Proceedings of the Eight
North American Caribou Workshop
Whitehorse, Yukon, Canada
20-24 April, 1998

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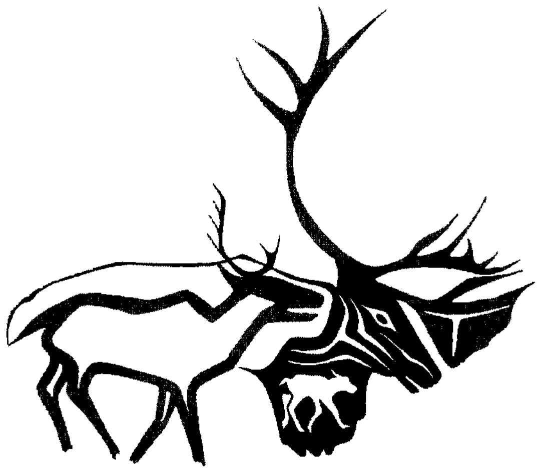

'A future for an Ancient Deer'

Whitehorse, Yukon, Canada, April 20 to 24, 1998

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Doug Urquhart studied biology at the University of Toronto (BSc) and the University of New Hampshire (MSc). In the early 1970s he studied the impacts of oil development on the caribou, muskox and arctic foxes of Banks Island NWT. Doug has been an environmental consultant in NWT, BC and Yukon for 20 years specializing in wildlife management planning. He was the Executive Director of the Porcupine Caribou Management Board for 10 years and wrote a syndicated newspaper column on Porcupine Caribou Management. Doug's biology background and vast experience with northern issues are reflected in his syndicated cartoon strip "Paws" and in the 12 cartoon books he has published over the past 25 years. Doug lives in Whitehorse with his wife Judy and their two children Robin and Kaitlyn. In his role as the Chief Strategist for the Arctic National Wildlife Refuge Campaign Canadian Leadership Group, Doug continues his efforts to help preserve the Porcupine Caribou Herd.

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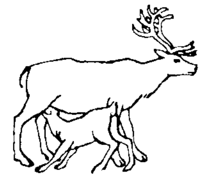


RANGIFER

Vol. 20 | 2000 | Special Issue No. 12

Proceedings of the Eight North American Caribou Workshop

Contents Page

Session Two – Co-Management

Session Three – Caribou & Human Activity

Session Four – Panel Discussion

Session Five – Nutrition & Physiology

Session Six – Habitat

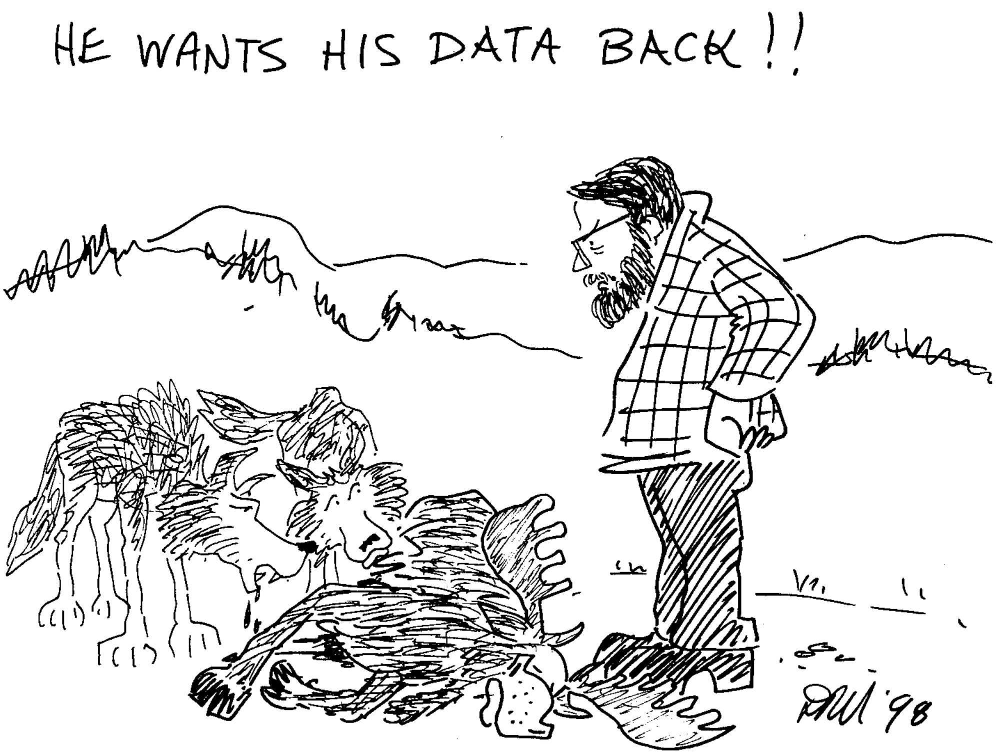
The Eight Notth American Caribou Workshop,
Whitehorse, Yukon, Canada,
20–24 April, 1998.

Preface

Two hundred and forty people attended the 8th North American Caribou Workshop. Attendees brought perspectives from government and private sector research, management, industry, boards, councils and First Nations. As well, the involvement of colleagues from Norway, Finland, Greenland and Russia diversified these proceedings. Over 60 papers covering broad areas of caribou resource interests were given in both the plenary and poster sessions.

