That is, the displacement equaled only about 12% to nearly 93% of the measured minimum distances traveled during each Movement Period (Table 3).

Productivity

The winter and spring of 1993-94 (and 1992-93) were highly favorable for caribou survival and the production and rearing of young. All five females captured on NE Bathurst Island had calves at heel in late July 1993 and in August 1993 2-3 weeks after capture and release. Visual observations obtained during VHF radio-tracking flights and other aerial search efforts between April and August 1994 indicated that all five 1993 calves survived to be yearlings and that all five cows again produced viable neonates on the known calving areas on NE Bathurst Island in the first week of June 1994 (Figs. 1-5). All of those calves and yearlings were still alive in August 1994.

All 5 females most likely calved about 3 June 1994, each of them had a newborn (1 or 2 d-old) calf at heel on 4 June when all five females were located visually during VHF radio-tracking helicopter searches. Female 93-01 calved on the west side of the major drainage running north-south from Young Inlet south to Stewart Bay. Female 93-05 calved at about the same latitude as female 93-01 but several kilometers to the west (93-05's offspring appeared no more than a day, and possibly only hours old, when seen on 4 June 1994). Female 93-02 calved near the head of Stewart Bay on the north side of the river flowing into the head of the bay (Stewart River). Female 93-04 calved several kilometers SE of the head of Stewart Bay and north of Dundee Bight. The fifth cow, 93-03, calved several kilometers inland from the east coast on NE Bathurst Island at about 76°N latitude.

Peak rutting activities apparently took place between 14 and 22 October 1993. The most likely date of breeding for all five PTT-collared females appears to be 18 October 1993, determined by back dating from 3 June 1994 for an assumed average 228-day gestation period (Bergerud, 1978). All five females participated in the rut on NE Bathurst Island (Figs. 2-5).

Discussion

Range use

All of the existing information indicates that Peary caribou on Bathurst Island favor northern Bathurst Island and particularly NE Bathurst Island (e.g., Tener, 1963; Miller et al., 1977a; Ferguson, 1987; Miller, 1987; 1989; 1995b; 1998). This study is, however, the first to document year-round use of NE Bathurst Island by individual Peary caribou. The findings indicate that caribou on Bathurst Island obtained their daily maintenance requirements on relatively small ranges, especially during wintertime. Use of larger sections of range during summer and autumn apparently simply reflect the widespread relative abundance and availability of forage and the foraging strategies employed at those times of the year (e.g., Miller, 1995b; 1998; Thomas et al., 1999).

An alternative in range-use patterns by Peary caribou involving multi-island seasonal ranges and collectively as annual range was exhibited by an additional female and a male Peary caribou during this study period (Miller, 2002). The female used five islands (Fig. 1: Vanier, Cameron, Alexander, Massey, and Marc), moving from one island to the next on 11 separate occasions throughout the year. The male used six islands (Fig. 1: Bathurst, Vanier, Cameron, Alexander, Massey, and Marc), moving from one island to the next on 16 separate occasions. As for the four female caribou on Bathurst Island in our study, their seasonal home ranges were the largest in summer and smallest in winter and their seasonal movements (displacements) greatest during pre-rut and pre-calving periods. The collective multi-island home range area of each of these two caribou was smaller in size than that of the four female Peary caribou that remained year-round on NE Bathurst Island: female, 1221 km^2; and male, 1607 km^2 vs. between 1735 to 2844 km^2 for the four females.

Gunn & Fournier (2000) satellite tracked four female caribou on NW Victoria Island from 1987 to 1989. Their findings were similar to ours: the animals occupied the smallest monthly home ranges in winter and the largest in summer and monthly movements (displacements) were greatest during pre-calving and pre-rut periods. They also found on a multi-year basis that the four individuals maintained similar annual home ranges from year to year on NW Victoria Island and did not move to other areas of the island.

Individual ranges

None of the PTT-collared females made any use of S Bathurst Island and only one made a slight excursion to NW Bathurst Island over the 'artificial boundary' between the survey strata of NE and NW Bathurst Island during the study period. It is most likely that the actual range used by each female for annual forage requirements on NE Bathurst Island is only a relatively minor proportion of the area that we encompassed by connecting the perimeter satellite location-data points for each caribou. Much of the area encompassed by each caribou might never have been used by them and what was used may be linked more directly to intra- and inter-specific interactions and variations in individual learned behavior rather than the forage supply *per se*. Even the relative unavailability of forage in winter and spring caused by snow and ice conditions did not appear to have been a major determinant in the favorable year of 1993-94.

We have no direct measure of the amount of range that was used to meet each animal's annual food budget. We can, however, estimate the theoretical minimum range necessary to meet a Peary caribou's annual forage requirements at a given rate of foraging that is sustainable by the vegetation being used. That is, we can assume from Miller (1998) that 730 kg dry matter (DM) of forage • caribou^{-1} • yr^{-1} is a reasonable estimate of the annual forage requirements of the small-bodied Peary caribou, based on findings from White & Trudell (1980a; 1980b), White et al. (1981), and R. G. White (pers. comm., 1998). For the sake of discussion, we will arbitrarily assume that Peary caribou within the Bathurst Island complex obtained an extremely low value, on average, of 0.1 g DM forage • m^{-2}. When we make this assumption, we find that one of those caribou could still realize its annual food requirements from as little as 7.3 km^2. This represents only an exceptionally minor proportion (0.3-0.4%) of the area encompassed by each of the four females on Bathurst Island in 1993-94 (Table 1).

This assumed rate of forage utilization would represent only 1% of an assumed standing crop of 10 g DM forage • m^{-2}. Most importantly, it represents only 0.3% of the average plant biomass estimated by Thomas et al. (1999) on adjacent eastern Melville Island in summer 1974, immediately after the major winter and spring die-offs of nearly half of all the caribou (and muskoxen, *Ovibos moschatus*) throughout the western Queen Elizabeth Islands (Miller et al., 1977a: ca. 99 000 km^2).

Detailed documentation of the relatively extensive displacements that were made in early winter, late winter, spring, and summer (Figs. 2-5) could be of great importance in evaluating range-use patterns. If those displacements had occurred in an environmentally stressful year, they would have been interpreted as responses to relative forage unavailability brought on by severe snow and ice conditions, or even an absolute forage shortage. However, summer 1993 to summer 1994 was a highly favorable period for the caribou under consideration, with high reproduction and survival of calves in 1993 and 1994, high recruitment from 1992 to 1993 and 1993 to 1994, and such low annual mortality among 1+ yr-old caribou that it went undetected during considerable search effort in each year (Miller, 1995b; 1997; 1998). The winter range was open with relatively little restriction of the forage supply. Therefore, there is no reason to believe that displacements were weather or food motivated in 1993-94. We should not, however, lose track of the fact that such displacements in unfavorable years could possibly be in response to widespread relative forage unavailability. If they were, however, they should be longer in duration and possibly with no return to origin. Perhaps, most importantly, extensive displacements should be associated with a detectable higher seasonal mortality, no mortality at all was detected during this study.

That all of the caribou maintained their smallest monthly ranges during wintertime (Figs. 2-5) warrants special consideration. As the forage supply is both absolutely and relatively more abundant and widely available during the remainder of the year, it seems reasonable that Peary caribou could live year-round on similar-sized areas. This supposition is strongly supported by subsequent satellite location data obtained from female 93-03 in 1994-96 (unpubl. data). In late December 1994, female 93-03 and at least her 1994 offspring moved off southeastern Bathurst Island and traveled eastward across the sea ice to Baring Island—a small, flat island only 21 km^2 in size and about 50 km east from Bathurst Island. They then remained on Baring Island for 13 months until late January 1996, possibly along with three bulls and a subadult male. We observed the three bulls and subadult male in association with female 93-03 and her yearling in July 1995. Even if the males remained on Baring Island for only 6 months (Jun-Nov 1995), the collective animal-months of range use would have totaled >4 yr or the equivalent, on average, of 5 km^2 • animal^{-1} • yr^{-1}. Each animal most likely would have ranged over the entire island during their stay there. When vegetation on Baring Island was visually inspected and sampled in summer 1998, no evidence of range overuse was detected (A. Gunn & G. Henry, 2001, pers. comm.). Therefore, we must conclude that when necessary, it is possible for Peary caribou to live year-round for at least 1 year on about 10 km^2 • $animal^{-1}$ • yr^{-1} at a mean density of about 10 caribou • 100 km^2 • yr^{-1} or possibly, even as little as on about 5 km^2 • $animal^{-1}$ • yr^{-1} at a mean density of about 20 caribou • 100 km^2 • yr^{-1}. It is interesting to note, although not directly comparable and perhaps solely by coincidence, that a 5 km^2 annual home range is a value reported for Svalbard reindeer (R. t. platyrhynchus) by Tyler (1987).

At first thought, the reader may think that severe reduction in the size of range used during winter is a common phenomenon among North American cervids. However, this wintertime restriction in the use of range by Peary caribou is not directly comparable to areas where deer use 'wintering yards.' Those deer concentrate when experiencing prolonged deep snow cover on relatively small areas within the animal's total winter range. Spatial restriction on tundra range where snow depth seldom interferes with travel per se is, seemingly, contrary to what would be expected for seriously food-stressed caribou. This appears especially true as Peary caribou live in a region of relatively low plant biomass. The most important distinction between deer yards and restricted winter range for Peary caribou is that deer in wintering yards have a 3-dimensional forage supply while Peary caribou have essentially only a 2-dimensional forage supply. That is, deer in wintering yards survive by feeding on vegetation that is available above the snow cover (3rd dimension). Peary caribou on high arctic tundra range must find low-growing forage plants during severe snow and ice periods on snow-free or shallow snow-covered sites (not ice-covered) in order to survive the prolonged rigors of a severe winter and spring.

The winter and spring of 1993-94 were highly favorable to caribou survival and to the subsequent production and early survival and rearing of calves in spring and summer 1994. Therefore, the small monthly home range sizes during winter 1993-94 may reflect the favorable environmental setting of that winter. Visual inspections were made of snow and ice conditions on sites throughout the Bathurst Island complex during late winter (Apr-May) and spring (Jun). Ice was absent until mid to late June in 1994. Much of the snowpack remained powdery with a 'sugar' base throughout the winter and until the melt began in spring. Some sites had hard packed crusts, but the caribou broke through the crusts with their hooves and the soft snow below was easily moved away to expose the vegetation. Wind action usually significantly packs the snow over large areas, if not range-wide, often to 'hardpan' by that time in most years. It is reasonable to argue that the restricted use of range in winter 1993-94, although probably only a reflection of the favorable conditions of that winter, could also be beneficial during periods of extreme forage unavailability brought on by snow and ice covers. Widespread inaccessibility of forage could promote restricted range use by caribou, as once a relatively favorable foraging area was found, it would be more beneficial to remain in that general area (e.g., 100 km^2 or more) where some forage was accessible on an ongoing basis rather than to keep moving to new areas in search of a possible, but unknown, accessible forage supply. Another consideration is that we were seeing movement patterns that actually were forged during less favorable years.

Evaluating the use of range on any one island, particularly during periods of extreme forage unavailability is complicated by the fact that there can be, in reality, free-movement between and among Arctic Islands for at least 9-10 months of each year. To further obscure the matter, Peary caribou on some Queen Elizabeth Islands can move nearly year-round (e.g., Miller 1995a). Annually occurring seasonal inter-island movements (migrations) have been documented for caribou on the Queen Elizabeth Islands and on the more southerly Arctic Islands (e.g., Miller et al., 1977a; 1977b; 1982; Miller & Gunn, 1978; 1980; Miller, 1990a). Thus, environmentally forced inter-island movements by some Peary caribou during prolonged periods of widespread or nearly range-wide, extreme relative forage unavailability should be expected (especially by Peary caribou living on relatively small islands). The benefits of the trade-offs for Peary caribou between remaining on familiar range vs. responding to extreme food stress by en masse long-distance emigrations beyond previously known traditional ranges are speculated about but in reality, such events have not been proven. Thus, the supposition for them, in the absence of any direct evidence that they have ever taken place, remains purely speculative and highly debatable. However, 'range shifts' during periods of food stress by some Peary caribou within their population's long time overall traditional range are known but for the most part, the magnitude and frequency of such events remains speculative. The value to the caribou making any of these displacements would be directly proportional to the intensity, duration and expanse of the environmental stressors which were in place at the time. Many Peary caribou are "reluctant to quit" traditional range and seek relief on unfamiliar ground during periods of extreme environmental stress—many of them dying on their then current home range instead (e.g., Miller et al., 1977a; Miller, 1998; Gunn & Dragon, 2002). However, some do respond by egress but most often, their subsequent fate is unknown (e.g., Miller, 1990a; 1998; Gunn & Dragon, 2002). Also, it is not known whether such environmentally-forced movements result in emigration and establishment of new ranges, or the surviving animals simply return to their previous range when conditions once again become favorable. Thus, the temporal scale of the data-set becomes the all-important factor in such evaluations (i.e., multi-year studies).

Displacement vs. minimum distance traveled

Values obtained from calculation of rates of minimum distances traveled for each consecutive duty-day from the beginning to the end of each of the 12 Movement periods are seriously misleading (Table 3). The minimum distance traveled differs considerably, on average, from the displacement distance by 45.0±43.8 km standard deviation.

Calculated rates for minimum distances traveled were unrealistically low, ranging from 0.09-0.40 km • h^{-1} and averaging 0.16±0.03 km • h^{-1}. It appears that from an ecological standpoint, the use of rates of travel obtained from >2 h time intervals (or, on occasion, even > 1 h) will cause a serious negative distortion of the resultant estimates of minimal distance traveled and associated rates of travel. The mean rate of travel of only 0.16 km • h^{-1} is grossly undervalued and represents <5% of the 3.6 km • h^{-1} mean value obtained for animals in the 0.2-1.0 h time interval. Based on the average rate of 3.6 km • h^{-1}, it appears that these caribou spent on average, only 5% (range 2.4-11.0%) of their respective Movement periods involved in travel - we believe this is obviously a misleading statistic that has no ecological foundation in fact.

The use of satellite location-data points for estimating actual distance traveled is dependent on the time interval between successive locations. This condition is especially confounded by not knowing the number of intervening rest or foraging periods between each bout of movement or travel. Such distance estimates are fraught with realized and probable error and thus, should be considered suspect without some form of independent validation (see Table 3: travel vs. displacement; and example in Methods). Ideally, such validation would take the form of direct timed visual observation and measurement of the exact path taken by the animal (cf. Miller et al., 1982). When possible, Global Positioning System (GPS) satellite telemetry could be employed in association with visual observations to obtain continual location data.

We know that caribou on arctic island ranges travel at 3-4 km • h^{-1} while foraging (Miller et al., 1982) and likely considerably faster when making changes in seasonal ranges or range shifts (e.g., Pruitt, 1960). We derived from Russell et al. (1993:15) that the average number of active hours in a day is about 14.8 h (based on yearly mean 'active/lying cycle' of 4.7 h with a mean 2.9 h active period). Therefore, we examined the apparent gross discrepancy in minimal distances traveled on their respective Wintering Area and the rates of travel for those movements for the two females (93-02 and 93-05) with complete usable records at 5-day intervals during 158 and 172 days of occupation on their Wintering Area, 24-km^2 (Fig. 2: 93-02) and 94-km^2 (Fig. 5: 93-05). Based on the sequential duty-day locations, female 93-02 supposedly moved only 78.4 km (average rate 0.02 km • h^{-1}) and female 93-05 134.5 km (average rate 0.03 km • h^{-1}) in these periods. When we apply the mean rate of 3.5 km • h^{-1} from Miller et al. (1982), at 8 h • d^{-1}, each female would have traveled 28 km • d^{-1} (i.e., movements during 54% of the daily active time derived from Russell et al. (1993), times 3.5 km • 8 h^{-1}). Therefore, 93-02 should have traveled a minimum distance of 4428 km during her 158 days on her Wintering Area and female 93-05 should have traveled a minimum distance of 4816 km during her 172 days on her Wintering Area. It appears from this exercise that our satellite location data can account for only <2 to <3% of 93-02's and 93-05's travel distances during their respective stays on their Wintering Area.

On a 365-day basis, at the average daily rate of travel of 3.5 km • h^{-1} for 8 h • d^{-1} for 365 days, we obtain a minimum distance traveled of 10 220 km. In contrast, the sum total sequential travel distance measured during the entire annual-cycle for female 93-02 was 678.7 km and for female 93-05 was 821.8 km. Thus, the satellite location-data points only account for 7 and 8%, respectively, of the distances likely traveled by those two female caribou throughout the annual-cycle of the study period. Even when the measured distances traveled are inflated from the 8 h the PTT was on to cover each 24-h period during 365 days, we can still account for only 45-54% of the distance that would be traveled by each of those females at a mean rate of 3.5 km • h^{-1} on each day of the year.

Productivity

The high productivity indicates that caribou on Bathurst Island and throughout the Bathurst Island complex were not being stressed by the limitations of the absolute forage supply or the relative unavailability of forage during the study period (Miller, 1995b, 1998; Gunn & Dragon, 2002; Miller & Gunn, this proceedings). Although the environmental conditions were highly favorable in winter and spring 1993-94, the cows all returned to previously known calving areas in June 1994. This most likely reflects the fidelity of caribou cows to their calving grounds (e.g., Gunn & Miller, 1986). Many sites on the calving areas on Bathurst Island (Figs. 1-5) have characteristics that result in at least some shallow snow and most importantly snow-free patches of ground at least just before, during, and immediately after calving. In a year with a severe winter and spring, these calving areas allow higher levels of survival among cows and higher initial production of viable neonates as well as subsequent better survival among those calves. Thus, although use of these calving areas is not necessary in all years—the collective overall calving area identified in Fig. 1 is particularly critical in the relatively few but more unfavorable years. In the few most extreme worst years, when major die-offs occur, use of even these calving area sites fail to make an appreciable difference—and major losses to near total or total calf crop failure occurs (Miller et al., 1977a; Miller, 1998; Gunn & Dragon, 2002).

Maintenance of fidelity (traditions) to calving areas most likely demands annual or near annual repetitive use by at least a core of individuals, even in the favorable years. Therefore, these calving areas (Fig. 1) should be protected at all times to foster the persistence of Peary caribou within the Bathurst Island complex, south-central Queen Elizabeth Islands, Canada.

Conclusions

Although our findings represent only a minute look into how Peary caribou use space over time, on a relative basis they represent a meaningful advance in our knowledge base. The findings in this study together with those in the sister study (Miller, 2002) indicate that different range-use patterns exhibited by Peary caribou incorporate feasible combinations of alternatives available to them.