Sessions featured presentations on population dynamics, co-management, habitat, nutrition and physiology. Many papers provided new and interesting perspectives. The new planning team approach for restoration of the Fortymile caribou herd using non-lethal wolf control will provide a test of socially acceptable methods of reducing predation on caribou. The finding of genotipic separation among small woodland caribou herds using DNA fingerprinting technology opens an avenue into better understanding of herd fidelity, historical distribution patterns, and genetic diversity. The importance of long-term research was clearly illustrated with the knowledge that calving ground locations may rotate over decades thus introducing uncertainty into land use management in the NWT. Finally, studies using similar and divergent techniques on caribou feeding site selection in Alaska, Yukon, British Columbia, and Alberta demonstrated how complementary inter-jurisdictional research is being carried out.

A full day was devoted to the controversial topic of caribou and human activity. The afternoon included a panel discussion on *'Human developments and their effects on caribou'*. The intent of this session was to examine what has transpired over the last 15



years as this topic was the theme of the First North American Caribou Workshop in Whitehorse, October, 1983. Participation from Norway provided an opportunity to contrast the European experience with that of North America. We wanted to determine whethet we were advancing the science or being long on rhetoric and short on fact. We asked ourselves what we needed in terms of research and how long this should be carried out. We also examined decision-making processes to determine what works and what does not. A healthy and respectful dialogue was carried out and its inclusion in these proceedings provides a benchmark on the status of this topic.

The Workshop organizers wanted to insure a wide range of content and meaningful participation of First Nation's people. The displays in the lobby and the catibou skin hut constructed on site greeted participants as they entered the Yukon Art's Center, the site of the conference. Elders told stories at the beginning of each session and these stoties set a respectful tone to the whole conference. One of these stories is presented in these proceedings. In addition each session was accompanied by a selection of cartoons by Doug Urquhart to bring humor to participants during breaks. A selection of these cartoons is included in these proceedings so that the lighter side of our work can be referenced in the permanent record.

The Workshop opened on April 20 with the film *'Beringia'* at the Beringia Interpretive Center reception. It ended April 23 with the presentation *'Ancient caribou, its evolution and place as one of the 'big 4' of the Beringian mammoth steppe fauna'* by guest speaker Dr. Richard Harington at the closing banquet. Dr. Harrington's talk helped us reflecr on the general Workshop theme *'A future for an ancient deer'*.

The organizers wish to thank all attendees for their participation and enthusiasm that made the 8th North American workshop a resounding success.

Rick Farnell, Head of the Organizing Committee and Conference Co-chair

Acknowledgements

We would also like to thank the following without whose help we could not have pulled this conference off:

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- Patrick Valkenburg, Research Biologist

First Nation Representation was by the following elders;

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- Stanley Johnathan, Selkirk First Nation
- John Joe Kay, Vuntut Gwichin First Nation
- Hanna Netro, Vuntut Gwichin First Nation
- Charlie Thomas, Vuntut Gwichin First Nation
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The Eight North American Caribou Workshop,
Whitehorse, Yukon, Canada,
20–24 April, 1998.

Elder's story

The boy who went to the moon

As told to Louise Profeit-LeBlanc by Mary Vittrekwa

Many years ago, when the people depended totally on the land, the Gwich'in people temember this story. It's the story about the boy who went to the moon.

There was a couple who had only one child. He was only a few months old and was fussing, so his mother took him out of their tent to show him the moon on a warm spring night. The little boy became very happy, he smiled and pointed to the moon and said the word for moon in his mother's language. He settled right down after this. His parents realised then that he must be special and in fact his fathet said "I think he comes from the moon people. He has a moon spirit. We must be good to him all his life."

Time passed until the year that the people wete suffering from famine. That was the year that the caribou had taken another trail in their migration. The snow and cold weather had come too quick and the people hadn't got enough to last them the winter. They didn't know how they were going to get through the winter and the whole village was worried. Some even cried because they knew that there was going to be great suffering.

This boy was about 14 years old now. Although he was this age, he was still as small as a young child. He nevet grew. He was a midget. His mother took pity on him and sewed him little marten skin pants to keep his legs warm and when they moved across the country she would carry him on her back, as walking over the tundra was very difficult. His parents treated him vety well.

"Mom, I know how to make caribou come to this place. I will make medicine for the people and bring caribou back from their trail." His mother was very surprised when her son told her what he could do to help the people.

The little guy went out of the skin-tent and pulled at a little clump of willows in the snow. It turned into a small calf caribou right before his parents' eyes! They killed that little caribou.

"Now take some of that meat and attach it to the fringes on my jacket. I'm going to make a song and dance for rhat bull caribou, to change his mind." His mother did as her son instructed and attached strips of the caribou meat to the fringes of his jacket. The young boy went outside the tent again. This time he plucked some willows and peeled the bark of them. He was going to use these for dancing sticks.

"Now befote I make my medicine to bring that chief caribou back, go tell all the people what I am going to do. Tell them that the only thing I want for my work is the stomach fat around the caribou's stomach. That's all I want. Now go and tell them quick, while I make a song for them."