The area encompassed by each satellite-collared caribou between 1 August 1993 and 31 July 1994 overestimates the annual minimum range required to sustain a caribou. Those values do, however, clearly show us that each animal remained within only a relatively minor portion of the range that was available to it on Bathurst Island and, of particular importance, did not even use all of the range on NE Bathurst Island. Subsequent to our study, female 93-03 lived for 13 consecutive months on only 21 km^2 (Miller, 1997, 1998, unpubl. data: Baring Island) but our satellite data indicated a home-range of 1735 km^2 in 1993-94. Thus, she was capable of living for 13 months on the equivalent of only 1% of the area we estimated in 1993-94 or over 82 times greater than the amount of annual range actually required.

The four individuals maintained seasonal ranges distinctly separate from each other: spatial separation was maintained for much of the year and temporal separation virtually year-round. The differences in range use (spatial and temporal templates) likely reflect variation in the individual's learned use of range compared to other caribou within the island complex, with overall limitations imposed by relative unavailability or absolute availability of forage.

Evaluation of the impact of environmental stressors on Peary caribou on an island basis can be seriously complicated and confounded because those caribou can make inter-island movements during winter and spring when environmental pressures are strongest. However, our findings indicate that Peary caribou can winter on relatively small areas, much smaller than previously thought by people investigating or otherwise interested in Peary caribou on the Queen Elizabeth Islands.

The use of the term 'movement' or 'travel' in evaluating supposed rate or distance measurements obtained from satellite telemetry is both confounding and at best of questionable ecological value. Although defining such a measurement as a 'displacement' is still limiting, the successive between-point values are most accurately described as displacements and the attendant limitations should become obvious to the reader. The magnitude of error associated with supposed measure of movement or travel is governed mainly by the time interval between obtaining successive location-data points. Together with longer time intervals, the actual pattern of movement or travel will also make a major contribution to the resulting error. Future workers should pay due heed to the potential for error when using such measurements in making biological and ecological evaluations.

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Caribou distribution during calving in the northeast National Petroleum Reserve–Alaska, June 1998 to 2000

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Abstract: Barren ground caribou (Rangifer tarandus granti) of the Teshekpuk Caribou Herd (TCH) inhabit the western portion of Alaska's Arctic Coastal Plain within the National Petroleum Reserve–Alaska (NPR-A). Alaska's North Slope communities, management agencies, and private industry are interested in this herd because of its importance as a subsistence resource and location relative to potential petroleum development. From 1998 through 2000, we monitored caribou distribution during the calving period within the Northeast Planning Area of the NPR-A using systematic strip-transect aerial surveys, as well as VHF and satellite telemetry for cow caribou. Aerial survey and telemetry data indicated cows with calves were distributed around Teshekpuk Lake, with a concentration south of the lake in 1999 and 2000. Inconsistencies in weather conditions, survey timing (both strip-transect and VHF surveys), 100% coverage survey areas, and small sample sizes confound interpretations of our results. However, several patterns were apparent. Later transect survey timing (7–12 June *versus* 4–7 and 5–8 June) resulted in more cow/calf pairs recorded. Our 18% coverage area, originally based on VHF telemetry data for the extent of TCH calving, covered a consistently high proportion (95% to 100%) of the annual calving ranges (95% kernel utilization distributions), but accounted for only 24% to 46% of the adult cows in the TCH based on the current Alaska Department of Fish and Game population estimate (1999) and average 1998-2000 herd composition. It appears that either our transect survey methodology significantly underestimated the true number of caribou cows in the study area, many cows calved outside the area or moved into the area and calved after our surveys, or we have over estimated the number of reproductive cows in the herd. Our 100% coverage transect areas covering oil and gas lease areas, contained 38% of the calving range with 23% of TCH cows in 1999; and 18% of the calving range with 8% of TCH cows in 2000. Based on 95% minimum convex polygon ranges, satellite collared cow/calf pairs were not stationary during either our survey period (14.7 ± 6.56 km^2; mean ± standard error of the mean; 4–12 June) or during the calving period (86.9 ± 72.30 km^2; 1–20 June) during 1998–2000. Site specific pre-development data on caribou distribution during calving in NPR-A will be useful for assessing the importance of specific areas to caribou during calving and for designing oilfields that minimize impacts should oil development occur.

Key words: Arctic Coastal Plain, barren ground caribou, oil and gas development, oilfield, Rangifer tarandus, Teshekpuk Caribou Herd.

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Introduction

Barren ground caribou (Rangifer tarandus granti) of the Teshekpuk Caribou Herd (TCH) inhabit the western portion of Alaska's Arctic Coastal Plain and range primarily within the National Petroleum Reserve–Alaska (NPR-A; U. S. Department of the Interior [USDI], 1998). North Slope communities, management agencies, and private industry are particularly interested in this herd because of its importance as a subsistence resource and location relative to potential oilfield development and existing oil and gas exploration.

The TCH was recognized as a separate herd from the Central Arctic (CAH) and Western Arctic (WAH) herds, which also range within NPR-A, in the mid 1970s (Davis & Valkenburg, 1978). Since

Table 1. Caribou number, density (caribou/km²), and mean group size (± standard error of the mean) recorded on 6 systematic aerial strip-transect surveys during calving in the National Petroleum Reserve–Alaska, 4–12 June 1998–2000. A sightability correction factor was applied to 18% and 100% coverage surveys during 1999 and 2000 to correct for poor sightability due to patchy snow cover (Lawhead et al., 1994).

Year	Area coverage	Survey dates	Cows	Calves	Total Caribou	Density (No./km²)	Number of Groups	Mean group size
1998	18% of 6509 km²	4–5 June	848	24	1062	0.91	246	4.3 ± 0.32
1999	18% of 7250 km²	7–11 June	455	169	662	0.51	119	3.0 ± 0.24
2000	18% of 7250 km²	6 June	551	19	624	0.48	128	2.6 ± 0.22
1998	100% of 1401 km²	5 and 7 June	1965	540	2668	1.90	501	5.3 ± 0.41
1999	100% of 2327 km²	9–12 June	2312	882	3369	1.45	444	4.0 ± 0.20
2000	100% of 2327 km²	5–8 June	837	55	1040	0.45	257	2.2 ± 0.08

1978, the Alaska Department of Fish and Game (ADFG), North Slope Borough Department of Wildlife Management (NSB), and Bureau of Land Management (BLM) have attempted to estimate the population size of the TCH through visual estimates and more recently through photocensus techniques. Visual survey estimates of the TCH were recorded in 1978 (3000–4000 caribou; Davis & Valkenburg, 1979), 1982 (4000 caribou; BLM, unpublished data), and 1985 (13 406 caribou; Philo et al., 1993). In 1984 the first photocensus of the TCH was completed and 11 822 caribou were counted (Silva, 1985). Additional photocensus estimates conducted in 1989 (16 649 caribou) and 1993 (27 686 caribou) documented increases in the TCH during the period 1984–1993 (Carroll, 1992; 1995), which was followed by a decrease in the herd in 1995 (25 076 caribou; Carroll, 1997). The exponential growth rate for this herd from the 1970s through the early 1990s (0.152 ± 0.087 [± 95% confidence interval]) was most similar to the WAH (0.116 ± 0.020) among Arctic Coastal Plain herds (Cronin et al., 1998). The most recent photocensus was conducted in 1999 where 28 627 caribou were counted (Carroll, 2001). Herd composition in 1998 and 2000 was, on average, 44% cows with 20% yearlings (Carroll, 2001) for about 10 077 adult cows in 1999.

Most TCH cows begin migrating to the Teshekpuk Lake area in May, and by early June most of the cows have moved into the calving area surrounding the lake (Carroll, 1999). Changes in the location of the calving area for the TCH have been documented since this herd was identified. During the mid 1970s, calving was reported on the west side of Teshekpuk Lake (Davis & Valkenberg, 1979; Silva, 1985). Since the mid 1990s, however, calving has been northeast, east, and southeast of Teshekpuk Lake (Carroll, 2001).

Although there has been oil and gas winter exploration within the Teshekpuk Lake area since the late 1940s (Silva, 1985), currently the TCH has no regular contact with industrial development (Murphy & Lawhead, 2000). Davis & Valkenburg (1978) recognized the importance of obtaining baseline data on the TCH prior to development of the NPR–A. Baseline data on herd size, distribution, and seasonal habitat use will be useful for planning to minimize impacts of likely future petroleum exploration and development on the TCH. Current abundance and distribution data will allow resource managers to make informed decisions regarding management of the herd's habitat.

The objectives of this study were to: (1) determine the current (1998–2000) number, sex/age composition, and distribution of caribou during the calving period near Teshekpuk Lake and within areas of potential oil and gas development and, (2) to investigate the importance of these areas of potential oil and gas development to the calving range for the TCH as defined by VHF calving sites. VHF telemetry data describe the extent of calving for each year of our transect surveys. Satellite telemetry data describe the potential for movement of cows with and without calves during both our transect survey period (2–14 June) and the calving period (1–20 June).

Study Area

The Teshekpuk Lake area of the NPR-A is west of the Colville River delta on Alaska's Arctic Coastal Plain (Fig. 1). We conducted surveys in the NPR-A at two effort levels covering approximately 18% and 100% of the areas (Figs. 2, 3). The 18% coverage survey area (6509 km²) in 1998 was roughly a rectangular block east of the Ikpikpuk River (northwest corner T17N, R11W, Teshekpuk quadrangle) to Atigaru Point (7250 km², southeast corner T10N,

Table 2. Estimated number of cow caribou for strip-transect surveys, proportion of calving range covered by transect survey areas, and the proportion of the estimated number of Teshekpuk Caribou Herd (TCH) cows within the transect survey area for 6 systematic aerial strip-transect surveys on 4–12 June 1998–2000, National Petroleum Reserve–Alaska. VHF calving range was modeled as the 95% fixed kernel utilization distribution for all calving locations recorded for each survey year (Fig. 3). The number and percent of cows were extrapolated from a sample of 11 transects covering 18% of the total survey area are reported with ± standard error of the mean (Caughley, 1977a). A sightability correction factor was applied to 18% and 100% coverage surveys during 1999 and 2000 to correct for poor sightability due to patchy snow cover (Lawhead et al., 1994).

Year	Area Coverage	Transect survey dates	Estimated number of cows	VHF calving range within transect area	VHF–TCH cow range within transect area	Proportion of cows in TCH[1]	VHF telemetry survey dates	Transect and VHF date comparison
1998	18% of 6509 km²	4–5 June	4649 ± 942	100%	67%	46% ± 9%	11–15 June	Earlier
1999	18% of 6509 km²	7–11 June	2463 ± 481	96%	80%	24% ± 5%	4–12 June	Within
2000	18% of 6509 km²	6 June	2968 ± 637	95%	67%	29% ± 6%	5–14 June	Within
1998	100% of 1401 km²	5 and 7 June	1965	45%	14%	19%	11–15 June	Earlier
1999	100% of 2327 km²	9–12 June	2312	38%	28%	23%	4–12 June	Within
2000	100% of 2327 km²	5–8 June	837	18%	15%	8%	5–14 June	Within

[1] Calculated as the per cent of the number of adult cows (10 077) based on the 1999 TCH census results (28 627 caribou) and average 1998- 2000 herd composition (44% cows with 20% yearlings; Carroll, 2001).

R12E, Harrison Bay quadrangle) and 50 miles inland, during the 1999 and 2000 surveys. This study area was designed to cover the documented extent of TCH caribou calving distribution based on VHF telemetry data (Carroll, 2001). The 100% coverage survey area (1401 km²) in 1998 extended north to the Beaufort Sea coast and was concentrated on the area east of Teshekpuk Lake. This survey area was designed to include documented concentrations of calving caribou (Carroll, 2001). In 1999 and 2000, the 100% coverage survey area was truncated north of Teshekpuk Lake and extended east to the Fish Creek delta and south to the Pik Dunes and Fish Creek areas covering 2327 km². This survey area focused on areas of potential oil and gas lease development where caribou calving had been documented (Carroll, 2001; USDI, 1997; Davis & Valkenberg, 1979; Reynolds, 1982; USDI unpublished data in Silva, 1985).

The composition of our 18% coverage survey transects in 1999 and 2000 was: 35% water (lakes and streams), 18% aquatic tundra, 6% wet tundra, 16% sedge/grass meadow, 17% tussock tundra, 3% moss/lichen tundra, 2% dwarf shrub tundra, and 3% sand dunes/barrens (Kempka et al., 1995; Pacific Meridian Resources, 1996). Our 100% coverage survey area in 1999 and 2000 were 27% water, 17% aquatic tundra, 8% wet tundra, 21% sedge/grass meadow, 21% tussock tundra, 1% moss lichen tundra, 2% dwarf shrub tundra, and 3% sand dunes/barrens (Kempka et al., 1995; Pacific Meridian Resources, 1996).

Methods

Aerial Surveys

Between 4–12 June 1998–2000, we conducted systematic, strip-transect aerial surveys (Caughley, 1977b) during the calving period from fixed-wing aircraft (Cessna 206). Transect centerlines were spaced at 9.6-km and 1.6-km intervals, using a 1.6-km transect width, resulting in 18% and 100% coverage of the survey areas, respectively. All transects were oriented north–south and centered on township and section lines mapped on 1:63 360-scale U.S. Geological Survey (USGS) topographic maps. Systematic surveys were flown 90 m

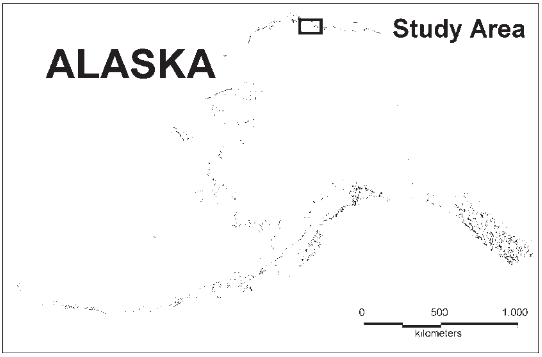

Fig. 1. Study area.

above ground level at 185–200 km/h airspeed. During surveys, two observers searched an 800-m wide area on each side of the transect centerline. A third observer entered data into a computer and assisted with spotting caribou during 1999 and 2000 surveys. Aircraft wing struts were marked with tape to enable visual control of transect strip-width (Pennycuick & Western, 1972) and estimation of group distances perpendicular from the transect centerline. Transect widths were also checked periodically with inclinometers and maps to assist in training observers.

As with previous aerial surveys in the Prudhoe Bay oilfield (Pollard et al., 1992; 1996), global positioning system receivers (GPS) were used to navigate the aircraft and provide position records during systematic surveys. Locations of animals were estimated by using the GPS in combination with visual estimates of their perpendicular distance to the transect centerline. At the time of sighting, all data were entered directly into a notebook computer that was linked to the GPS receiver (Geolink version 6.1, Michael Baker Jr., Inc., Jackson, MS). The computer software associates a real–time GPS position (latitude and longitude of the survey aircraft) for each animal sighting entered with related attributes (e.g., number of individuals in the group and sex/age classification). When possible, behavior and habitat types, along with the group attributes and time of sighting, were recorded into the computer or an audio recorder.

We counted and classified caribou as bulls, cows, calves, or unclassified, based on body size, antler development, pelage, and calf presence. Unclassified caribou were adults or yearlings that couldn't be classified with confidence. Caribou near the outer margin of transect strips were most difficult to classify. During patchy snow cover sightability of caribou was diminished and a sightability correction factor (SCF=1.88) developed for 20-70% snow cover on Alaska's North Slope (Lawhead et al., 1994) was applied to survey results. The total number of cows within the 18% coverage survey area was extrapolated and the variance was calculated based on the sample of 11 transects within the 6509 km^2 area (Caughley, 1977a). June weather data was obtained from National Oceanic and Atmospheric Administration weather stations at Deadhorse, Alaska for 1998 and Nuiqsut, Alaska for 1999 and 2000. Data were unavailable for the Nuiqsut station for June 1998.

Satellite and VHF Telemetry

Through a cooperative project involving ADFG, NSB, and BLM, caribou were captured using a skid-mounted net gun from a Hughes 500 helicopter (Carroll, 2001). Platform Transmitter Terminal (satellite radio collar transmitters or PTTs) or VHF (Very High Frequency) collars were attached to captured caribou; and satellite collars were programmed to transmit on a 6-h per 48-h cycle (Carroll, 2001). Data were received from 6 collared animals by downloading satellite location data (monthly summaries) from the Argos Data Collection and Location System (ARGOS) in Landover, Maryland. VHF radiotracking flights collected information on 27–36 animals year^{-1} between 2–16 June to determine caribou movements, distribution, and reproductive status (Carrol, 2001).

VHF calving locations defined as the first sighting of an individual cow with a calf (Carroll, 2001) were used to calculate "calving ranges" as the fixed kernel utilization distribution (Worton, 1989) with least squares cross validation (Silverman, 1986) using the Animal Movements extension (Hooge and Eichenlaub, 1997) for ArcView® Geographic Information System. Calving ranges for cow caribou based on VHF telemetry from 2–16 June were calculated separately for cows with (n = 16–23 cows year^{-1}) and cows without (n = 4–14 cows year^{-1}) calves.

Satellite-collared cow ranges were calculated as 95% minimum convex polygons (MCP, Range Manager© v. 1.0.1, Data Solutions, Topsail, Newfoundland, Canada, for MapInfo Professional®). These MCP ranges for satellite-collared cows were based on movements of 6 individual cows during 1–20 June (calving period, n = 28–58 locations per cow) and during our transect survey period from 4–12 June (n = 6–22 locations per cow).

All mean values are reported with the standard error (SE) of the mean. Spatial comparison of calving ranges and study area coverages was completed using MapInfo Professional®. Mean range values were compared using 2-sample t-tests without the assumption of equal variance (Snedecor & Cochran, 1980).