His mothet went to tell the people. Meanwhile the boy came outside of the tent and with those dancing sticks in each hand, proceeded to sing a special caribou song, a song which even the oldest of the Elders no longer remembers the words to. He danced, clacking the sticks together to make the same sound that caribou horns make when they are in a latge herd moving across the land. Pretty soon, on top of the nearest rise, the young man saw the silhouette of a bull caribou. The chief for the caribou people. He knew that there were thousands more behind him.

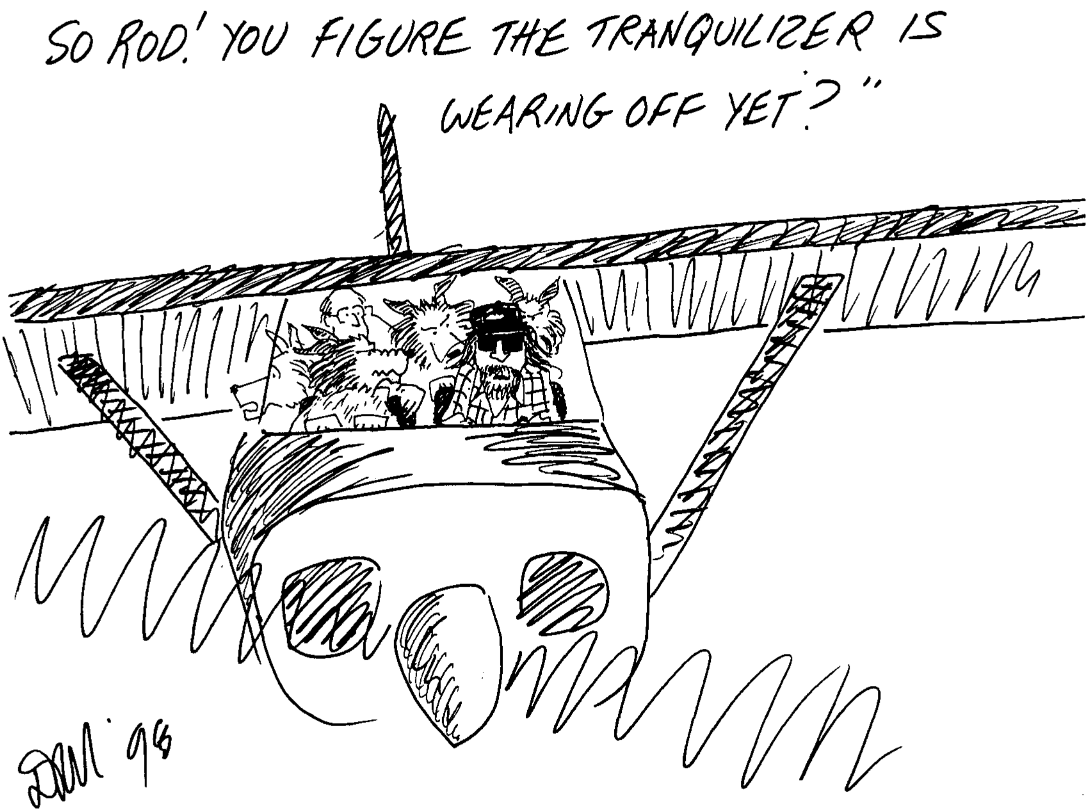
The people ran around frantically, herding the caribou into the caribou cottals, spearing and shooting them with arrows. They were in a state of frenzy. Many caribou were taken that day, and the young boy waited patiently in his tent with his mother. Nobody came.

"What's the matter with my people? How can they forget their promise so quickly? His mother insisted that he wait a little longer. They are busy with the meat, my son. Be patient, they won't forget you."

The boy waited until nightfall. He became very upset. He cried. He cried over this condition of the people. "I want to go back to my people. Back to the moon, for these people here have no more respect. They forget promises. I don't want to live among such people anymore."

His parents begged the boy not to leave them. In fact, that night when they went to bed, they put the child between them so he could not leave. In spite of their attempts, however, in the morning, he was not there. They awakened to discover only his little marten skin pants hanging from the smokehole in the middle of their tent. Their son had returned to the moon.

Now, to this day, if you look closely at the moon, you will see a young boy holding something in his hand, something that looks like lace fat from around a caribou's stomach. And this boy is still controlling the caribou. On the first full moon in rhe fall and rhe first full moon in the spring, the catibou begin their migration as they have done since the beginning of time.



Session one

Population Dynamics

The Eight North American Caribou Workshop,
Whitehorse, Yukon, Canada,
20–24 April, 1998.

The Fortymile caribou herd: novel proposed management and relevant biology, 1992–1997

Rodney D. Boertje[1] & Craig L. Gardner[2]

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Abstract: A diverse, international Fortymile Planning Team wrote a novel Fortymile caribou herd (*Rangifer tarandus granti*) Management Plan in 1995 (Boertje & Gardner, 1996: 56–77). The primary goal of this plan is to begin restoring the Fortymile herd to its former range; >70% of the herd's former range was abandoned as herd size declined. Specific objectives call for increasing the Fortymile herd by at least 5–10% annually from 1998–2002. We describe demographics of the herd, factors limiting the herd, and condition of the herd and range during 1992–1997. These data were useful in proposing management actions for the herd and should be instrumenral in future evaluations of the plan's actions.