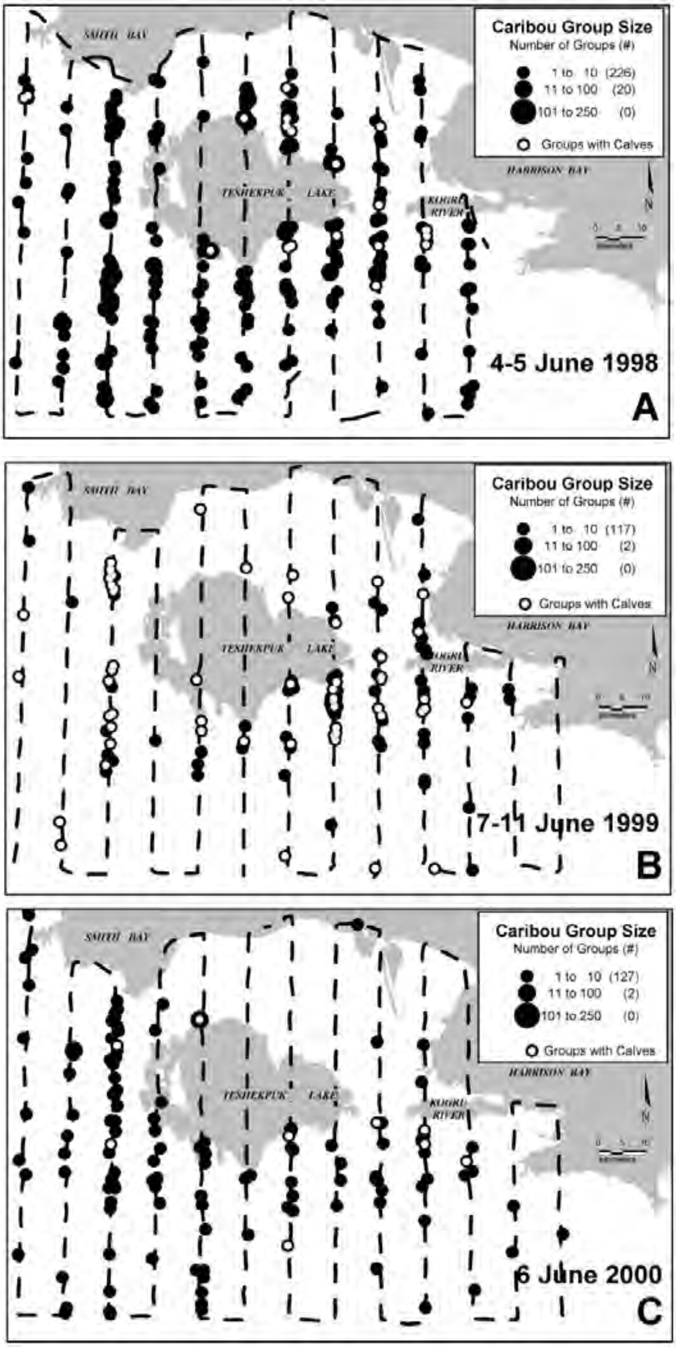

Fig. 2. Caribou groups located during 18% coverage systematic aerial strip-transect surveys in the National Petroleum Reserve–Alaska, June 1998–2000.

Results

Aerial Surveys

We completed 3 aerial surveys at 18% coverage and 3 aerial surveys at 100% coverage in the Teshekpuk Lake area during the caribou calving period between 4–12 June 1998–2000. Snow melt was nearly complete during the survey in 1998, but patchy snow cover leading to poor sighting conditions occurred in 1999 and 2000. Areas north of Teshekpuk Lake were 80% to 100% snow covered while areas south of the lake were 30% to 70% snow covered during surveys in 1999 and 2000. Mean daily temperature during 1–15 June declined steadily over our surveys during 1998–2000: 4.26 ± 0.57 °C in 1998, 3.04 ± 0.90 °C in 1999, and 2.04 ± 0.99 °C in 2000.

18% coverage area

We observed fewer total caribou of all classes and lower caribou density in the 18% coverage area in 1999 and 2000 than in 1998, even after application of the SCF (Table 1). However, more cow/calf pairs were recorded in 1999 (Table 1). In general, cow/calf pairs were closer to Teshekpuk Lake in 1998 and 2000 than in 1999 when survey timing was later (Fig. 2). In 1999, more cow/calf pairs were west of Teshekpuk Lake and at the southern border of the study area than in the eastern study area (Fig. 2). In the 18% coverage area, cows without calves generally occurred over a larger area than cow/calf pairs during 1998 and 2000, with more cows without calves occurring west and southwest of Teshekpuk Lake (Fig. 2).

Based on the 11 transects sampled consistently during 1998–2000 in the 18% coverage area, the estimated number of cows declined from the number observed in 1998 by 47% in 1999, and 36% in 2000 (Table 2). Our estimated number of cows within this area ranged from 24% to 46% of the estimated total of 10 077 cows in the TCH, based on the 1999 ADFG population estimate (Table 2).

100% survey area

In 1998, cow/calf pairs occurred throughout the 100% coverage area centered on the area northeast and southeast of Teshekpuk Lake (Fig. 3). In 1999 and 2000, cow/calf pairs were concentrated in the northwestern half of the survey area, southeast of Teshekpuk Lake and south of the Kogru River (Fig. 3). In 2000, we

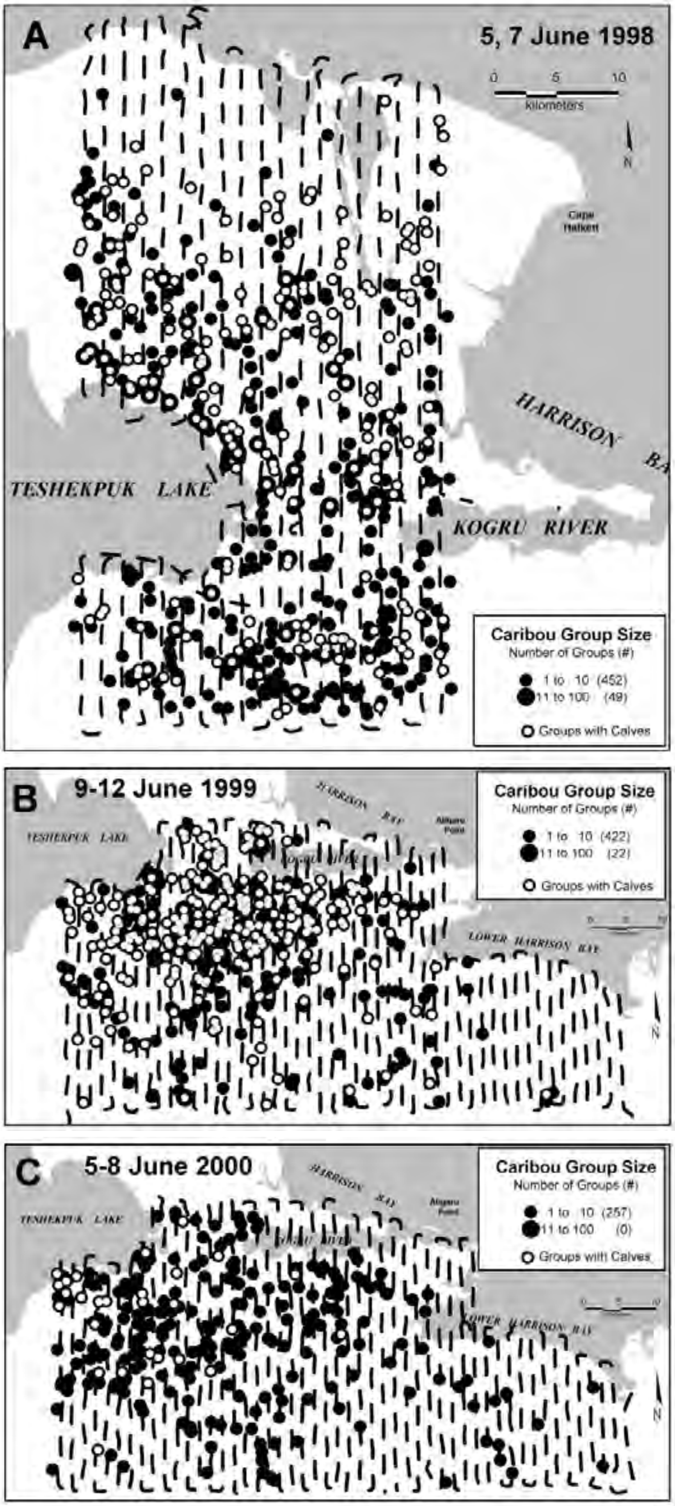

Fig. 3. Caribou groups located during 100% coverage systematic aerial strip-transect surveys in the National Petroleum Reserve–Alaska, June 1998–2000.

observed lower caribou densities, fewer total caribou, and fewer cow/calf pairs within the 100% coverage survey area than in the same area in 1999 (Table 1). Survey timing in 1999 was later (9–12 June) than in 2000 (5–8 June). Mean group size declined steadily during the 1998–2000 survey period (Table 1). The eastern extent of calving in the 100% coverage area appears to be Atigaru Point; only 1 cow/calf pair was sighted east of Atigaru Point (Fig. 3).

The 100% coverage area during 1998 included 19% of TCH cows. Survey coverage, focused on areas of potential oil and gas development, included 23% of TCH cows in 1999 and 8% in 2000 (Table 2). As in the 18% coverage area, a higher proportion of cow/calf pairs was recorded during 1999 than in either 1998 or 2000.

VHF and Satellite Telemetry

During early June 1998–2000 radio-collared caribou calving locations (n=63 locations) were distributed around Teshekpuk Lake, within 97 km of the lake shoreline (Carroll, 2001). Cows without calves (n=30 locations) were generally located west of Teshekpuk Lake within 123 km of the lake (Fig. 4; Carroll, 2001). During the 3 years of surveys, cows without calves occurred over a wider area (15 210 ± 2080.0 km^2) than cow/calf pairs (3874 ± 1221.1 km^2, t=-4.70, P=0.02, df=3). Radio-collared cows with calves during the 3 years of surveys were also closer together (mean distance = 32.9 ± 8.21 km) than cows without calves (mean distance = 65.9 ± 2.58 km; t=-3.51, P=0.04, df=3). Calving ranges appeared more concentrated in 1998 (2210 km^2) and 1999 (3158 km^2) than in 2000 (6254 km^2, Fig. 4). This was consistent with group size observations for both the 18% and 100% coverage survey areas which indicated mean group sizes declined from 1998–2000 (Table 1).

Based on the limited data available for this period, satellite-collared cows with calves (n=4 caribou) during 1–20 June 1998–2000 were generally south and southeast of Teshekpuk Lake and cows without calves (n=2 caribou) were

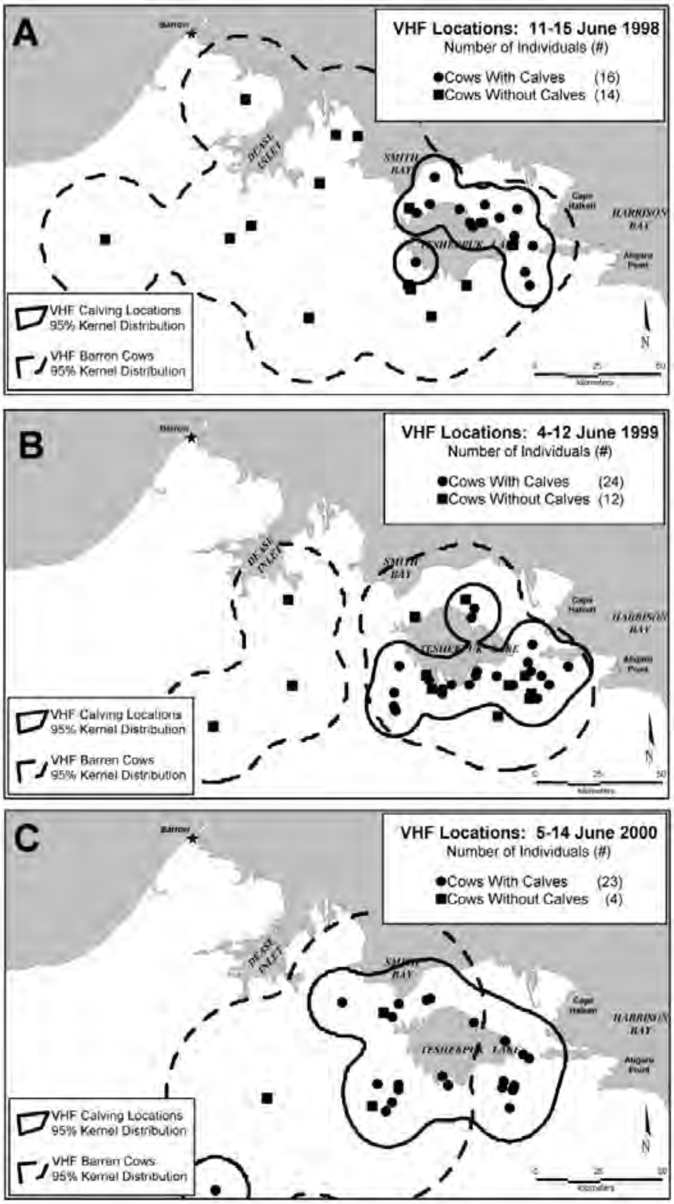

Fig. 4. Caribou calving locations determined by VHF radio telemetry from 4–15 June 1998–2000 (Carroll, 2001) and fixed kernel utilization distributions for calving locations and for cows without calves in the National Petroleum Reserve–Alaska.

west of the lake. Cow caribou MCP ranges between 1–20 June (28–58 locations per cow, n=6 cows) were similar for cow/calf pairs (621 ± 524.3 km^2, n=4 cows) and cows without calves (468 ± 303.3 km^2, n=2 cows). MCP ranges for satellite-collared cows during our 4–12 June survey period (6–22 locations per cow, n=6 cows) were smaller and less variable for cow/calf pairs (15 ± 6.6 km^2, n=4 cows) than for cows without calves (87 ± 72.3 km^2, n=2), although this difference was not statistically significant.

Mean distances traveled per day during 1–20 June were similar for cows with and without calves (2.5 ± 0.69 km/d and 3.7 ± 1.56 km/d, respectively). Mean distances traveled per day during our 4–12 June survey period were also similar to movement rates during the calving period (2.5 ± 0.85 km/d with calf, and 3.3 ± 0.50 km/d without calf). Total distance traveled during our 4–12 June survey period showed an increasing trend across years from 23 km in 1998, 37 km in 1999, to 45 km in 2000. This trend was inconsistent during the 1–20 June calving period with 155 km in 1998, 101 km in 1999, and 183 km in 2000.

Discussion

The TCH calved southwest of Teshekpuk Lake in 1976 and 1977, and northeast of the lake in 1978 (Davis & Valkenburg, 1979). Since the mid 1990s, calving has been northeast, east, and southeast of the lake (Carroll, 2001). Philo et al. (1993) reported that 3 out of 5 collared cows calved southeast of Teshekpuk Lake. Aerial survey and telemetry data suggest that the entire area surrounding Teshekpuk Lake is used by caribou during calving.

In general, calving dates for the TCH range from 2–16 June, with most cows moving into the area in early June (Carroll, 2001). When our strip-transect surveys were initiated, we focused on the distribution of calving locations, believing that the peak of calving, near 5 June, would be similar to the Central Arctic Caribou Herd. We considered that after this date most cows would have moved into the Teshekpuk Lake area and would have calved.

Carroll (2001) noted that most calves were located during VHF telemetry surveys after 7 June 2000, which he indicated was slightly later than normal. During surveys for waterfowl in the 100% coverage survey area on 15–19 June 2000, Noel et al. (2001) recorded nearly 3 times the total number of caribou and a much higher proportion of cows with calves (61 calves:100 cows) than during our 5–8 June 2000 survey (Table 1). Apparently cows moved into this area after our survey on 5–8 June, either before or after parturition.

More cow/calf pairs were observed on our transect surveys in 1999 than in either 1998 or 2000 apparently because survey dates in 1998 and 2000 were before most cows had calved. Patchy snow conditions and cooler temperature from 1–15 June were likely responsible for the decreased numbers of caribou recorded within our 18% coverage survey area in 1999 and 2000 (Table 2). Calving ranges were larger in 1999 and 2000 than in 1998, indicating that cows/calf pairs were spread across a larger area in these years. VHF determined calving ranges during 1998–2000 were potentially influenced by (1) survey timing, (2) small sample sizes, and (3) weather conditions.

We recommend that calving period transect surveys be flown after 15 June, when most calves have been born, and the ADFG VFH calving surveys have been completed. This later timing may be less disruptive to pre-parturient and parturient cows and should allow documentation of a higher proportion of cow/calf pairs. Also, because VHF determined calving ranges will already be established, this may allow a more accurate comparison between the proportion of TCH cows and the proportion of the TCH calving range represented by the area of interest for potential development.

Annual variation in calving distributions is evident from the few years of survey data presented here, and is potentially influenced by snow cover, weather conditions, survey timing, and possibly sample size. Comparing the proportion of the calving range within a particular transect survey area should indicate how important any particular area is for the calving period during a given year. Our comparison of calving ranges based on VHF surveys to estimates for the number of TCH cows within the 18% coverage transect survey area suggests that the VHF determined calving ranges may underestimate the calving range of the TCH, for these years. Satellite telemetry data for 1998–2000 indicate cows were not static either during our survey period or during the calving period.

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Brief communication

Multi-scale habitat selection by mountain caribou in West Central Alberta

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Introduction

Woodland caribou (*Rangifer tarandus caribou*) populations in Alberta are in decline, which may be partially attributed to habitat loss and alteration resulting from industrial activities, such as timber harvesting. These effects may be direct (e.g., loss of forage), or indirect (e.g., through changing the abundance and distribution of predators). An understanding of caribou habitat requirements is a fundamental first step towards conservation of the species. In this study, we analysed winter habitat selection by mountain caribou, a migratory ecotype of woodland caribou, in west central Alberta (1998-2001). The habitat requirements of these caribou have been identified as a knowledge gap by government and industry. Since habitat needs may differ over space (e.g., locally and regionally) and over time (e.g., as snow conditions change over the winter), selection was analysed at multiple spatial and temporal scales.

Study area

This study was conducted within the Redrock/ Prairie Creek caribou winter range (54°N, 119°W), which runs along the eastern slopes of the Rocky Mountains. This upper foothills landscape is intersected by ridges and many small drainages. The forest is composed primarily of black spruce (*Picea mariana*), Engelmann spruce (*Picea engelmannii*), white spruce (*Picea glauca*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine (*Pinus contorta*). Wolves (*Canis lupus*) are present in the study area. Industrial use includes timber harvesting, oil & gas exploration and development, and coal mining. Recreational use of linear features associated with development activities, by ATV's (all terrain vehicles) and snowmobiles, is widespread.

Methods

Global Positioning System (GPS) collars, deployed on adult female caribou over three winters (for 21 caribou-years), were used to collect locations that were both accurate (within 14-100 m, 95% of the time), and frequent (1-24 locations/day). Using digital forest inventory maps, and a Geographic Information System (GIS), we determined the forest characteristics within a study area (defined by the minimum convex polygon of historic caribou locations), within caribou home ranges, and at GPS caribou locations (referred to as general habitat use). Caribou home ranges were created by buffering daily locations by 2.8 km (the 90th percentile of the daily distance travelled by caribou, averaged across all animals). Using multiple logistic regression and compositional analyses, we analysed selection for home ranges within the larger study area, and for general habitat use within home ranges. We also used snow tracking over two winters to collect data on habitat and snow conditions, as well as on foraging strategies. Caribou in this area use two strategies to feed: they either dig through the snow for terrestrial forage (referred to as "cratering"), or they feed on arboreal lichens, which are suspended from tree branches. Multiple linear regression was used to determine how caribou foraged over a range of snow conditions, and multiple logistic regression was used to associate habitat and snow conditions with foraging sites.