The following points summarize herd biology relevant to management proposed by the Fortymile Planning Team:

1. Herd numbers remained relatively stable during 1990–1995 (about 22 000–23 000 caribou). On 21 June 1996 we counted about 900 additional caribou in rhe herd, probably a result of increased pregnancy rates in 1996. On 26 June 1997 we counted about 2500 additional caribou in the herd, probably a result of recruirment of the abundant 1996 calves and excellent early survival of rhe 1997 calves. The Team deemed that implementing management actions during a period of natural growth would be opportune.
2. Wolf (*Canis lupus*) and grizzly bear (*Ursus arctos*) predation were the most important sources of mortality, despite over a decade of the most liberal regulations in the state for harvesring of wolves and grizzly bears. Wolves were the most important predator. Wolves killed between 2000 and 3000 caribou calves annually during this study and between 1000 and 2300 older caribou; 1200–1900 calves were killed from May through September. No significant differences in annual wolf predation rates on calves or adults were observed between 1994 and early winter 1997. Reducing wolf predation was judged by the Team to be the most manageable way to help hasten or stimulate significant herd growth. To reduce wolf predation, the Team envisioned state-sponsored wolf ttanslocations and fertility control in 15 key wolf packs during November 1997–May 2001. Also, wolf trappers were encouraged ro shift their efforts to specific areas.
3. To increase social acceptance of the management plan, the Fortymile Team proposed reducing the annual caribou harvest to 150 bulls for 5 years beginning in 1996. Reducing annual harvests from 200–500 bulls (≤2% of rhe herd, 1990–1995) to 150 bulls (<1% of the herd, 1996–2000) will not result in the desired 5–10% annual rates of herd increase.
4. We found consistent evidence for moderate to high nutritional status in the Fortymile herd when indices were compared with other Alaskan herds (Whitten *et al.*, 1992; Valkenburg, 1997). The single evidence for malnutrition during 1992–1997 was the low pregnancy rate during 1993 following the abnormally short growing season of 1992. However, this low pregnancy rate resulted in no strong decline in Forrymile herd numbers, as occurred in the Delta and Denali herds (Boertje *et al.*, 1996). No significant diseases were found among Forrymile caribou.
5. Winter range can support elevated caribou numbers borh in regards to lichen availability on currently used winter range and the availability of vast expanses of winter range formerly used by the herd.

Key words: Alaska, condition, fertility control, mortality, nutrition, predation, pregnancy rate, translocation, sterilization.

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Introduction

We describe the Fortymile Herd Management Plan (Boertje & Gardner, 1996) as a "novel" plan because of its unique holistic approach to wildlife management, its nonlethal proposals for reducing wolf predation, and the divetsity of interests