Results

For their home ranges, caribou selected stands over 80 years old, with the highest preference for 120-160 year old stands. They also preferred stands with 71-100% crown closure relative to all other stands. At a finer scale, for general habitat use within their home ranges, caribou showed an even greater preference for older stands: stands under 120 years were avoided relative to stands over 160 years old, which were most preferred (on average, 21% of caribou locations were in these 160 year old stands). Again, caribou preferred denser stands, but to a lesser extent, since only stands with less than 30% canopy closure were avoided relative to stands with 71-100% canopy closure (the most preferred category). At the finest scale, cratering sites were associated with moderately dense stands (around 50% canopy closure). Arboreal feeding sites were associated with old stands containing greater amounts of spruce. Caribou selected many of the same habitat attributes at multiple scales, reinforcing their importance. For example, older stands were selected at all scales, even though older forest was abundant at each level (because it had been selected for at coarser scales).

Snow conditions also influenced habitat selection. For home range selection and general habitat use, caribou showed a greater preference for older stands in the late winter, when snow conditions were generally harsher (deeper and harder) than in the early winter. This is consistent with greater arboreal feeding during harsh snow conditions, since arboreal lichens were found to be more abundant in older stands. In addition, caribou fed on arboreal lichens more when snow was harder, and selected areas of relatively shallow, soft snow for cratering.

Conclusions

This research suggests that mountain caribou select a suite of winter habitats, at multiple spatial scales, and under a range of snow conditions. Our findings lead to several management recommendations. In general, habitat selection by caribou necessitates management over large spatial and temporal scales. Specifically, there must be management at multiple spatial scales to maintain older stands and a range of stand densities, as density requirements vary among scales. Patches of old spruce forest must be maintained with good dispersion across ranges, and in proximity to areas of suitable habitat, in case harsh snow conditions necessitate their use for arboreal lichen feeding. Such harsh conditions could limit the caribou population in this area if critical habitat is not available. Our research provides useful information for government and industry to make knowledge-based decisions when planning for the long-term conservation of caribou habitat.

Source

Szkorupa, T. S. 2002. Multi-scale Habitat Selection by Mountain Caribou in West Central Alberta. MSc thesis. University of Alberta, Edmonton, Alberta, Canada.

Session eight

Conservation, Husbandry, Management and Co-management

Inuit Elder's Story:

Edward Flowers, Labrador Inuit Association, Nain, Newfoundland

Edward Flowers spent his childhood years with his family at Aullasimavet in Voisey's Bay and on the west side of South Aulatsivik Island. As a young man he was a member of a cod fishing crew on the Queens Lakes, and in the autumns, he crewed with some of the best sealers in Nain at a sealing station called Ivilik. He has hunted the George River caribou herd all his life, often following the caribou across the border into Québec. Edward is currently employed by the Labrador Inuit Association (LIA) as a member of the Land Claims Negotiating Team. Whenever he gets a chance, he continues to hunt, fish, and gather from his Aullasimavik on Paul's Island. He also enjoys fishing for arctic char, hunting seals north of the Kiglapait Mountains, and hunting the George River Caribou. He is recognized for his skills and knowledge of the land. The Torngâsok Cultural Centre employs Edward and his wife to teach skills on the land and sea to young Inuit teenagers at Inuktitut immersion camps.

The Ninth North American Caribou Workshop,
Kuujjuaq, Québec, Canada,
23–27 April, 2001.

Evaluation of satellite collar sample size requirements for mitigation of low-level military jet disturbance of the George River caribou herd

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Abstract: Wildlife radio-telemetry and tracking projects often determine a priori required sample sizes by statistical means or default to the maximum number that can be maintained within a limited budget. After initiation of such projects, little attention is focussed on effective sample size requirements, resulting in lack of statistical power. The Department of National Defence operates a base in Labrador, Canada for low level jet fighter training activities, and maintain a sample of satellite collars on the George River caribou (Rangifer tarandus caribou) herd of the region for spatial avoidance mitigation purposes. We analysed existing location data, in conjunction with knowledge of life history, to develop estimates of satellite collar sample sizes required to ensure adequate mitigation of GRCH. We chose three levels of probability in each of six annual caribou seasons. Estimated number of collars required ranged from 15 to 52, 23 to 68, and 36 to 184 for 50%, 75%, and 90% probability levels, respectively, depending on season. Estimates can be used to make more informed decisions about mitigation of GRCH, and, generally, our approach provides a means to adaptively assess radio collar sample sizes for ongoing studies.

Key words: adaptive assessment, caribou season, Kernel home range, probability, radio-telemetry, radio-tracking.

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Introduction

When initiating wildlife radio telemetry and tracking research projects, researchers must initially determine transmitter sample sizes that suit project objectives. With conventional Very High Frequency (VHF) telemetry, this usually involves a trade-off between number of transmitters and relocation frequency (Garton et al., 2001). With satellite telemetry, relocation frequency is a function of collar programming and therefore dependent on the objectives of the project and the financial resources required for transmitter purchase and system access (Rodgers, 2001). Due to the relatively high cost of satellite telemetry, these projects are often used either to augment conventional VHF telemetry projects, or proceed with the maximum number of collars that can be maintained within a specified budget. Such constraints lead to reduced statistical power of subsequent data analyses (Steidl et al., 1997).

The Canadian Department of National Defence (DND) operates a low-level jet training base for foreign military aircraft out of 5 Wing Goose Bay military base in Goose Bay, Labrador, Canada (53°21'N, 60°25'W). Part of the Military Training Area (MTA) overlaps in space and time with the George River caribou herd (Rangifer tarandus caribou) (GRCH). As a result DND, in cooperation with provincial governments, attempts to minimize noise disturbance by maintaining spatial and temporal separation between jets and individual caribou fitted with Platform Terminal Transmitters (PTTs, Telonics, Inc., Mesa, AZ) using satellite telemetry (Service Argos). When location data indicate the presence of caribou inside the MTA, DND erects either blanket closures around groups of collars or buffers around individual collars, to reduce the probability of disturbing caribou. It is assumed that due to the gregarious nature of caribou, randomly collared individuals provide a reasonable approximation of caribou herd location and movement, assuming adequate sample size.

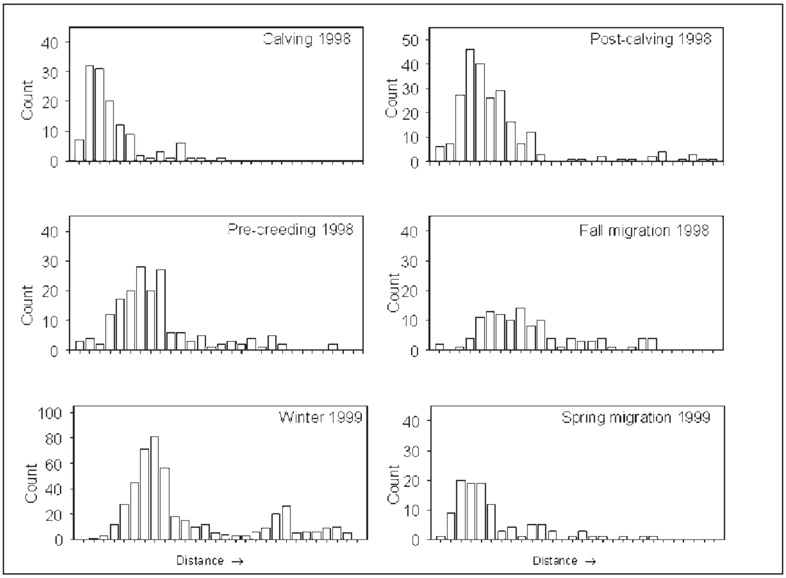

Fig. 1. Distance class from centroid histograms for satellite collared caribou, by caribou season, George River caribou herd, 1998-1999. Note difference in y-axes scale for Post-calving 1998 and Winter 1999 seasons.

Past reviews of this mitigation program have concentrated on attempting to determine the variance of numbers of animals associated with collared animals (Renewable Resources Consulting Services, Ltd., 1994) or correlating collar presence with visual observations of groups of animals (Trimper & Chubbs, this issue). To date, however, there has been no effort to estimate collar sample size requirements for this type of program, central to determining effectiveness of mitigation efforts. Additionally, statistical analyses could suffer from lack of power (Steidl et al., 1997). It is noteworthy that earlier studies have identified potential negative impacts of the jet activity on caribou (Harrington & Veitch, 1991; Harrington & Veitch, 1992). We present an evaluation of the estimated sample size requirements for mitigation of the George River caribou herd in Labrador and Quebec exposed to low level jet fighter activity.

Methods

Individual animals from the George River caribou herd were captured using a net fired from a helicopter, physically restrained, and fitted with ST-3, ST-4 or ST-14 Platform Terminal Transmitter collars (Telonics, Inc., Mesa, AZ, USA). Animals were eartagged, and standard morphological measurements obtained. Captures were in support of an ongoing telemetry project of the Department of National Defence, Goose Bay.

We used location data of quality (NQ) >0, from 1 June 1998 to 31 May 1999 (Keating, 1994). Lower quality (NQ≤0) locations were not used because of inherent imprecision, resulting in a data set containing locations for multiple individual caribou with a precision of 1 km or less (Rodgers, 2001). Collars transmitted on both 4- and 5-day cycles. To ensure that each collared animal had the opportunity to be present in each 5-day period, all locations were then divided into consecutive, 5-day periods. When more than one location was present for an animal within a 5-day period, the higher quality location was retained or where locations were of the same quality, the earlier location was retained. Each 5-day period was then assigned to one of six annual caribou seasons: calving, post-calving, pre-rut, fall migration, winter, and spring migration (Bergman et al., 2000). Five-day periods that overlapped two successive seasons were omitted, removing from the analysis locations recorded on the cusp of season changeover. During the study period the number of collared animals per 5-day period ranged from 9 to 21 animals.

For each five day period, we generated a Jennrich-Turner ellipse (JTE), including centre of mass, for all individual animals (Jennrich & Turner, 1969). We then calculated the distance from the centre of mass to each individual animal location. For the six caribou seasons, we pooled all centroid distances, creating one larger list of centroid distances for each caribou season.

We defined caribou groups based on a defined radius around a point in space. For our analysis, we used a 27.8 km buffer, one of the larger radial distances currently used by DND to create no-fly zones around satellite-collared caribou. Using a relatively large buffer will produce a relatively smaller estimate of required collars, while the smallest buffer could produce collar number estimates that are unrealistic. This approach suited the original intent of the analysis (spatial avoidance mitigation), avoids the potential pitfall of attempting to define caribou groups based on variation in distance between animals, and facilitates modifying grouping criteria to assess effect on sample size estimates. We generated histograms of centroid distances for each caribou season, using 27.8 km as bin width (Fig. 1). This method provided an objective means of determining bin width which is important since histogram shape is highly dependent on bin width.

The number of caribou locations in each distance class was determined for each caribou season by extrapolating the proportion of locations to the estimate of herd size (700 000, Russell et al., 1996; Couturier et al., 1996). We converted the distance class measure to caribou group size by using the equation: Y=mX+b, where, Y=caribou group size and X=distance class. This equation assumes a linear decline in group size as distance from centre of mass increases; i.e., that caribou locations at greater distance from the centre of mass represent smaller groups of caribou than locations closer to the centre of mass. This assumption was supported by field observations (S. Couturier & R. Otto, unpubl. data). To determine the slope of the equation, we assumed the average distance class corresponded to the average caribou group size and the maximum distance class corresponded to one caribou.

Because caribou density changes with season (Bergman et al., 2000) we calculated, for each of the six caribou seasons a 95%. Kernel Home Range (KHR) using Animal Movement Analysis software (Hooge & Eichelaub, 1997) and Arcview GIS (Environmental Systems Research Institute, Redlands, CA), employing the ad-hoc smoothing option. This method is a fixed-kernel range estimate, and appears to be the best method for calculating range estimates from location data (Seaman & Powell, 1996, Seaman et al., 1999, Kernohan et al., 2001). We used these estimates of area to calculate the density of 95% of the estimated herd size (665 000). Knowing the number of caribou within a group and the total number of caribou within each bin allowed us to calculate the number of caribou groups within each bin and, therefore, the total number of groups for each caribou season.

Table 1. Minimum and maximum caribou group size estimates for each caribou season, by distance class, George River caribou herd, 1998-1999.

	Group size estimates (Means)	
Season	Min	Max
Calving	1 872	28 228
Post-calving	192	12 940
Pre-breeding	319	10 040
Fall migration	188	31 099
Winter	10 036	11 946
Spring migration	297	14 295

We defined protection probability as the chance that any one randomly selected caribou would be "captured" within one of the caribou "groups" found inside the associated KHR. By repeating the above density calculations for 75%, and 50% (525 000 and 350 000 animals, respectively) of the total herd size, it was possible to adjust our overflight tolerance from 5%, to 25% and 50%. For the 75% and 50% estimates, we calculated the number of groups, starting from the largest (and therefore closest to the centre of mass), that were required to contain 525 000 and 350 000 animals respectively.

Results

Our procedure for extracting and omitting locations from the analysis resulted in a range of 110 to 469 locations per caribou season (Table 1). There was large variation in the minimum mean estimated group sizes between seasons, almost two orders of magnitude, while maximum mean estimated group sizes varied by only a factor of three (Table 1). The number of locations per season was primarily the result of the length of the particular caribou season (range 30 to 152 days), but also depended on the presence of high-quality location data.

Calculated KHR's ranged from 10 845 to 37 690 km^2 for the 50% probability level, 24 773 to 87 279 km^2 for the 75% probability level, and 73 597 to 228 629 km^2 for the 95% probability level (Table 2). Estimated group sizes of caribou varied by season, with minimums ranging from 188 to 10 036 and maximums ranging from 10 040 to 31 099 caribou (Table 2). Estimated satellite collar sample sizes also ranged by caribou season, from 36 to 184 for the 95% probability level, from 23 to 68 for the 75% probability level, and from 15 to 52 for the 50% probability level (Table 3).

Table 2. Areas (km²) of Kernel Home Range, by caribou season and percent range, for the George River caribou herd 1998-1999. Number of locations used in calculations are indicated in brackets.

	Percent of total range		
Season	95%	75%	50%
Calving (127)	73 597	24 773	10 845
Post-calving (237)	157 121	53 340	19 737
Pre-breeding (175)	227 102	58 762	22 565
Fall migration (114)	90 510	44 966	23 041
Winter (469)	228 629	87 279	37 690
Spring migration (110)	150 956	39 826	23 802

Table 3. Estimated number of satellite collars required to protect individual caribou from the George River caribou herd, by probability level, 1998-1999. Rank, smallest to largest, of sample size for given probability level, as well as overall rank (bold), is given in parentheses.

	Probability level		
Season	95%	75%	50%
Calving 1998 **(1)**	36 (1)	23 (1)	15 (1)
Post-calving 1998 **(2)**	100 (4)	48 (4)	32 (3)
Pre-breeding 1998 **(6)**	131 (5)	68 (6)	52 (6)
Fall migration 1998 **(4)**	184 (6)	26 (2)	18 (2)
Winter 1998 **(5)**	64 (2)	49 (5)	34 (4)
Spring migration 1998 **(3)**	97 (3)	44 (3)	35 (5)

Discussion

The procedure used to extract and filter location data resulted in a small percentage of locations (NQ<1) being omitted from the analysis. Briefly, collars used to collect location data were on four-day cycles, and some were on five-day cycles during the study period. Thus, in order to maximize number of locations used to calculate JTE's, the five-day period was chosen as our sampling interval. This meant that multiple locations for an individual caribou were used in the JTE and distance-to-centroid calculations. However, we do not believe this approach constitutes pseudoreplication (Hurlbert, 1984). Recall that our intention was to estimate total seasonal ranges used by the GRCH for spatial mitigation, as well as the distribution of caribou locations throughout the season within the associated KHR, requiring all locations of all collared animals.

Our method of fitting a regression line to the distance class histograms probably over-estimates the number of collars required to "capture" the smaller and more distant groups of animals. This is due to the regression line extending to the extreme distal end of the histogram, where there were usually relatively few and usually low histogram values, meaning the curve was actually above the true values, and hence overestimating number of caribou groups. However, the converse is true as well; at small to medium distance classes (larger caribou groups) the estimate was probably too low as the curve would be below the actual values, and hence underestimating number of caribou groups. The degree of trade-off between these competing forces was not investigated for the purpose of this analysis, and is probably minimal. Further, regardless of the assumption and model used to perform this portion of the analysis, a similar trade-off will occur, although the relative weight of under- and overestimation will probably vary.

The large variation in the minimum mean estimated group sizes indicates that the core area of use, by season, remained much more stable than the peripheral areas, with small minimum mean values indicating very dispersed distributions and higher rates of movement. The minimum mean value for Winter is substantially higher than the next lower value, and probably reflects the large number of locations derived from Winter season, the longest of the six caribou seasons, as well as the fact that groups of the GRCH move relatively little during the winter (Bergman et al., 2000).

The KHR analysis revealed large variations in the total range estimate for the GRCH, indeed, more than an order of magnitude (Table 2). A seasonal pattern did emerge, with Winter consistently exhibiting the largest KHR's, and Calving the smallest KHR's. It is not surprising that calving season had the smallest range estimates, as congregation of females on calving grounds is one characteristic of the migratory caribou ecotype (Gunn & Miller, 1986), like the GRCH. Additionally, the winter range of the GRCH can span the entire land mass from Hudson Bay to the Labrador Sea, north of 53°N, and this cumulative range is expanding (Schmelzer & Otto, this issue). The winter distribution of the GRCH is probably multimodal, graphically reflected in the winter distance to centroid distribution (Fig. 1). Two modes are more obvious, although rigorously determining number of modes can be problematic (Silverman, 1981; Manly, 1996).

Multimodality would cause the KHR to be relatively large, causing an underestimate of density of caribou, hence overestimating the number of collars required for that season. The other seasons exhibited variability in ranking of range estimate (Table 2), most likely reflecting movement distance and rate of travel between calving grounds and winter foraging ranges.

Estimated collar sample sizes varied both by season and probability level (Table 3). A distinct pattern emerged here as well, with Calving having the lowest estimated required sample sizes and Prebreeding and Winter seasons having generally the highest estimated required sample sizes. Aside from season, important variables that will modify the required collar number estimate is the spatial seasonal range use in relation to the boundaries of the military training area (MTA) as well as seasonal training period for aircraft. Jet training usually commences in late March or early April and usually finishes by early November. Also the identified MTA encompasses only a portion of the total range of the herd. Caribou are usually present in the MTA during Winter, Spring migration, Post-calving, Pre-breeding, and Fall migration, but not during Calving. Protection of the GRCH at any desired probability level can be as easy as choosing the highest estimated number of collars of those seasons exhibiting spatial and temporal overlap with the MTA. Alternatively, mitigation can employ minimum collar sample size estimates for some caribou seasons, and invoke other mitigative measures for remaining seasons. For example, during Pre-breeding, the GRCH usually overlaps with a relatively small portion of the MTA, where block closures to flight training could provide increased protection from overflights. Further, variable buffering distances around individual collars can be used as well. Both of these measures are presently used by DND to protect caribou from overflights, but both implicitly depend on being able to extrapolate from collar locations to herd distribution.

This analysis serves as a basis from which decisions can be made about the degree to protect the GRCH from jet overflights. Such decisions can be made based on estimated sample size requirements, level of probability of protection, costs associated with such programs, and augmentation of avoidance of collars with other mitigative measures. But further, these procedures and results form an alternative to pure statistical evaluation of sample sizes. Our approach allows researchers to adaptively evaluate sample size requirements for radio telemetry and tracking studies where a portion of data already exist, producing estimates based on the life history characteristics, movement patterns, and abundance of the animals studied.

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Caribou co-management in Nunavut: Implementing the Nunavut Land Claims Agreement

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Abstract: In 1993 the Nunavut Land Claims Agreement (NLCA) was signed and this lead to the creation of Nunavut in 1999. Under the NLCA caribou and other wildlife in Nunavut are co-managed by government and Inuit. The Nunavut Wildlife Management Board (NWMB) is the main instrument of wildlife management, working with its government and Inuit co-management partners to manage caribou within the principles of conservation outlined in the NLCA, using both western scientific knowledge and traditional knowledge. When caribou herds cross provincial or territorial boundaries, management boards or management planning committees are established.

Key words: Nunavut Wildlife Management Board, conservation, wildlife, management, traditional knowledge, Inuit.

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Introduction

On April 1, 1999, Nunavut became Canada's newest territory. Previously a part of the Northwest Territories, Nunavut was created as a result of the Nunavut Land Claims Agreement (NLCA). Nunavut occupies over 1.9 million square kilometers or approximately 1/5th of Canada's land mass (Fig. 1). The NLCA was signed in May, 1993, and implementation of the claim has been ongoing since that time.

Under the NLCA, wildlife (defined as all flora and fauna) in Nunavut is managed jointly by the Inuit of Nunavut and the Government. This system is termed co-management. In Nunavut, this means Inuit and the appropriate level of government (federal or territorial) working together. It also means that wildlife management decisions are made based on information from both western science and Inuit Qaujimajatuqangit (IQ or Inuit traditional knowledge). IQ is Inuit knowledge, values and beliefs about wildlife and reflects knowledge that has been passed down through generations, and/or the knowledge that has been gained through a long association with the land. IQ provides an Inuit perspective on the resource. Where a scientific survey provides information on a herd at only one point in time, IQ often provides a better long-term picture of the herd and changes in patterns of behaviour, movement patterns and interactions.

Caribou Co-management

The organizations, or co-management partners, who work together to manage caribou (Rangifer tarandus) in Nunavut include the Nunavut Wildlife Management Board (NWMB), Hunters and Trappers Organizations (HTOs), Regional Wildlife Organizations (RWOs), Nunavut Tunngavik Incorporated (NTI) and the Government of Nunavut, Department of Sustainable Development (DSD) (Fig. 2). Each of these partners has a role to play in managing caribou in Nunavut.

The NWMB is an Institution of Public Government (IPG), but is not directly a part of the federal or territorial government. The NWMB is also a co-management board, with four members appointed by Inuit organizations and four by government (federal and territorial). The eight Board

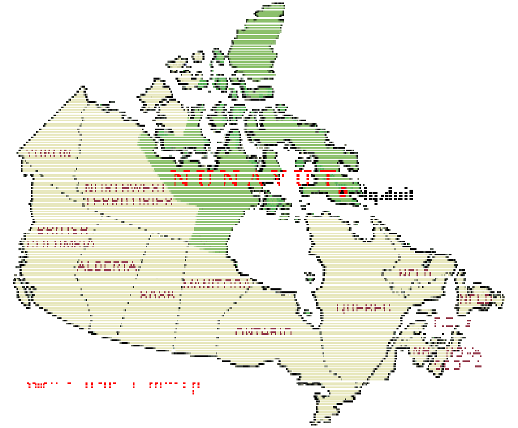

Fig. 1. Map showing the Territory of Nunavut within Canada. The Nunavut Settlement Area (NSA) includes all of the Territory of Nunavut except for Hudson Bay and the southern part of Hudson Strait, but does also include the Belcher Islands in Hudson Bay. Maps courtesy of www.theodora.com/maps, used with permission.

members choose the independent chairperson. The Board is not an Inuit organization, but rather represents the public in general.

The NWMB is the main instrument of wildlife management in the Nunavut Settlement Area (NSA), subject only to the ultimate authority of the appropriate government Minister. The NWMB's mandate includes establishing quotas or non-quota limitations on harvesting (non-quota limitations include seasons, hunting methods etc.). The Board also approves all management or conservation plans and approves the designation of all species (endangered etc.) within Nunavut.

Each of the 27 communities in Nunavut has an established HTO with membership comprised of the Inuit beneficiaries of that community. Each HTO regulates the harvest of wildlife by its members and reviews issues affecting wildlife in the vicinity of the community. In making decisions about wildlife that will affect a community, the NWMB will consult with the appropriate HTO prior to making a decision.

In each of Nunavut's three regions - Kitikmeot, Kivalliq and Qikiqtaaluk – there is an RWO. The membership of each RWO consists of the chairpersons of the HTOs in that region. The RWO has similar responsibilities to the HTOs, regulating harvest by the members of HTOs in the region, where a population/stock/herd is harvested by more than one community. The RWO also reviews issues affecting wildlife in the region. As with HTOs, the NWMB will always consult with the relevant RWO(s) when making decisions regarding wildlife in each region.

NTI is the Inuit birthright corporation, representing the Inuit of Nunavut and promoting Inuit interests. It is the primary Inuit land claims organization. NTI oversees Inuit rights established under the NLCA and works to ensure that other co-management partners are meeting their obligations established under the NLCA.

The Department of Sustainable Development, Government of Nunavut has two roles in the management of caribou in Nunavut. Under the terms of the NLCA, the Minister of Sustainable Development has the ultimate authority in wildlife management decisions respecting caribou (and other terrestrial wildlife) in Nunavut. However, the Minister can only overrule a decision of the NWMB on the grounds of conservation, public health and safety or interference with Inuit harvesting rights (Government of Canada, 1993).

DSD's biologists are responsible for conducting research on caribou (and other terrestrial wildlife). The biologists and other Nunavut Wildlife Service staff provide advice to the NWMB when the NWMB is preparing to make a decision on an area within the Government of Nunavut's mandate.

Principles of Conservation

In making decisions with respect to wildlife, the NWMB is guided by the Principles of Conservation outlined in the NLCA. The Principles of Conservation are:

(a) The maintenance of the natural balance of ecological ecosystems within Nunavut Settlement Area;
(b) The protection of wildlife habitat;
(c) The maintenance of vital, healthy, wildlife populations capable of sustaining harvesting needs as defined in the NLCA; and
(d) The restoration and revitalization of depleted populations of wildlife and wildlife habitat. (Government of Canada, 1993, pp. 27-28).

Caribou Populations and Management

There are at least 12 different caribou populations in Nunavut. These include the Bathurst, Bluenose East, Ahiak, Beverly, Qamanirjuaq, Dolphin-Union, Northeast Mainland, Northeast Baffin Island, North Baffin Island, South Baffin Island, Queen Elizabeth Islands and Prince of Wales – Somerset Islands herds. The Northeast Mainland and Queen Elizabeth Islands populations may also contain sub-populations.

The management of the different herds in the NSA varies depending on whether the herd is shared

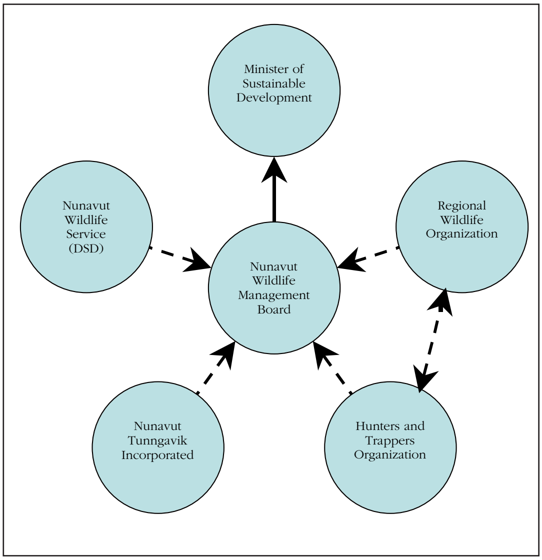

Fig. 2. Relationship between co-management partners responsible for caribou management in Nunavut. Dashed lines indicate advisory relationship, solid line indicates decision authority. Arrows show the direction of flow.

with another region or whether they are found entirely within the NSA. For those caribou herds found entirely within the NSA, the co-management partners outlined above work together to manage the herds and develop management plans as appropriate. However, several herds are shared with other neighboring jurisdictions and these herds require cooperation with the appropriate management organizations in those jurisdictions. The level of development of these management measures varies with different herds.

The Beverly and Qamanirjuaq herds are shared between Nunavut, the Northwest Territories, Manitoba and Saskatchewan and are managed together. The Beverly-Qamanirjuaq Caribou Management Board (BQCMB), with government and aboriginal representation from all four regions is responsible for overseeing the management of these two herds. With respect to Nunavut, the BQCMB makes recommendations to the NWMB. The NWMB then makes a decision and forwards this decision to the Minister of Sustainable Development.

The Bathurst Caribou herd is shared between Nunavut and the Northwest Territories. Currently the Bathurst Caribou Management Planning Committee is working to develop a Management Plan for this herd. The Committee has representation from governments of both territories and from Dene and Metis from the South Slave and North Slave claim areas in the NWT and Inuit from the Kitikmeot region of Nunavut. The Management Plan developed will require approval of the NWMB.

The Bluenose East caribou herd was previously considered to be part of the larger Bluenose herd. However, recent satellite tracking and genetic work has shown this herd to be separate from the Bluenose West herd. The Bluenose East herd is shared between Nunavut (Kitikmeot region) and the Northwest Territories (North Slave and Sahtu – Dene and Metis). A draft management plan was previously developed for the larger Bluenose herd. However a management plan for the Bluenose East herd has yet to be developed.

For the South Baffin caribou herd, work has begun on a management plan, and is still underway. For the remaining herds, management plans have not yet been developed but in future will follow similar approaches to those described above for other herds.

Summary

The signing of the NLCA and the establishment of Nunavut has seen the development of a co-management system for caribou in Nunavut. Co-management requires government and Inuit work together to manage caribou in the NSA. The NWMB works with its co-management partners: DSD; NTI; RWOs; and HTOs to manage caribou within the principles of conservation outlined in the NLCA. Where trans-boundary populations of caribou occur, management boards or management planning committees have or are being established.

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Twenty-five years of co-management of caribou in northern Québec

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Abstract: The Hunting Fishing and Trapping Co-ordinating Committee (HFTCC), created at the signature of the James Bay and Northern Quebec Agreement has been meeting regularly since 1977. Early in the process, it became clear that the perception of the role and powers of the Committee were not commonly shared by the native and non-native members of the Committee. Nevertheless, the Committee has been used primarily as a consultative body for wildlife related issues. Of all the files on which the Committee worked, Caribou management, (including the development of outfitting and commercial hunting for this species) has been among one of the most discussed subjects during the meetings. An analysis of important decisions taken and of the process that led to them reveal that very rarely was the Committee able to formulate unanimous resolutions to the Governments concerning caribou management. In fact, only a few unanimous resolutions could be traced and many were ignored. This took place during a period of abundance and growth of the caribou herds. As a result, the Committee has gone through the cycle of growth of the George River Herd without a management plan, without a long term outfitting management plan and for the last 8 years, without a population estimate of the herds. This situation did not prevent the Committee from allocating quotas for a commercial hunt, open a winter sport hunt and to give permanent status to outfitting camps that were once established as mobile camps. It was hoped then that increased harvest would help maintain the population at carrying capacity. This short-term reaction however, never evolved into a more elaborate plan. Of course this must be looked at in the context of the HFTCC having a lot more to worry about than the Caribou. Although all members know of the population cycles of caribou, the decision process that must be triggered, should a crisis occur is not in place. This presently results into a polarization of concerned users (fall outfitters vs. winter outfitters, subsistence and sport hunters vs. commercial hunt, Outfitters Associations vs. HFTCC and eventually George River Herd users vs. Leaf River Herd users. The HFTCC may have to make difficult decisions during the coming years but did not gain much constructive experience through its first 25 years of existence. It is unfortunate that the authority of the Committee is binding the governments only in times of crisis when an upper limit of kill needs to be established. Because of the unpredictability of caribou herd numbers, the upper limit of kill should be established on a yearly basis. This would insure that the committee is fed information continuously in order to make informed decisions and would also re-establish the authority of the HFTCC over this resource.

Key words: Cree, Inuit, Naskapis, sport hunting, subsistence harvest.

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Introduction

The conclusions contained in this paper are those of the author and may not coincide with those of current or past members of the Hunting Fishing and Trapping Coordinating Committee. I base my opinions on my nine years of experience as an advisor to the Cree members of the said Committee.

The James Bay and Northern Quebec Agreement (JBNQA) was signed in 1975 and the Northeastern Québec Agreement in 1978. The territory covered by these comprehensive Agreements is approximately one million km^2 in Northern Québec. The Northern Québec Inuits, the James Bay Cree of Québec and the Naskapi Nation of Kawawachikamach are beneficiaries of these Agreements. Section 24 of the JBNQA established the Hunting Fishing and Trapping Regime, and section 24.4, the Hunting Fishing and Trapping Coordinating Committee (HFTCC), which is an expert body, composed of an equal number of Native and Government voting members. It is primarily a consultative body to the governments of Québec and Canada and is intended to be the preferential and exclusive forum where the beneficiaries of the Agreements and the two governments may jointly formulate regulations and supervise the administration of the Hunting Fishing and Trapping Regime.

The Coordinating Committee enjoys the authority to establish the upper limit of kill for moose and caribou for Native and non-Natives and subject to the principle of conservation, such decision bind the responsible Minister of government who must make such regulations as are necessary to give effect thereto. This authority is unique among co-management boards in Canada.

Sport hunting for caribou in northern Québec is open since 1964. At first, there was only one hunting zone, which covered all the area north of the 50th parallel. In 1973, the zone was sub-divided into four zones. The main zones where sport hunting took place were zone 03 and 04. Zone 04 was for Québec residents exclusively whereas in zone 03 the use of an Outfitter was required for all sport hunters, except for residents of Shefferville and Fort Chimo.

Hunting pressure was controlled then through the number of hunting permits made available to the Outfitters. For instance, the number of permits available varied from 700 in 1975 to 1300 in 1979 in zone 03 (Mallory, 1980).

The HFTCC started meeting regularly in 1977. A difference in the perception of the role of the Committee was evident between the Native and Government parties. Native parties saw themselves as equal partner in the Management of wildlife resources whereas the Government representatives saw the committee role as advisory to the responsible governments. This has contributed to mutual frustrations and impatience on the part of the Québec Government party and the three Native parties (Juniper, 1994).

In this paper, I will examine the evolution of the regulatory changes, which influenced some aspects of the development of Caribou sport hunting and the role played by the HFTCC. This historical perspective is essential in order to better understand the context into which the Committee may have to make difficult decisions should the George River Herd decline to a level requesting restrictive measures.

Upper limit of Kill

In 1980, information indicating that the number of female caribou on calving grounds had declined and that the percentage of calf in the population was low was provided to the Committee. A discussion of these results with the biologists of the government led the Committee to the conclusion that restrictive measures were necessary. The HFTCC adopted for the first time an upper limit of Kill of 3300 caribou for zone 23 and 24 (formerly 03 and 04). The resolution was put in application by issuing a limited number of hunting permits (4000). Quebec representatives on the Committee abstained from voting on the said resolution. It was the first time that the Committee made a decision that bound the responsible minister. It can be found in the Minutes of the meeting that Québec representatives wanted to control access to the territory through a restricted number of permits rather than reducing the harvest of caribou. Following that important decision, the Committee reviewed the upper limit of kill for caribou every year until 1987.

In 1981, as a result of a detailed analysis of population indicators demonstrating clearly that the caribou population was augmenting, the upper limit of kill was established at 5500 with most of the increase in zone 24. That time the Naskapi representative abstained from voting on the resolution arguing that it would be necessary to improve our understanding of the biology of the George River Herd prior to making such decision.

In 1982, the adoption of the upper limit of kill was heavily discussed because Native Parties were frustrated with the lack of progress made with the hiring of Native Game Wardens and because Québec was suggesting to increase the size of zone 24 and possibly the harvest. An upper limit of kill of 5500 was finally adopted, with the representative of Québec voting in favour, the Cree against and the Naskapi and Inuit abstaining. Later in that year, the Committee discussed for the first time the possibility of allowing two caribou per permit and the opening a winter hunt. It is clear from the Minutes that the members of the Committee shared the opinion that the herd was increasing and that sport hunting was not limiting this increase. An upper limit of kill of 2700 caribou for the winter hunt was established through a unanimous resolution and for the first time two caribous would be taken for each sport-hunting permit. The resolution also called for the drawing up of a management plan.

In 1983, the Minutes of the HFTCC indicate clearly that the members agreed that the herd could be exploited more intensively but argued about the lack of economic spin-off for the Natives. At the time, the procedure for the establishment of new outfitting operations was not finalized and the native promoters were limited to operations taking place in territories surrounding their communities. The proposal from Québec was to implement an earlier hunting season (bow and arrow), to allow two caribou per permit for the fall hunt and to fix the upper limit of kill at 10 000. The HFTCC finally adopted a resolution fixing the upper limit of kill at 5500 and decided to adopt another resolution for the winter hunt. The total number allocated to sport hunting would not be higher than 10 000 animals. Québec representatives voted against this resolution. It was later reported to the HFTCC that the outfitters were not ready to augment the number of caribou to two per permit because of logistical problems such as air transport. The committee then adopted a resolution establishing the upper limit of kill for the winter hunt at 1500 animals. A second resolution rejecting the proposal to have two caribou per permit was adopted, with Québec representatives voting against.