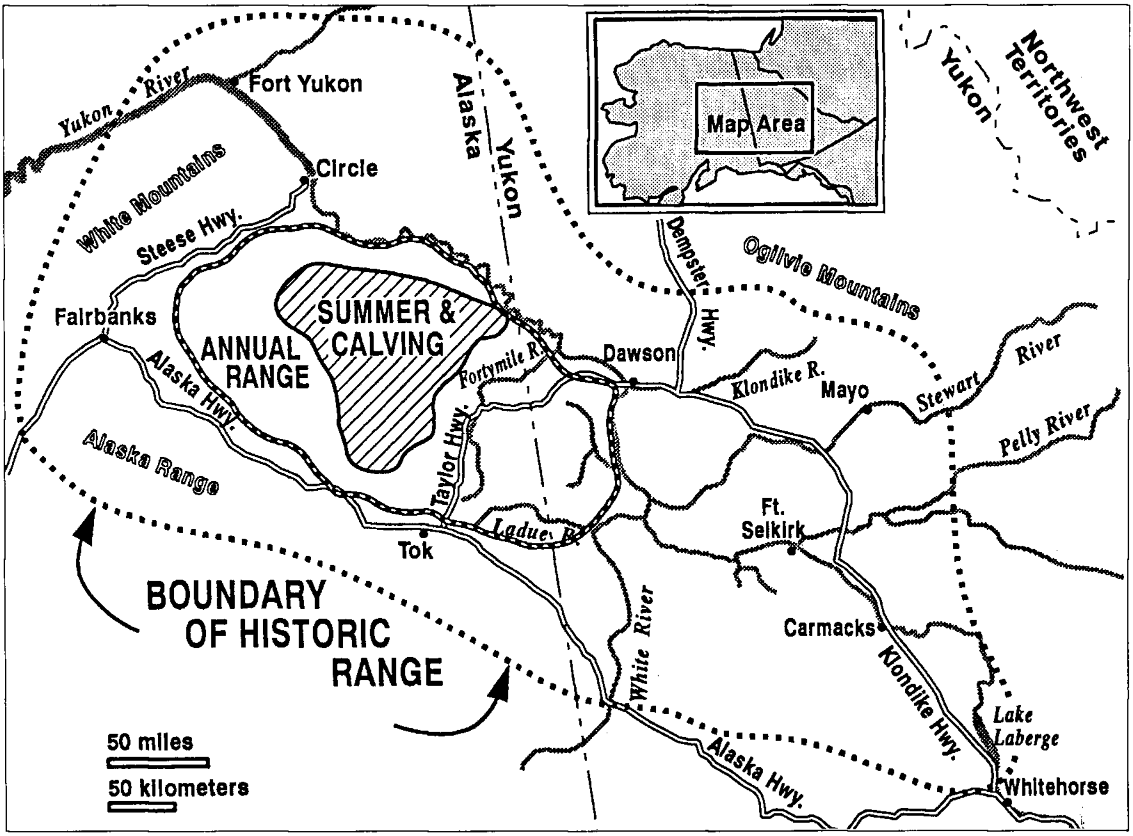

Fig. 1. Range of the Fortymile caribou herd, 1984–1997, and historic range during the 1920s.

involved, representing Alaska and Yukon villages, environmentalists, hunters, and several governmental agencies. No similar plan exists to our knowledge. Although the management plan emphasizes habitat protection objectives, these details are beyond the scope of this paper. This paper provides the 5-year baseline pretreatment data for the study area and presents hetd responses following recent management actions, i.e., increased wolf harvest and decreased caribou harvest. We summarize demographics of the herd, factors limiting the hetd, and condition of the herd and range during 1992–1997. These data wete useful in proposing management actions for the herd and should be instrumental in evaluating the effectiveness of proposed management actions.

Background

The Fottymile caribou (*Rangifer tarandus granti*) herd has the potential to be the most economically important wildlife population in Intetior Alaska and the southern Yukon, both for consumptive and nonconsumptive uses. Potential for growth is indicated by Murie's (1935) extrapolated estimate of 568 000 caribou during a 20-day herd migration across the Steese Highway in 1920, compared to an aerial photocensus of 25 912 caribou on 26 June 1997. The herd's low point was in 1973 with about 6500 caribou.

Caribou herds typically restrict range use as herd size declines. For example, the Fortymile herd has not migrated across the Steese Highway since 1963 and rarely enters the Yukon because of its teduced size. The herd's historical range encompassed 220 000 km^2 (Murie, 1935) compared with about 50 000 km^2 total for all years since 1968 (Valkenburg *et al.*, 1994; Fig. 1) and about 30 000 km^2 annually in recent years. Today, the historical range of the herd is largely devoid of caribou.

Population objectives for increasing the Fortymile caribou herd have wide public support in Alaska and the Yukon for consumptive and nonconsumptive reasons. Public support has flourished because most of the herd's former range was abandoned as herd size declined and because current low numbers are, in part, a result of past management decisions.

We have learned much from past management of the Fortymile herd. Valkenburg *et al.* (1994) detailed a case history of the herd from 1920 to 1990. The decline in the herd from about 50 000 in 1960 to only 6500 in 1973 was partly a result of errors in the prevailing management beliefs. Overharvest was allowed in the early 1970s, and, simultaneously, high numbets of wolves (*Canis lupus*) and unfavorable weather contributed to the herd's decline to ctitically low levels (Davis *et al.*, 1978; Valkenburg & Davis, 1989; Valkenburg *et al.*, 1994). Had this overharvest been prevented, the herd probably would have declined to only 10 000–20 000 caribou during the early 1970s and may have increased to 30 000–50 000 during favorable conditions in the 1980s.

Ovetharvest was allowed in the early 1970s in part because of the belief that poor range condition was the major factor causing low-yearling recruitment. Thus, managers allowed high harvests and largely ignored wolf predation while awaiting a compensatory rebound in yearling recruitment from improved range. However, it was a futile vigil; calf caribou became increasingly scarce through 1973. It was mistakenly believed hunters and predators usually killed animals that were about to die anyway (before successfully reproducing), and wolf and grizzly bear (*Ursus arctos*) predation were minor influences on the herd. Also, the size of the Fortymile herd was grossly overestimated and the trend in herd size inadequately monitoted (Davis *et al.*, 1978; Valkenburg & Davis, 1989).

Today harvest ptograms for caribou are managed much more conservatively than in the early 1970s. During natural declines of caribou to low levels, harvests are eliminated or restricted to small percentages of bulls or are carefully monitored using permit systems. Since 1973, substantial teductions in the human harvest of Fortymile caribou have made harvest an insignificant factor affecting herd growth compared to predation by wolves and bears (Valkenburg *et al.*, 1994; Appendices A, B, & C). Since 1984, radiocollaring of Fortymile caribou has given biologists the ability to efficiently estimate herd distribution to ptedict huntet success, particularly along roads. Othet benefits from radiocollaring include efficient estimates of herd size, recruitment, mortality, causes of mortality, and relative nuttitional status (Valkenburg & Davis, 1989; Valkenburg *et al.*, 1994; Valkenburg, 1997).

Today managers know adverse weather can initiate declines in caribou hetds (Valkenburg *et al.*, 1994; Adams *et al.*, 1995a; Boertje *et al.*, 1996). Adverse weathet in Interior Alaska in the early 1990s and the simultaneous decline of several Interior Alaskan caribou herds were, in part, the stimuli for this renewed study of the Fottymile herd. During periods of adverse weather, herd condition can decline and ptedation and wolf numbers can increase (Mech *et al.*, 1995; Boertje *et al.*, 1996). Predation can accelerate declines because of increased vulnerability of prey and under-utilization of carcasses (Peterson & Page, 1983). After weather improves, the increased wolf numbers may prolong declines in caribou herds until wolf numbers also decline. Examples exist where the proportion of a herd killed by wolves increased during adverse weather because caribou were more vulnerable and because wolf numbers increased as caribou declined (Adams *et al.*, 1995a; Mech *et al.*, 1995; Boertje *et al.*, 1996).

Today it is a well-accepted belief that wolf and bear predation are often the major factors limiting caribou and moose (*Alces alces*) at low densities (Davis *et al.*, 1978, 1983; Gasaway *et al.*, 1983, 1992; Boertje *et al.*, 1987; 1988; Larsen *et al*, 1989; Valkenburg & Davis, 1989; Adams *et al*, 1995b; Boertje *et al.*, 1996). Several studies summarized historical and recent predator-prey relationships in the Fortymile area and documented that predation was a major factor limiting recovery of caribou and moose populations (Davis *et al.*, 1978; Boertje *et al.*, 1987; 1988; Valkenbutg & Davis, 1989; Gasaway *et al.*, 1992).

From 1981 through 1987, management actions were implemented to reduce gtizzly bear and wolf predation in a portion of the Fortymile hetd's range (Valkenburg & Davis, 1989; Gasaway *et al*, 1992). Control of wolf numbers by department petsonnel was terminated before desired reductions were achieved, and grizzly bear numbers were only moderately reduced in a small portion of the range. Subsequent 7–10% annual increases in caribou numbers could not be definitively linked to predator control because pretreatment studies were lacking and only small reductions in predator abundance occurred in the annual range of the Fortymile herd (Valkenburg *et al*, 1994). Increased harvests of wolves and grizzly bears in the 1980s were insufficient to allow for herd growth during

1990–1995, presumably because predators were not sufficiently reduced and adverse weather occurred.

To definitively test the effectiveness of predatot control, large reductions in predator abundance are necessary for several years (Crete & Jolicoeur, 1987; Larsen & Ward, 1995; Boertje *et al.*, 1996; Farnell & Hayes, unpubl.). Large reductions in wolf numbers for several years resulted in dramatic increases in caribou numbers in central Alaska (16% per year; Gasaway *et al.*, 1983; Boertje *et al.*, 1996) and eastcentral Yukon (18% per year; Farnell & MacDonald, 1988; Larsen & Ward, 1995; Farnell & Hayes, unpubl.). In both studies, late winter wolf numbers were 69–85% lower than precontrol autumn wolf numbers during the 4–6 winters of effective control efforts. These are the only well-documented studies where large reductions of wolves wete maintained for more than two winters and wolves were subsequently allowed to recover.

Management planning, presentations, and objectives

International draft management objectives from the mid–1980s through 1995 called for increasing the herd to 50 000 adults or 60 000 caribou by the year 2000. These management objectives wete written when the herd was growing at 7–10% per year and when population objectives were expected to be reached without further management actions. Instead, hetd numbers were nearly stable between 1990 and 1995 at about 22 500 caribou.

By 1994, conflicting interagency management objectives and stagnant low caribou numbers stimulated an interagency and international meeting focusing on Fortymile herd management in Tok, Alaska on 9 February 1994. Following this meeting, a divetse Fortymile Planning Team was cteated to write a new Fortymile Herd Management Plan. The Team completed the management plan and the Board of Game endorsed the plan in October 1995. The Team met 8 times between autumn 1994 and autumn 1995 to develop the plan, and continues to meet to address issues of importance. Ten public meetings wete held in various places to gathet input on the plan. The Board of Game approved a detailed implementation plan for the Fortymile Management Plan in spring 1997, and we began implementation (wolf fertility control and translocations) in November 1997. We also drafted a new 5-year research plan (1997–2002, Boertje & Gardner, 1996), which was edited by 10 independent, international scientists familiar with wolf biology and/or predatot/prey relationships.

We presented our findings in 5 editions of *The Comeback Trail;* a newsletter written to inform the public and agencies of Fortymile hetd planning, management, and research. This newsletter is published by the Alaska Department of Fish and Game and mailed to 3 300 interested parties for theit input. We also assisted Northern Native Broadcasting of Whitehorse in the production of a 52-minute documentary video on Fortymile herd history, planning, and biology. This video was released in January 1998.

The primary goal of the new Fortymile Management Plan is to restore the Fortymile herd to its former range, which entails initiating management actions to inctease herd size. Specific objectives include increasing herd numbers by at least 5–10% pet year through the year 2002. Management actions are to include fertility control in dominant wolf pairs in up to 15 key packs, translocation of the remaining wolves in these 15 packs, reduced caribou harvest quotas, encouraging trappers to shift trapping to specific areas, and possibly translocation of grizzly bears from calving areas during the final spring. Herd response to these management actions will depend largely on changes in wolf and bear predation, weather, and caribou distribution and productivity. Thus, response to the proposed management actions could vary considerably among years.