In 1984, discussion went much easier. Even though Québec proposed to not establish an upper limit of kill, the HFTCC adopted a resolution establishing the upper limit of kill for the territory and for both fall and winter hunt to 7000 caribous. The date for the opening of the hunt in zone 23 was also changed to an earlier date.

In 1985, the HFTCC adopted again a resolution establishing the upper limit of kill at 7000 caribous. The Cree representatives abstained from voting on this resolution.

In 1986, Québec representatives were arguing that the establishment of an upper limit of kill for caribou was a useless administrative procedure, but the Native representatives insisted to establish the limit to 9000 animals on the basis that such an exercise aimed at protecting their priority of harvest on the Territory. Québec representatives abstained from voting on this resolution. This was the last time a resolution fixing the upper limit of kill was adopted.

For the 1987-88 season, it was agreed to not fix an upper limit of kill as in the past. First, the upper limit of kill would be based on biological data. This number would be established for a period of approximately 5 years but could be reviewed every year. The number would include subsistence hunting. This exercise would take place in the framework of the drawing up of a management plan for caribou. No upper limit of kill would be fixed for 1987-88. Such a number would only be established in 1988-89 and for a period of 5 years.

During that period the province authorized the use of mobile camps for outfitters. Although the sites used for mobile camps were to be allocated on a temporary basis, the 11 outfitters in operation were allocated a total of 83 sites and were able to increase instantaneously their lodging capacity without the administrative weight of the use of permanent sites. It was hoped then that an increased harvest would contribute to maintain the herd at carrying capacity. Of course, it did not happen, and the outfitters soon requested that the sites become permanent sites. The status of these sites remains unclear today and could create problems should restrictive measures be necessary.

During the following year, the representatives of Québec tabled a document describing scenarios of harvest based on caribou populations of 300 000 or 600 000. The document concluded that it was "useless to plan for the long term" (...) it must be clear for every one involved that harvest needs to be readjusted frequently when new information becomes available. Discussions on this topic were postponed until a new survey was carried out. No other mentions in the minutes of the HFTCC appeared until 1998 when the big game working group was again mandated to draft a management plan. A majority of the meetings of this task force have been postponed, and as a result the HFTCC has yet to see the draft version of the plan.

The need for a management plan

As previously seen, the discussions that led to the establishment of an upper limit of kill between 1980 to 1987 were often influenced by other issues concerning caribou, such as the lack of a management plan, problems associated with Native participation to the outfitting industry and others.

In this section, the discussions relating to the need for a management plan are reviewed. At present, the HFTCC in the course of its work can refer to management plans for almost all game species such as moose, black bear, Atlantic salmon, and important species for subsistence such as beluga. Ironically, we have no management plan for the species that could be rated most important both for subsistence and the outfitting industry. Such a situation is not the result of an absence of funds or the lack of biological information. In fact, millions of dollars have been spent researching caribou biology and behaviour. Hydro Québec conducted a research programme to study the impacts of reservoir creation on the migration of caribou and the government of Canada spent important sums of money to monitor impacts caused by NATO low level flights in Labrador.

At the meeting of the HFTCC in 1980, a discussion on caribou management took place during which the Inuit party offered to assume part of the responsibility for caribou management provided they were given the necessary funds by the government. This discussion was continued during a second meeting. The Inuits argued then that their experience and their vested interest in the resource placed them in a privileged position to assume more responsibilities. The available funds should be allocated to them for that purpose. Of course the representative of the Québec government replied that they had no intention of sharing funds for the management of caribou nor did Québec intend to abdicate legal responsibility in the management of this species.

During the period from1981 to 1987, four different censuses of the George River herd were conducted by the Québec and Newfoundland-Labrador governments, the results of which were confusing and hampered efforts to adopt a reliable population estimate for management purposes. Nevertheless, government managers were concerned with the large size of the herd in relation to its habitat, and recommended measures to stabilize its numbers (opening of a winter hunt and a bag limit of two).

The Inuits expressed concerns in adopting such liberal regulations in the absence of a management plan. When the resolution endorsing the opening of a winter hunt and the increased bag limit was adopted in 1983, it also called for the drawing up of a management plan which would allow more benefits for Native people. The approval by the Natives for liberal regulation was later suspended by way of another resolution however, which also requested the Committee's task force on Big game to draw up a management plan for the George River Herd. At the time, the task force was occupied with moose management and it was not until December 1986 that this body addressed caribou management, when the Government of Québec tabled a draft management plan. The government representatives assured Native parties of their guaranteed participation and added that because the minister himself had requested a management plan for caribou, the project automatically enjoyed the highest priority.

Further discussions on a Caribou management plan between Québec representatives and the Native parties continued sporadically including meetings with the Ministers responsible for Wildlife resources. However, a Québec government management plan for caribou has yet to be adopted. The native members on the HFTCC have shown much patience and persistence and went to the extent of supporting the organization of the 9Th Conference in Kuujjuak in order to stimulate more interest from the governments. Hopefully these efforts will eventually pay off!

Winter hunt in the Cree Territory

The development of a winter sport hunt in the Cree territory (zone 22) was first proposed in 1984, but was rejected by the Cree representatives until other administrative issues would be solved. Before the opening of the winter hunt, the sport hunting industry of caribou was absent from the Cree territory.

In 1985, Québec tabled a preliminary draft document to modify the law and authorize winter caribou sport hunting for the Québec residents in the area of Radisson. The Native parties were strongly opposed to such a hunt and blamed the government representatives for not consulting the Committee appropriately. The government representatives decided to postpone the opening of the hunt.

Bilateral discussions between Québec and the Cree continued until July 1988, when a presentation was made to the Committee explaining the progress made so far in the discussions between Québec and the Cree.

During the next meeting, in October, a proposal by Québec was tabled for discussion. The parties were divided on the issue. The Inuit and Naskapi were opposed to open a hunt without the obligation to use the services of an outfitter. Moreover, they thought that no more caribou should be allocated for sport hunting until a census would be carried out. The Cree were not opposed to a winter sport hunt of caribou, but were worried that the proposed regulations were not adequate. More specifically, they were in disagreement with the size of the zone, they wanted to exclude the road from the hunting zone, more surveillance and a shorter season than what was proposed. Québec announced then that the opening of the season would be delayed for another year to continue discussions with the Cree. No changes were made to the proposed regulations however before the opening of the season in 1989-90. Dissatisfaction with this type of hunt was evident when Cree Trappers complained that they were being displaced from their trapline because of the danger caused by the hunt and the lack of surveillance.

In June 1990, the Québec representatives presented their analysis of this first year and proposed changes such as a shorter season and the inclusion of reserved territories in the zone so that a Cree outfitting industry could be developed in order to make the hunt more acceptable to the Cree. In 1992, a new zone exclusive to the outfitters was created which was a precedent for the Committee. This development of the winter hunt has been so successful since then, that in the recent years more caribou are taken from this zone than from zone 23 where the Fall sport hunt was first established. Cree owned outfitting camps are now well established in the area.

Discussion

The responsibility of the Coordinating Committee in the management of wildlife is evident. Since its establishment in 1975, the committee has attempted to fulfill its responsibility. Disagreements in the interpretation of the role and mandate of the Committee made this difficult during the early days of the Committee (Juniper, 1996). Tight schedules and crowded meeting agendas have resulted in discussion of important decisions being referred to working groups. Bi-lateral discussions between responsible governmental departments and the concerned native parties contributed to compromises, but never to unanimous decisions by the Committee. In fact, in the case of the development of the winter hunt along the Trans-Taiga road, these bi-lateral discussions have divided the Committee.

Twenty years after having mandated a working group to elaborate a management plan, the HFTCC still does not have any and must take case-by-case decisions. Since then, there have been numerous staff changes and native parties are gradually losing interest in the process.

In retrospective, it seems that as soon as the Committee loosened its hold on the caribou situation and stopped establishing the upper limit of kill in 1987, it lost control over its exploitation and regulation. Following that decision, the Committee started to act as if there were too many caribous and that intense exploitation was beneficial to the population. Only when the George River Herd showed signs of a decline did the Committee became interested again to develop a management plan.

For the committee to function efficiently it has to be fed information on a continuous basis and it must spend the necessary time analysing the said information. The review of the upper limit of kill, even though considered by government officials a heavy administrative exercise, should be done on an annual basis in order to insure that the global situation is taken into consideration.

In the absence of the Coordinating Committee involvement, outfitters, hunters and native organizations are trying to pressure the government and are therefore diminishing and weakening the status of the HFTCC. The authority of the HFTCC must be re-established for Native parties to fully participate and trust government management decisions.

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Reindeer avoidance of pasture contaminated with sheep and reindeer faeces

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Abstract: Contamination by excrements will increase in areas with high animal densities, such as snow free patches with accessible forage in winter and holding paddocks. Avoidance of faeces dropped by other grazers may result in interference competition by reducing optimal forage intake, or offer protection from the transfer of parasites or disease. We conducted two enclosure experiments investigating reindeer (Rangifer tarandus) reactions towards faeces. The first experiment tested whether reindeer avoid pasture contaminated with faeces from reindeer or sheep (Ovis aries). Both high (0.5 kg/m^2) and low (0.05 kg/m^2) concentrations of faeces reduced reindeer grazing compared to no faeces. Reindeer grazed significantly less in areas with high concentration of faeces compared to areas with low concentrations, with equally strong avoidance regardless of faeces source. The second experiment analysed the defecation pattern (random or not) of reindeer in a 50 m x 40 m enclosure to investigate how this pattern might change following the introduction of female sheep or additional female reindeer. Both reindeer and sheep defecated in a non-random pattern that was related to their preferred bedding sites. When sheep visited reindeer, the species' faeces distributions were positively correlated, indicating that reindeer and sheep had an overlap in area utilization, at least while bedding. When additional reindeer were introduced and then removed, the combined resident and visiting reindeers' faeces distributions were negatively correlated with the resident reindeers' faeces distribution following the removal of the visiting reindeer. This suggested that resident reindeer avoided the visiting reindeers' faeces. Resident reindeer also produced fewer total droppings when visited by new reindeer, while the number of droppings did not change when visited by sheep. Thus, resident reindeer were more adversely affected by the introduction of new reindeer even after their removal than by the introduction of sheep. In conclusion, the amount and distribution of excrements will play an important role in reindeer grazing and area use in pastures maintaining high densities of reindeer or reindeer and sheep.

Key words: competition, faeces distribution, grazing, spatial overlap, sympatric ruminants, parasite aversion.

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Introduction

Norway currently manages the remaining Fennoscandian populations of wild tundra reindeer (Rangifer tarandus tarandus) in the mountains of South-Norway. In addition to wild reindeer, reindeer herdsmen (almost exclusively Sami) maintain approximately 183 000 semi-domestic reindeer in the northeastern part of South-Norway and in North-Norway. Domestic sheep are prevalent with wild and semi-domestic reindeer on alpine summer range, exceeding densities of 30 sheep per km^2 in some areas, e.g. in Setesdal-Ryfylke in southwestern Norway (Colman, 2000). To a large extent, reindeer and sheep overlap in plant resource utilization (Skogland, 1984; Ballari, 1986; Colman et al., 1998; Mysterud, 2000). Thus, direct competition between reindeer and sheep would be expected when resources are limited.

Limited information exists on competition between sympatric ruminants like reindeer and sheep (Ballari, 1986; Warren & Mysterud, 1986; Colman, 2000). An indirect form of interference or competition may occur if the species avoid feeding in locations that contain excrements from the other species (Putman, 1996). Data from a stall-fed experiment (Moe et al., 1999) showed that reindeer avoid eating when faeces from either species were mixed in their rations. Questions remain whether reindeer or sheep avert from otherwise preferred pasture locations because of the presence of faeces from the other species.

The amount of excrement and its distribution may be important factors influencing avoidance behaviour, but little is known about the defecating patterns for reindeer on pasture. Reindeer often use small areas of pasture due to spatially limited resources, for example in winter when cratering for forage through snow. Semi-domestic reindeer may also be held in pre-slaughter pens or holding paddocks before or after transportation. In such areas, high animal densities relative to foraging area will increase contamination by excrements.

From a previous pen experiment with reindeer (Moe et al., 1999), we expected reindeer to reduce feeding time on pasture contaminated with reindeer and sheep dung. Although never specifically tested, data from Moe et al. (1999) indicate that reindeer are more avers towards sheep faeces than to reindeer faeces. Studies of within species systems also show that avoidance increases with increased level of contamination (Hutchings et al., 1998). Thus, we tested the following hypothesis:

1) Reindeer spend less time feeding in areas contaminated with faeces from either reindeer or sheep.
2) Reindeer avoidance of areas contaminated with sheep faeces is stronger than towards areas contaminated by reindeer faeces.
3) Reindeer avoidance of areas increases with the faecal concentration regardless of the faecal source.
4) Reindeer defecate in a random pattern that reflects their grazing pattern and not their use of bedding sites.
5) Introducing sheep into an enclosure with reindeer increases interspecies avoidance due to faeces avoidance between species. This reduces areas of faeces overlap both during the co-inhabitation and after the removal of the sheep.
6) Introduction of naive reindeer into an enclosure with resident reindeer will result in co-use of areas by both groups of reindeer. This would suggest a mixing of faeces, measured by comparing faeces overlap following the removal of the visiting reindeer.

Methods

Site description

The study was conducted in an open farm landscape in the Bognelv river valley, about 5 km from Langfjordbotn, Finnmark county, North-Norway (22°19'E, 69°59'N). The experimental area was a level 2 ha field at sea level. It has not been ploughed or sowed during the last 25 years and consist of a homogenous mixture of native and planted grasses. The experiment's location in an open agricultural area, combined with a short distance from the ocean and a cold-water river system, provided an almost constant wind over the experimental area (registered during the experimental period (Eidesen, 2002)). This probably reduced harassment on animals by parasitic flies compared to inland areas.

Experimental design

Experiment 1

This experiment was designed to test reindeer avoidance of sheep and reindeer faeces (predictions 1, 2 and 3). Three 10 m x 10 m enclosures were set up on a level field where no animals had previously grazed, and thus, was free of excrements. Vegetation in the 3 enclosures consisted of a homogenous mixture of earlier planted grasses cut to 15 cm in height two days prior to releasing animals onto the pastures. A height of 15 cm was chosen to facilitate and maintain green growth, provide an average height similar to natural grass pastures, and allow the excrements to be evenly distributed within each treatment square. Each enclosure was divided into 25 squares of 4 m^2. The size of the enclosures and squares was chosen to represent the approximate size of a free ranging reindeer's feeding radius and specific grazing patches while grazing intensely for approximately 30 minutes (Colman, 2000). The inside corners of each 4 m^2 square were measured to the nearest 1 cm and marked with a small white circle of paint on the grass clearly visible to the observer, who sat in a 5 m high observation tower placed 5 m away from the enclosures. The outside corners of the 4 m^2 squares were marked with white paint or a white ribbon on the fence surrounding the enclosure. Four treatments and a control, with 5 replicates in a randomised design were used in each of the 3 enclosures (Table 1). The treatments were high (0.5 kg/m^2) and low (0.05 kg/m^2) concentrations of reindeer (RH, RL, respectively) and sheep (SH, SL, respectively) faeces. The dry matter content in the faeces used was about 50%. This provided a dry matter concentration of 250 g and 25 g per m^2 for high and low faeces concentrations, respectively. If 35% of 80 kg faeces were distributed on 5% of 1 hectare, this would give 56 g

Table 1. The treatment and animal densities used during the 3 periods for the faeces distribution experiment, northern Norway, June 1999.

		Enclosures		
Period	Date	1	2	3
1	10. - 16. June 1999	3 reindeer	3 reindeer	3 reindeer
2	17. - 23. June 1999	3 reindeer + 3 reindeer	3 reindeer + 3 sheep	3 reindeer + 3 sheep
3	24. - 30. June 1999	3 reindeer	3 reindeer	3 reindeer

dry matter per m^2 and about 112 g wet weight per m^2 from one sheep or reindeer (as was supported by the results of experiment 2). Considering that sheep tend to aggregate in camp areas to bed at night (Hilder, 1966; Colman, 2000), and reindeer are occasionally restricted to limited pasture area, the level of faecal contamination in some areas is likely to greatly exceed the highest concentration of 250 g dry matter of faeces per m^2 used in this experiment.

Fresh reindeer faeces (mixture of 1 to 13 days old) were obtained from adjacent pastures one day prior to the onset of the experiment. Sheep faeces were collected from a sheep farm 12 hours before the experiment began, and were a mixture of 1 to14 days old. Both reindeer and sheep faeces were wet in tepid water 12 hours before the onset of the experiment to provide an equal amount of moisture (i.e. "simulated freshness") to all the faeces. Faeces were then spread as evenly as possible by hand wearing rubber gloves. To facilitate feeding during the experiment, the animals were offered water but not fed for 12 hours prior to the onset of the experiment. Six female reindeer yearlings were used in the experiment. One animal at a time was released into an experimental enclosure for 30-min each. Using 3 enclosures and 6 animals required that only 2 consecutive experimental trials were used per enclosure (3 repetitions in "pasture" with a repeated measure by 2 reindeer in each paddock). This provided the dual advantage of minimising contamination and overgrazing by the first animals.

All 6 reindeer were habituated towards humans and thus, our presence did not appear to influence their behaviour during the experimental trials. The reindeers' feeding time and position within the enclosure was recorded using focal observations (Altmann, 1974). Using a stopwatch with up to 1000 "lap-times", the animals' activities and positions were recorded to the nearest second and included; feeding, standing, walking, and running (the animals never laid down during trials). Feeding was only considered an act of ingesting forage with the animals' muzzle down and actively biting vegetation (grass), and did not include the activity in which the animals were searching the immediate feeding site for food. The acts of biting or searching were clearly visible (and biting was audible) by the observer at all times. The position of the reindeer within the enclosure (within which of the 25 4 m^2 squares the reindeer was located) was recorded together with every change in activity. Duration of all trials was 30 minutes. For each reindeer, we then tabulated the total amount of feeding combined for each treatment and the control. Differences in the combined time reindeer grazed within treatments were tested using Kruskal-Wallis ANOVA on ranks followed by Student - Newman - Keuls pair-wise multiple comparison procedure (Glantz, 1992).

Experiment 2

Here, we originally used a set up of 6 enclosures each 50 m x 40 m arranged sequentially. The enclosures were homogeneous, i.e. similar with regard to size, shape and vegetation. The fences between the enclosures were covered with fabric to inhibit visual contact among the animals. All corners in each individual enclosure were covered with the same fabric to provide animals with shelter and shade. Two water buckets with running water were placed opposite each other in the middle of the 50 m side in each enclosure to provide the animals with drinking water. All enclosures were cleared of dung at the start of the experiment.