Materials and methods

Caribou capture

We radiocollared 49 adults and 129 autumn calves since September 1990. Each autumn we collared 14 or 15 calves. Adults were collared during 1991, 1992, and 1996 to provide a sample of productive, older caribou. Blood samples and body measurements were routinely collected. Radiocollats transmitted for 6 or 7 years (Telonics, Mesa, Arizona, USA and Advanced Telemetry Systems, Isanti, Minnesota, USA).

To immobilize adult caribou, we currently use 3 mg carfentanil citrate (3 mg/ml, Wildnil®, Wildlife Pharmaceuticals, Fort Collins, Colorado, USA) and 100 mg xylazine hydrochloride (100 mg/ml, Anased®, Lloyd Laboratories, Shenandoah, Iowa, USA) administered in a 2-cc dart with a 1.9-cm barbed needle using a short-range Cap-Chur pistol fired from a Robinson R-22 helicopter. To reverse the immobilization, we inject 275 mg naltrexone hydrochloride (50 mg/ml, Trexonil®, Wildlife

Pharmaceuticals) and 27.5 mg yohimbine hydrochloride (5 mg/ml, Antagonil®, Wildlife Pharmaceuticals) intramuscularly. Our current dose for immobilizing autumn calves includes 1 mg carfentanil citrate and 67 mg xylazine hydrochloride reversed with 125 mg naltrexone hydrochloride and 12.5 mg yohimbine hydrochloride inttamuscularly.

We radiocollared 50 newborn calves in May 1994, 52 in May 1995, 60 in May 1996, and 55 in May 1997 using techniques and collars described by Adams *et al* (1995b), except that we used a 2-person, Robinson R-22 helicopter. Usually a person was dropped off to capture the calf by hand, but occasionally the helicopter was used to slowly herd the cow and calf toward the hidden person. Most calves selected for collaring had a collared dam, and we distributed the remaining collars both geographically and temporally to mimic the calving of collared dams. Handling took <1.5 minutes/calf. Radiocollars transmitted fot about 17 months.

Estimating herd numbers and growth rate from photocensuses

We estimated minimum numbers of Fortymile caribou between 14 June and 1 July 1990, 1992, and 1994 through 1997 using a radio-search, total search, aerial photo technique (Valkenburg *et al.*, 1985), as in previous estimates of herd size during the 1970s and 1980s (Valkenburg & Davis, 1989). The entire summer range was divided among observers in 4 or 5 light aircraft during a 1-day census. These aircraft and a separate radiotracking plane communicated locations of caribou groups to the pilot of a DeHavilland Beaver aircraft equipped with a 9 x 9 format camera. This camera was used to photogtaph all groups numbering over about 100 caribou; usually 20–30 groups were photographed during a census. Smaller groups totaling about 500 caribou were visually counted. Photographed caribou were counted using 10X magnification. Counts probably include a high proportion of the total calves, but we are certain some calves are missed because of their small size and because of varying photo quality. We suspect that a fairly consistent proportion of the calves are counted among years, but counters cannot consistently sepatate calves from adults in the photos, so we have no way of testing this hypothesis.

To date, we have used photocensus data to calculate growth rates of the herd (Boertje *et al.*, 1996). We also used data on herd composition, pregnancy, and mortality to model population ttends, because photocensuses have, on occasion, substantially underestimated catibou numbets in the Delta herd (Boertje *et al*, 1996).

Explaining causes for herd fluctuations and estimating trend from data on herd composition, pregnancy, and mortality

We developed simple conceptual models to assess how productivity and various mortality factors affected herd size among years. Data on herd composition and total numbers allowed us to calculate the number of potentially productive cows in the herd, i.e., cows ≥36 months old (Appendices A, B, & C). We then calculated the number of calves born (pregnancy rate x number of cows ≥36 months old). Finally, we calculated the numbet of calves and adults dying from various causes using proportions of mortalities among collared samples. This allowed us to calculate net tecruitment (calves surviving 12 months minus the number of adults dying during those 12 months).

To estimate herd composition, we classified caribou from a helicopter during late September or early October 1991–1997 using the distribution of radiocollared caribou to randomly select catibou for counting. Cows, calves, and small, medium, and large bulls were counted during the 1-day survey each year. Caribou bulls and cows are more randomly mixed during this period than the temainder of the year. The helicopter crew relied on a Bellanca Scout pilot to relay locations of radiocollared caribou. After each count, we verified that the proportion of caribou counted in an area closely matched the proportion of radiocollars in that area, and we corrected biases in the counts using ratios when necessary.

We estimated ptegnancy rates of the herd during mid to late May by documenting the presence or absence of a calf, hard antlers, and/or a distended udder among radiocollared female caribou ≥24 months old (Whitten, 1995). Pregnancy was easy to confirm using these techniques. To confitm nonpregnancy, we repeated observations at least twice during 11–31 May 1984–1997.