This was part of a larger experiment to study reindeers' within and between group synchronicity and their behaviour response towards sheep (Colman, 2000; Eidesen, 2002). The experiment was divided into three time periods (10-16 June 1999, 17-23 June 1999 and 24-30 June 1999) (Table 1). Three reindeer yearlings (resident reindeer) were released in each of the enclosures at the beginning of period 1. At the beginning of period 2, three sheep were released in 2 enclosures, and three new reindeer were released into 2 other enclosures (visiting reindeer and sheep, respectively). The two control enclosures did not receive visitors. At the end of period 2, the visiting animals were removed from the enclosures and the resident reindeer remained for period 3.

The enclosures were separated into squares by extending string between the fences and the number of pellet groups (defined below) was counted in each square. Due to time limitations in regards to the

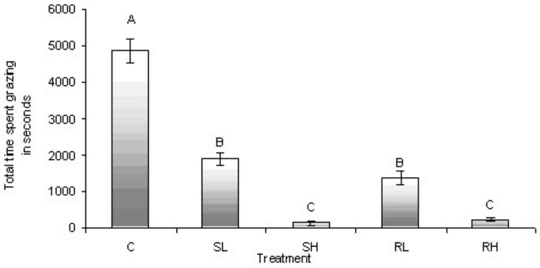

Fig. 1. Reindeer (n=6) grazing time (±SD) on areas contaminated with different concentrations of sheep and reindeer faeces. C-control, SL-low concentration of sheep faeces, SH-high concentration of sheep faeces, RL-low concentration of reindeer faeces, RH-high concentration of reindeer faeces. Columns with the same capital letter are not significantly different (ANOVA on ranks followed by Student-Newman-Keuls multiple comparison method, P<0.05).

behaviour experiment, we were unable to count faeces in all 6 enclosures. Enclosure 1 and 3 were separated into 48 squares, each 42 m^2. Because the fence poles were placed closer together in enclosure 2 than in enclosure 1 and 3, enclosure 2 was separated into 56 squares, each 36 m^2. Square size was defined out of practical purposes and on the basis of balancing the largest possible size of squares within the enclosure and an adequate number squares for a successful statistical analysis for faeces distribution. We controlled for unequal square size by analysing averages, i.e. relative values. We also assumed that there were enough squares in both cases (48 squares or 56 squares) and that they were similar enough in size (each 42 m^2 or 36 m^2, respectively) to properly represent the true faeces distribution in each enclosure.

After each of the 3 periods, we counted and recorded the location of sheep and reindeer faeces in the three enclosures. Faeces were recorded as the number of pellet groups in a square. One pellet group indicated one animal's defecation. The pellet groups were either soft deposits of faeces or a group of hard, often scattered, pellets, both easily identified as a single, independent pellet group. No faeces were removed in any of the enclosures during the experimental periods and this led to a high accumulation of faeces during the experiment. The average number of defecations per reindeer or sheep per day was calculated as the total number of pellet groups deposited in each enclosure at all periods added up and divided by the number of animal grazing days.

With this experiment, we first aimed to investigate the defecation pattern (random or not, and average number of defecation's per animal per day) for reindeer in an enclosure situation (prediction 4). We used a χ^2- test for agreement with a Poisson series (Elliott, 1977) to test whether reindeer pellet groups were randomly distributed inside the enclosures. When the variance is larger than the mean, aggregation occurs. If the variance was equal to the mean, the distribution was random. If the variance was less than the mean, distribution was regular. If the defecation pattern were to be random (and not related to bedding sites), we could then assume that reindeers' defecation pattern reflects their grazing pattern. If this were to be true, we could then test whether reindeer avoided grazing where there were faeces from either species using the same correlation analyses described below. We assumed that this part of experiment 2 was not compromised by the lack of recordings in all 6 enclosures.

We also explored how the defecation pattern changed for resident reindeer following the introduction of 3 adult female sheep or additional 3 adult female reindeer into the enclosures by testing for a positive or negative correlation (overlap) between the animals' faeces distributions (prediction 5 and 6). In connection with this, we also tested whether the resident reindeers' faeces distribution was correlated after the removal of the 3 visiting animals in order to test for an eventual avoidance of faeces from either species as a result of their visit. We used a Spearman rank order correlation to compare distribution of sheep and reindeer faeces, spatial changes in distribution of faeces between the different periods, and changes in distribution of faeces with increasing and then decreasing animal density following the introduction and then removal of additional animals (avoidance towards faeces from either species). The lack of recordings in all 6 enclosures meant that we were unable to include the original replications for each treatment. All statistical analyses were performed using the program Sigmastat (Jandel Scientific, 1994).

Results

Experiment 1

Each reindeer was allowed 30 minutes in the experimental enclosure and as expected, spent most of that time, from 63.9% to 97.2%, grazing. Reindeer spent significantly less time grazing in both the high- and the low-contaminated squares compared to the control for both reindeer and sheep faeces treatments (ANOVA on ranks, P<0.05; Fig. 1). This would suggest faecal contamination of a site reduces its preference as a site for foraging. Reindeer spent significantly less time grazing in high-contaminated

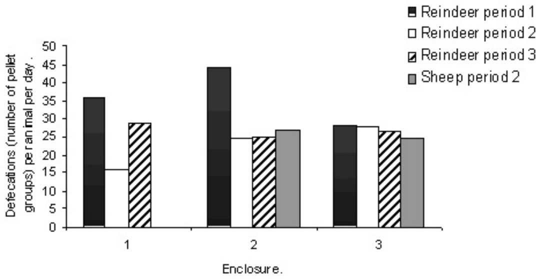

Fig. 2. Mean number of defecations (recorded as pellet groups) per animal per 24 hour in 0,5 ha enclosures 1, 2 and 3 during June 1999 (period 1: 10-16, period 2: 16-23 and period 3: 23-30).

squares with sheep or reindeer faeces compared with low-contaminated squares regardless of faecal source (ANOVA on ranks, P<0.05; Fig. 1), lending support to prediction 3. However, no significant difference (P>0.05) was found between source of faeces and its influence on avoidance of a contaminated area (ANOVA on ranks, P>0.05; Fig. 1). Thus, reindeer apparently do not avoid areas contaminated with sheep faeces moreso than similar areas contaminated with reindeer faeces.

Experiment 2

The mean number of defecation's per 24 hour for reindeer and sheep (among all three periods) was 27.3 (±7.26 SD) and 25.8 (±1.10 SD), respectively. When 3 visiting reindeer were introduced, the mean number of defecation's per reindeer per day for the resident reindeer dropped from 35.5 in period 1 to 16.1 defecations in period 2. This may reflect a reduction in grazing among individuals that in turn likely reflects increased inter-specific competition within the group. This was further supported when the mean number of defecation's per reindeer per day for the resident reindeer rose again to 28.9 in period 3, following the removal of the visiting reindeer (Fig. 2). Compared with visiting sheep, the mean number of defections per reindeer per day did not change during or after the sheep were introduced in either group 2 or 3 (Fig. 2).

Spatial distribution of reindeer pellet groups was not uniform across the area; 35% were distributed on 16% of the area (χ^2-test for agreement with a Poisson series, P<0.01). For sheep, the spatial distribution of pellet groups indicated 35% of the faecal output was found on 19% of the area (χ^2-test for agreement with a Poisson series, P<0.01). Both species usually defecated within one minute after rising from a lying bout. In light of this, and also contradicting prediction 4, we could not relate the reindeers' faeces distribution to their grazing pattern and thus, no further assumptions towards this relationship could be made.

Concentrations of sheep and reindeer faeces were positively correlated (r=0.32, P=0.001, n=104) following the period sheep and reindeer had been together (recorded at the end of period 2 in enclosure 2 and 3). This indicated that reindeer and sheep did not segregate themselves, at least while bedding. When the sheep were removed, no significant correlations (r=-0.14, P>0.05, n=104) were found between the resident reindeers' faeces at the end of period 3 and all the sheep and reindeer faeces combined from period 2. Faeces avoided by the resident reindeer towards the visiting reindeer most likely occurred, reflected in a negative correlation (r=-0.33, P=0.02, n=48) between the faeces distribution for the resident reindeer in period 3 and the combined faeces for resident and visiting reindeer in period 2. Furthermore, a positive correlation (r=0.43, P=0.003, n=48) was found when comparing the resident reindeers' faeces distribution after period 3 with their distribution after period 1, indicating a return for the resident reindeer to a "normal" pre-additional-reindeer-visit pattern when the visiting reindeer were removed.

Together with the results from the number of defecations per reindeer per day, the inter- and intraspecies faeces correlation analyses demonstrate that the introduction of additional reindeer resulted in a considerably stronger negative effect on the resident reindeer than the introduction of sheep.

Discussion

Reindeer avoided pastures contaminated with dung compared to uncontaminated areas of the pasture (control). This supports the theory that reindeer avoid foraging in areas contaminated with faeces. Furthermore, as faeces concentration increased, a stronger avoidance was recorded. This would indicate that faecal density does affect use of areas in which reindeer forage. However, we found no significant (P>0.5) difference in pasture use depending on its source of faecal contamination, i.e. from reindeer or sheep. Van der Wahl et al. (2000) found that Svalbard reindeer avoided pastures having a high density of reindeer dung. Other intraspecific experiments have shown sheep reject pasture contaminated with sheep faecal material, with a stronger avoidance associated with increasing faecal concentrations (Hutchings et al., 1998).

Besides Moe et al.'s (1999) stall-fed study, studies of indirect interference competition in the form of faeces avoidance between sympatric herbivores are lacking. Although some have shown otherwise (White & Hall, 1998; Clutton-Brock et al., 1987), selective grazing by large herbivores to avoid faecal contaminated areas on pastures is well documented (Marten & Donker, 1964; Hafez, 1975; Forbes & Hodgson, 1985; Hutchings et al., 1998; 1999). Such grazing distribution patterns may affect pasture utilisation (Arnold, 1962). On the other hand, the deposition of faeces may create patches of grass with a relatively high level of nutrients and energy (Haynes & Williams, 1993). These relatively nutrient rich patches can attract herbivores for grazing. However, they may also represent a risk of parasitic infection to herbivores as a result of the migration of helminth parasite larvae from the faeces to the sward (Sykes, 1978). Van der Wahl et al. (2000) hypothesised that Svalbard reindeer (R. t. platyrhynchus) minimised their risk of gastro-intestinal nematode infection by avoiding patches having a high faecal density. Helminth parasites have been shown to affect the growth rate, fecundity and probability of mortality of their hosts (Anderson, 1978; Gulland, 1992). In the light of this, there should be a strong selective force on the host to minimise the detrimental consequences of parasitism through faecal avoidance (Hutchings et al., 1998; 1999). Reindeer and sheep share many abomasal nematodes (Bye, 1987) that those reduce growth in sheep (Sykes, 1978) and may potentially also reduce growth in reindeer. Thus, reindeer growth rates on summer ranges may be improved if they avoid foraging on areas contaminated with reindeer or sheep faeces if other forage is not limited. In West Greenland, Clausen et al. (1980) found a severe drop in cow/calf ratios from 70 to 24 calves per female from June to August. They showed that the death of most calves was a result of severe E. coli infections presumably transmitted through faeces consumed while grazing in intensively contaminated (faeces concentrations of 4500 kg/ha) Poa pratensis grassland areas (Clausen et al., 1980). Our study suggests that reindeer have evolved a strong inter and intraspecific faeces avoidance behaviour and this may drastically improve their fitness to contracting parasite and/or E. coli infections.

Sheep faeces distribution in our second experiment showed that sheep tend to defecate more in certain areas than others, as was expected. King (1993) and Hilder (1966) found that a third of the faecal output was in less than 5% of the paddock area for merino sheep in Australia. White & Hall (1998) on the other hand, found in their study of lambs that a third of the faecal output was concentrated in 15.7% of the paddock area. That amount is similar to our study, where 35% of sheep faecal output was on 19% of the area, and 35% of reindeer faecal output was on 16% of the area, i.e. reindeer pellet groups were non-randomly distributed in the enclosures. This was a new finding for reindeer. At least in an enclosure situation, reindeer defecation patterns were strongly related to preferred bedding sites, as it was for sheep. Wild reindeer do not usually have preferred bedding sites that they return to in any consecutive manner. However, sheep and semi-domestic reindeer often return to bedding sites within their home range or pre-arranged grazing areas, both while free ranging and especially when held in paddocks. We suggest that reindeer and sheep would defecate in a similar pattern as we recorded regardless of whether they were free ranging or not, i.e. mostly within one minute of standing up following a laying bout and consequently, close to a bedding site. Thus, at least for semi-domestic reindeer, care should be taken to include enough area in a paddock to allow for grazing and bedding sites as two separate areas.

Information concerning dunging behaviour of free ranging animals is limited, and it is unclear to what extent the behaviour patterns observed in an enclosure are merely an effect of confinement, as suggested by Odberg & Francis-Smith (1976) and Edwards & Hollis (1982). However, our results are consistent with Putman (1996), who discussed that animals generally deposit more excreta on areas where they congregate, or at specific latrine sites within a home range or territory. Grazing behaviour of 20 lambs was investigated after sheep faeces were removed from randomly chosen areas, and the removal of faeces had no effect on grazing behaviour (White & Hall, 1998). The only correlation between faecal abundance and behaviour was that night lying tended to be on areas where faecal abundance was high (White & Hall, 1998).

When introducing sheep to reindeer inhabited enclosures we found that the locations of reindeer and sheep faeces were positively correlated. In period 2 when six reindeers were together, the average number of defecations per reindeer per 24 hours dropped from 35.5 in period 1 to 16.1 in period 2, indicating less food intake. Importantly, the average number of defecations per reindeer per day rose to 28.9 when the animal density was halved again. In the enclosures where sheep were introduced to reindeer, reindeer defecations remained constant and similar to pre- and post-treatment levels. Thus, resident reindeer appeared more negatively affected by the introduction of new reindeer than by introduction of sheep, lending support to the claim that interspecific competition is stronger than intraspecific competition (Caughley & Sinclair, 1994). These results were supported by the behaviour data recorded for the same experiment (Eidesen, 2002). For example, the behaviour study showed that reindeer in the reindeer groups were considerably more aggressive towards each other than the animals in the reindeer-sheep and control groups.

In a pasture situation, we predicted reindeer to avoid contaminated areas only as long as food unaffected by faeces is available. The reindeer in the first experiment were hungry at the onset of the experiment and grazed intensively, in addition to being limited by the size of the enclosure. We would expect less hungry, free ranging reindeer to show more avoidance towards faeces than hungry and enclosed reindeer, similar to what was found for sheep (Hutchings et al., 1998). We also suggest that in a high density, high-contaminated situation, reindeer grazing, and ultimately their condition, will be less than optimal regardless of resource availability because of their avoidance of faeces.

Reindeer and sheep utilize similar preferred vegetation (Skogland, 1984; Colman et al., 1998), and we have shown that reindeer may also avoid areas with an accumulation of sheep and especially reindeer faeces. As a consequence, reindeer may be loosing access to important range if animal densities are high and preferred vegetation is limited. This effect may be strengthened if bedding sites are located in or near preferred areas within a pasture, as they often are (Colman et al., 1998; Colman, 2000). Thus, avoidance of faeces dropped by other grazers most likely results in interference competition by reducing optimal forage intake. However, the same avoidance should provide protection from the transfer of parasites or disease, and thus, also act on improving the animal's overall survival and fitness (Van der Wahl et al., 2000).

The lack of replication in the second experiment undermined the value of its results. However, the behaviour data from this experiment (Eidesen, 2002), using all 6 enclosures, lends strong support to the results presented here. Another concern is whether enclosure size in either study allowed for the animals to express their full range of behaviours studied. Wild and semi-domesticated reindeer alike are occasionally restricted to limited pasture where high densities will lead to limited movement and increased contamination by excrements. We also extrapolated information on the feeding and movement behaviour of free ranging reindeer (Colman, 2000) when designing the size of our paddocks. Thus, in terms of measuring reindeers' reaction towards faeces while feeding and other "dunging" behaviour, we maintain that the size of our enclosures were adequate.

In conclusion, the amount and distribution of excrements from either species may play an important role in reindeer grazing and area use, especially in pastures maintaining high densities of reindeer or reindeer and sheep. In light of this, management decisions towards pasture size and animal density should include calculating separate areas for bedding sites where faeces concentrations are high and grazing utilization is low.

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Brief communication

The Caribou Québec Corporation: one step toward caribou conservation

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Key words: management, George River caribou herd, Labrador, Leaf River caribou herd.

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The Québec and Labrador Peninsula is home to two large migratory caribou herds, which recently have totalled close to 1.1 million. This said, one out of every three North American caribou lives in this area. These caribou inhabit the northern part of the Peninsula, regularly crossing the tree line. The George River herd (GRH), the largest herd in the world in the early 1990s, is the most known and spends its year in north-eastern Québec and Northern Labrador. The Leaf River herd (LRH), which only lives in Northern Québec is relatively large too, with several hundred thousand head. We know very little about the smaller Torngat Mountains herd, which is thought to be of the mountain ecotype, such as those found in western North America. South of these migratory caribou herd, we find smaller, isolated herds in the boreal forest, between 50°N and 54°N. An example of this is the Lac Joseph herd, currently reduced to a few thousand head. Located east of Fermont and south of Churchill Falls, this small herd is faced with increasing human activity, as the area becomes more accessible and supports major projects in hydroelectric development and military training.

The caribou of Northern Québec and Labrador are of great cultural value to the Inuit, Cree, Naskapi and Innu peoples and allow them to practice a traditional way of life. In addition, caribou are at the base of an important industry in Québec: that of sports hunting, which brings in about $30 000 000 to $50 000 000 annually to the regional economy namely in local communities such as Kuujjuaq, Schefferville, and Radisson.

After two decades of abundance, many people worry about the future of our caribou herds as native elders remember major historical fluctuations. Their lives having been painfully marked by famine when the herds disappeared in the early 1900s, many are cautious as to what the future will hold. There are disturbing signs suggesting the beginning of another decline in caribou numbers. This decline would no doubt jeopardize the native way of life and culture. The uncertain future of the caribou in Québec has led to the project to create a non-profit organization called Caribou Québec, with the following objectives:

- Promote the wildlife resources of Northern Québec particularly caribou, both within Quebec and abroad, while at the same time developing tourism in all its forms;
- Educate the public about caribou and Northern Québec;
- Encourage involvement and promote training of native people in projects related to caribou and northern wildlife;
- Encourage the involvement of native people in caribou related projects by transferring the necessary expertise to local organizations.

The operation of Caribou Québec will be based on the general principle that the resource users (native and non-native people and communities, outfitters, sport hunters, commercial users, etc.) in collaboration with related government organizations, participate actively in conservation and management projects. During the last decade in North America, it has been observed that wildlife management is rapidly evolving, especially in the arctic. Through different ways, caribou users, mainly native people are being included in the management process. Everywhere, initiatives are out together where natives and the governments are exploring new avenues of co-management. The Beverly-Qamanirjuaq Caribou Management Board; the Porcupine Caribou Management Board; the Nunavut Wildlife Management Board; the Borderlands Ecological Knowledge Society, are just a few models of which Caribou Québec could draw interesting elements.

For its very first year of operation, Caribou Québec has worked under a temporary council composed of three (3) outfitters of the Kuujjuaq, Lac Pau and Schefferville regions. Outfitters had expressed their concerns for the fate of the caribou for many years and their involvement has led to the creation of Caribou Quebec to actively participate in research efforts in the summer 2001. One of the major objectives of the corporation was to sponsor a study on the physical condition of the caribou of the GRH and the LRH. The corporation also joined in with the Québec wildlife agency, Société de la faune et des parcs du Québec, and the Newfoundland and Labrador Government to help on the caribou census of the GRH and LRH in the summer of 2001.

Caribou Québec is presently working on an educational program for school groups, in order to help the public discover the Northern Québec region and its treasures. The proceeds of this program will be entirely distributed in future research projects. The corporation finally plans to put together its first administration council to reflect the Northern Québec reality, by involving major stakeholders such as outfitters, natives, scientific and research professionals, as well as caribou users. All this with the hopes that caribou research will become a common and unifying goal.

Abstracts

The Ninth North American Caribou Workshop, Kuujjuaq, Québec, Canada, 23–27 April, 2001. S2

Indigenous knowledge and caribou management: the terms of a new alliance

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Abstract: Since the beginning of the 1980s, interest in regards to indigenous knowledge has only grown. As aboriginal populations have established themselves as partners who cannot be ignored on the national and international scene, this knowledge has become a strong identifying marker and a new avenue for cultural and political affirmation. Moreover, its legitimacy as a source of pertinent information for the protection of ecosystems and the management of land and natural resources (more specifically, the caribou) and the understanding of environmental phenomena has been recognized on numerous occasions by governments of various countries and most notably, by Canada. This recognition is also seen in the specific provisions in international conventions aimed at their protection and transmission. The present conference will allow us, in the first instance, to shed light on this emerging field of study and to clarify the main theoretical and methodological issues from a social science and environmental sciences viewpoint. In the second instance, the discussion will focus on the specific case of the caribou and will examine the meeting of indigenous knowledge and scientific knowledge.

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The Ninth North American Caribou Workshop, Kuujjuaq, Québec, Canada, 23–27 April, 2001. S3

Cumulative impacts of hydro-electric power development on the distribution and productivity of wild reindeer

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Abstract: Monthly systematic snowmobile surveys during winter and ground surveys during summer of approximately 1500 reindeer were annually conducted prior and following the construction of the Blue lake hydroelectric reservoir in south-western Norway 1977-1987. We analyzed pre- and post development distributions in relation to location of constructed 300 and 420 kV power lines, roads and dams on 54 sites, each 25 km^2. Infrastructure was present in 17% of the sites in 1977, increasing to 71% of the sites in 1987. Following development after 1980, annual reindeer density was reduced by 72% within the study area, the far majority as a result of an 88% reduction in use of developed sites in winter, without changes in undeveloped controls. During summer, distribution of reindeer away from power lines resulted in a 53% reduction in use in near half of the sites, and a subsequent 137% increase in use of remaining undisturbed sites. The proportion of large insect-harassment-related aggregations of reindeer also declined significantly in developed sites and increased in undeveloped formerly low-use sites. Production 3-10 years after development was, in spite of near absence of predators, ca. 30-40 calves/100 females in June, corresponding well with very low body weights in spite of relatively stable herd size, giving some of the lowest reproductions in wild reindeer in the world. The Blue lake development resulted in: 1) Reduced availability of winter ranges; 2) physical barriers and reduced availability of summer ranges; 3) possible lower availability of insect relief habitat; 4) enhanced use of remaining scattered undeveloped sites, and 5) most likely lowered production.

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Cumulative impacts of human development on wild reindeer

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Abstract: We investigated the effects of infrastructure on wild reindeer in five major reindeer ranges in southern Norway, including some of the most intensively developed *Rangifer* habitats in the world. The investigation was based on systematic aerial and ground based surveys, including over 200 000 reindeer observations 1977-1998, snow measurements and vegetation surveys on >500 vegetation sites. During winter, reindeer abundance was 50-97% lower within 2,5-5 km from roads, power lines and ski resorts compared to comparable habitat in undisturbed areas. During summer, patterns were more diffuse, mainly due to varying sensitivity caused by insect harassment, although a 30-50% reduction in use also was observed in summer. Redistribution of reindeer away from development resulted in a 137-470% increase in use of the few remaining, scattered undisturbed sites, with apparent resultant overgrazing. Smaller groups of animals, mainly bulls, could be observed under all levels of disturbance. Combinations of linear structures, such as two power lines in combination or a road and a power line combined generally resulted in not only avoidance but also barriers to migration. Exceptions existed mainly for periods of starvation. No apparent habituation had occurred up to 30-80 years after construction, in spite of short distances to available forage in demand. Overall, range availability in southern Norway, and hence, carrying capacity, has been reduced by 50-70% in the last half of the 20th century due to human development.

The Ninth North American Caribou Workshop, Kuujjuaq, Québec, Canada, 23–27 April, 2001. S6

Isolation and genetic diversity of caribou ecotypes in Québec, Canada

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Extended abstract: Three caribou ecotypes are present in eastern North America: the mountain caribou which is found in the Chic-Choc mountains (Gaspésie Peninsula) and, possibly in the Torngat mountains, the barren-ground caribou which calves in the tundra and the forest-dwelling ecotype which lives all year long in the boreal forest. In this study, 226 blood and muscle samples were collected from seven locations and characterized at eight microsatellite loci to test the hypotheses that forest-dwelling and barren-ground ecotypes constitute a single metapopulation and that geographical isolation results in reduced genetic diversity through genetic drift. The highest mean number of alleles per locus was found in the barren-ground population while the lowest value was observed in the smallest forest-dwelling population. Expected heterozygosity did not vary among populations, whereas genetic differentiation was detected between all pairs of populations, confirming that they were genetically distinct. Correspondence analysis showed three groups of samples, corresponding to the three ecotypes. Gene flow estimates were moderate or high among all forest-dwelling populations and particularly between those <200 km apart. Our results suggest that the three caribou ecotypes represent three distinct genetic entities. Our findings also indicate that the forest-dwelling populations form a metapopulation and that barren ground caribou are not part of this metapopulation. The mean number of alleles per locus and heterozygosity of the studied populations were similar to or greater than those measured in other caribou populations or other cervid species. Genetic drift was noticeable in isolated populations but does not seem to be of immediate concern for conservation. However, we propose that management strategies should favor increase in caribou numbers in order to avoid extinction due to stochastic events and to maintain local biodiversity, particularly in isolated populations. In the boreal forest caribou range, conservation strategies of populations must be planned on large scales and should favour maintenance of occasional exchanges among populations, thus preserving genetic diversity.

The Ninth North American Caribou Workshop, Kuujjuaq, Québec, Canada, 23–27 April, 2001. S6

Environmental variability and live body mass of reindeer calves at weaning

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Abstract: Factors which influence variation in the body mass of ungulates may be classified according to whether they are (i) largely dependent on or (ii) largely independent of prevailing environmental conditions. Given that reindeer in Arctic and sub-Arctic habitats experience substantial annual variation in both population numbers and the weather conditions which affect quality and availability of forage, we predicted that the live body mass of reindeer calves at weaning (September, calves=4 mo. old; LBM4) would be influenced principally by factors dependent of prevailing environmental conditions. Body mass data were collected from 1992 to 2000 in a herd of approximately 400 individually marked semi-domesticated reindeer which grazed all year round at natural mountain pasture in northern Norway. Body mass was highly variable (mean=37.5 kg, $s_{between\ \mathrm{year}}$=1.3 kg, $s_{within\ \mathrm{year}}$=4.6 kg, n=789). A general linear model of a sub-sample revealed that (i) calves' sex (β=1.9, $F_{1,450}$=33.9, P<0.0001), (ii) mothers' body mass in late winter (β=0.4, $F_{1,450}$=243.1, P<0.0001) and cohort year of birth ($F_{1,450}$=10.8, P<0.0001) together explained 45% of this variation after controlling for date of weighing. Neither mothers' age nor mothers' reproductive status in the preceding year had any significant additional effect on LBM4. The results suggest environmental conditions in the current year are important for the growth of male and female reindeer calves directly by changing abundance or quality of forage and indirectly by changing resource allocation from their mothers.

The Ninth North American Caribou Workshop, Kuujjuaq, Québec, Canada, 23–27 April, 2001. S6

Urinary creatinine ratios in snow samples as a non-invasive nutrional monitoring tool for caribou

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Abstract: Nitrogen (N) balance can be critical for caribou in winter. Low nitrogen content, especially in lichens, can induce severe protein mobilisation under natural conditions. Efficient monitoring tools are needed to properly assess animal nutritional status in the wild. Biochemical indicators of catabolism would simplify appraisal of the physiological status and food limitation during the winter months. Previous studies have shown that purine derivatives, lost through urine, are reliable indices of ruminant nutritional status. The Urea Nitrogen:Creatinine (UN:C) and Potassium:Creatinine (K:C) ratios have showed promising results in nutrition quality monitoring. A newly developed method was tested using urine samples collected from fresh snow. As little experimentation has been done to date on caribou, the present study tests hypotheses related to this technique with a group of caribou under controlled conditions. It was carried out in captivity at the Saint-Félicien "Wild" Zoo on caribou recently captured from the Leaf River Herd in N. Québec. Less than one week after a gradual reduction in N intake (from a 14%-protein pellet formula to a 3%-protein lichen diet), UN:C and K:C ratio results declined and echoed the deterioration of nutritional condition of the study individuals. Five weeks later, still under reduced N intake, both ratio values started to rise slightly again, probably due to the onset in protein catabolism. This U-shape tendency was similar to previous results obtained from other species of ungulates and represents a problem in the application of the snow-sampling technique in the wild. No circadian differences in ratio values were found even though ratio variability increased as diet conditions deteriorated. Under a high protein diet, UN:C for fawns did not differ from that of adults. However, K:C seemed higher for fawns than for adults under the same high protein diet. This could be used in the wild to differentiate fawn from adult snow urine samples, as age effect was pointed out as a possible drawback for the snow sampling method. Although preliminary results suggest that snow-urine sampling shows some potential as a nutrition monitoring tool, further studies are required to establish baseline values for caribou.

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Genetic relatedness of caribou herds in Northwest Territories, western Nunavut and the northern Yukon Territory

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Abstract: We studied nine herds of caribou in northern Canada. Five herds, Porcupine, Cape Bathurst, Bluenose-West, Bluenose-East and Bathurst (*Rangifer tarandus granti* and *R. t. groenlandicus*) occupy ranges on the mainland. Three herds, Melville Island, Banks Island, and Minto Inlet (*R. t. pearyi*) occupy ranges on the arctic islands. The Dolphin-Union herd (*R. t. pearyi*) occupies both mainland and island ranges. Preliminary analysis of microsatellite loci showed more genetic differentiation amongst caribou on arctic islands than those on the mainland, a small genetic difference between Banks and Melville Island caribou and that Banks Island and Minto Inlet herds were not genetically distinct. Subsequently, additional genetic material has been analyzed to increase sample size so we could elaborate on the preliminary results and further elucidate the relatedness of caribou found on arctic islands and the mainland.

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Patterns of seasonal range use of Cape Bathurst, Bluenose-West, and Bluenose-East barren-ground caribou and its implications for management

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Abstract: Cape Bathurst, Bluenose-West, and Bluenose-East barren-ground caribou herds occupy parapatric ranges in northern Northwest Territories and western Nunavut. Since March 1996, we have obtained information on the movements of satellite-tracked radio-collared caribou in these herds. Collars provided location data on the same days and months over multiple years. For those caribou with >1 year of movement data, we measured all possible distances between locations on a given day and month to provide a measure of fidelity to areas used during the year. Caribou in all three herds showed as high a degree of fidelity to areas used during early August to early October as they did to those used during calving and post-calving. The lowest degree of fidelity occurred during winter. The relative importance of ranges used by barren-ground caribou during seasons other than calving and post-calving need to be considered in light of current and proposed development activities

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The effects of sample interval on estimating movement rates, habitat use, and home ranges: a case study employing GPS technology on overwintering caribou

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Abstract: GPS-based animal tracking systems are well suited for a variety of spatio-temporal investigations. While researchers have traditionally struggled to collect sufficient data with conventional radiotelemetry, GPS technology can quickly amass large samples of relocation data. To optimize the use of GPS systems, we need to understand effects of sampling interval, and therefore sample size, on ecological estimates we obtain. We investigated the effects of sampling interval on estimates of movement rate, habitat use, and home range size by sub-sampling hourly relocation data collected from three GPS collars deployed on female caribou in the Fortymile Herd during October 1998-April 1999. We also evaluated diurnal patterns of habitat use to compare "round-the-clock" sampling via GPS technology with "daylight only" sampling characteristic of conventional aerial radiotelemetry. Our results will provide some insight into the ramifications of and difficulties associated with estimating ecological parameters using different data collection schemes.

Is the metapopulation theory useful in caribou herds conservation? - A test with the Québec-Labrador caribou

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Abstract: Since the 1950s, North American caribou herds have been defined and named on the basis of their calving ground locations. As most censuses are conducted at or near calving time, this herd definition is appropriate for short-term management decisions. However, over larger time and spatial scales, the herd may not be the most effective conservation unit. The metapopulation theory may prove to be useful in the area of long term caribou conservation. Metapopulation is a system of geographically or ecologically isolated populations whereby there is sufficient emigration among populations to have a significant impact on either the demography or genetic profile of each component population. In the large mainland area west of Hudson Bay, caribou herd ranges overlap in a continuum of varying caribou abundance, small-scale exchanges may occur between neighbouring herds. The ranges of the migratory and sedentary caribou ecotypes also overlap, a fact that requires study of the ecological factors involved, and more importantly, of the long-term conservation effects on the fragile sedentary ecotype. East of Hudson Bay, on the Québec-Labrador Peninsula, a similar caribou population continuum exists but on a smaller spatial scale. This situation provides an opportunity to test the metapopulation theory. This paper will use this new approach to formulate hypotheses for better management of caribou herds and metaherds. Satellite monitoring data have recently confirmed emigration of caribou from the George River Herd (GRH) to the Leaf River Herd (LRH). Data also confirmed that after a fourfold increase from 1971 to 1993, the GRH contracted its annual range by 40% from 1994 to 2000. The LRH calving ground, first surveyed in 1975, has gradually shifted so that by 1992 it had moved 400 km to the north, from low altitude landscape south of the tree line to a 530-metre high tundra plateau-habitat. Since 1993, this herd has used the same area with little annual variability. As revealed by Inuit traditional ecological knowledge, the current (1992-2000) LRH calving ground was used in the late 1880s at the metaherd's previous population peak. This paper will suggest that emigration plays an important role in Québec-Labrador caribou herd dynamics and that annual small-scale changes to calving grounds are one of the mechanisms involved. Emigration from the GRH may have led to the creation and the growth of the LRH in the 1970s. Throughout history, caribou herds have fit into the source-sink metapopulation system, whereby one-source populations, typically large in size or occupying prime habitat (*i.e.*, GRH), produce an excess of individuals that disperse to smaller sink populations in less than optimal habitats (*i.e.*, LRH). Very little is known about the genetics of Québec-Labrador caribou, and it should be investigated further to better understand gene flow between the herds and within the metaherd.

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A North American caribou database – a step in assessing impacts of climate change and industrial development

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Abstract: In recent years much focus has been directed to the fate of our large migratory caribou herds. Climate change and numerous development projects combine to pose a potential threat to the well being of these herds. Management agencies and co-management bodies need to have the best information possible to generate effective policy decisions related to the mitigating possible impacts. A recent survey across the north indicates that there is a wide disparity in the amount of baseline data that is available for these herds. We feel that by integrating all the data that exists for the populations and their habitats, we can create herd specific datasets that can be input for an integrated assessment tools. To that end, a MS Access database is being developed for mainland migratory caribou in North America. In this presentation we discuss the structure of the database, provide a few examples of comparisons among herds and outline a process to use the database as an integrated assessment tool.

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A 'rediscovered herd' - the Ahiak (Queen Maud Gulf) herd of barren-ground caribou in Canada's central arctic

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Abstract: In 1996, the Ahiak herd numbered about 200 000 barren-ground caribou *Rangifer tarandus groenlandicus* which makes it the fourth largest herd in the Northwest Territories and Nunavut, Canada. Yet the herd is almost unrecognized outside its range because its numerical increase and re-occupation of seasonal ranges is recent. The herd's recognition was confirmed when we fitted five cows with satellite collars in April 1996 and flew calving surveys in 1986 and 1996. The collared cows calved along the Queen Maud Gulf (Ahiak) coast and their winter range extended to below the treeline. The Ahiak herd's seasonal ranges overlap with ranges of the Bathurst herd, the Beverly and the Dolphin and Union herd.

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Is a park a guaranty for the survival of the Gaspésie caribou?

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Abstract: The regression of caribou distribution in North America is well known and unfortunately irreversible. In the East, the last individuals of the herds that once occupied the Atlantic Coast are now restricted to the area of the *Parc de la Gaspésie* (Gaspésie Park). The word "park" might lead to think that every possible conservation step has been carried out. A closer look at the park's history shows that the status of herd is still precarious. Many protection measures for the caribou were taken over the last century. Caribou hunting was prohibited; the forestry reserve was modified to a Conservation Park in 1981; a recovery plan was implemented from 1990 to 1994; an essential habitat area was established in 1993; and a forestry plan was concluded in 1999 for a 293 km^2 area outside the park. In spite of all these conservation efforts, a recent telemetry study shows that the caribou population is smaller than expected. From a population size of 273 in 1983, the herd steadily declined to 126 in 2000 ($y=-7.2932x+244.29$; $R^2=0.5029$). Previous efforts probably slowed, but did not stop, the caribou decrease. The situation of naturally isolated small populations, such as the Gaspésie caribou, will always be precarious. Apart from a conservation park, constant survey studies and research programmes are essential if we ever want to have a chance to preserve these relic populations.

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