We estimated mortality rates among different age classes from October 1992 to October 1997 by radiolocating all collared caribou 1 or 2 times monthly. In addition, during 1994 through 1997, we flew daily between 11 May and 31 May, 10 to 13 times in June, and weekly during July through September. Radiocollars contained a mortality

Table 1. Estimated numbers, harvest, natural mortality, pregnancy rates, and composition in the Fortymile herd, 1984–1

Year	Estimate of herd size		Estimated harvest[a] M	F	% Mortality of collared caribou 4–16 mo old for year ending 1 Oct (*n*)		% Mortality of collared females 17–28 mo old for year ending 1 Oct (*n*)	
1984	13 402	(19)[c]	430	20				
1985	–	–	421	20				
1986	15 307	(19)	360	20				
1987	–	–	229	20				
1988	19 975	(39)	645	150				
1989	–	–	401	100				
1990	22 766	(16)	321	22				
1991	–	–	495	10	21	(14)		
1992	21 884	(64)	432	35	57	(14)	8	(12)
1993	–	–	335	11	8	(12)	10	(10)
1994	22 104	(91)	313	15	17	(12)	10	(10)
1995	22 558	(85)	203	22	20	(30)	10	(10)
1996	23 458	(97)	145	5	18	(39)	14	(7)
1997	25 910	(113)	143	8	18	(44)	9	(11)

[a] Some harvest occurred during Jan, Feb, or Mar of the subsequent year, but was included in the autumn tally of the pre

[b] *n*=number of females ≥1 year old classified.

[c] Number of caribou with radiocollars during census.

[d] In 1993, 5 of 12 (42%) females 3 years old were pregnant, and 27 of 36 (75%) females ≥4 years old were pregnant. Pre square test of proportions, 2 x 2 tables, $P \leq 0.12$).

[e] Pregnancy rate in 1996 was significantly greater than other rates during 1994–1997 (chi-square test of proportions, 2

sensor that doubled the pulse rate if the collar remained motionless for 1 hour (newborn calf collars) or 6 hours (other collars). Annual mortality rate (M) was calculated as M = A / B x 100, where A = the number of caribou dying during the 12-month petiod, and B = the total number of collared caribou at the beginning of the 12-month period. We used the chi-square test of proportions to test for statistical differences among proportions (Conover, 1980).

Evaluating causes of natural caribou mortality

When a mortality was detected during daily May flights, we investigated the site via helicopter, usually within 4 houts of detection. Aftet May, we investigated mortality sites as soon as possible, usually within 1 day of detection. We necropsied carcass remains either on site or in the laboratory and noted wounding patterns. Hemorrhaging associated with puncture wounds, blood (non-coagulated) on collars, or blood on remnants of hide served as evidence of a violent death. In these cases scats, tracks, wounding patterns, other signs, and season of kill (bears hibernating in winter) served to identify the predator involved (Ballard *et al.*, 1979; Adams *et al.*, 1989). Bears often scraped up portions of the tundra mat and buried portions of the carcass or left crushed, cleaned bones in a small area with the collar. Wolves often left the carcass intact, cached whole or half carcasses in snow or muskeg without obvious digging, or carried the bloody collar some distance from the kill site. A collar soaked in blood indicated lynx (*Lynx canadensis*) predation, based on evidence of lynx predation in the snow at several sites.

Estimating caribou harvest

Procedures for estimating total and female caribou harvest varied, depending on the type of harvest reporting system. We considered harvest reports collected from permit hunts accurate estimates of total harvest because about 97% of permittees responded. In addition, we added estimates of illegal harvest from checkstations and by including

ℰ Mortality of)llared females :28 mo old for year ending 1 Oct	(n)	Pregnancy rate ofı collared females ≥36 mo old	(n)	Bulls or Calves:100 females Sep to Oct Bulls	Calves	(n)[b]
10	(21)	87	(23)	–	–	–
9	(22)	100	(19)	50	36	(574)
17	(24)	95	(21)	36	28	(842)
5	(19)	95	(19)	40	37	(1274)
9	(33)	95	(20)	38	30	(770)
19	(27)	–	–	27	24	(1182)
40	(20)	88	(16)	44	29	(1002)
17	(12)	91	(11)	39	16	(931)
17	(35)	87	(39)	48	30	(1416)
10	(51)	68[d]	(47)	46	29	(2095)
11	(37)	82	(45)	44	27	(1710)
8	(40)	85	(41)	43	32	(1879)
5	(42)	97[c]	(39)	41	36	(2601)
8	(61)	85	(46)	46	41	(3313)

in 1993 was significantly lowet than rates for each of the other years on this table (chi-

≤0.02).

caribou shot but not retrieved along roads and trails. All harvest since 1993 and most harvest during 1990–1992 was conducted under permit hunts. During general season hunts, harvest was reported by mandatory mail-in report cards without the benefit of reminder letters. Correcrion factors for general season hunts were derived from road surveys and surveys of transporter services during 1973. The surveys and subsequent mail-in harvest reports were treated as a mark-recapture sample to estimate total harvest. Harvest reported from general season hunts was multiplied by 1.59.

Estimating wolf harvest rates in the herd's annual ranges

To estimate wolf harvest rates within the respective annual ranges of the Fortymile caribou herd for the years 1992–1993 through 1996–1997, we delineated annual ranges ofı the herd based on monthly telemetry flights beginning 1 October. We then digitized the size ofı the annual ranges used by the herd, and estimated wolf numbers in the tespective annual caribou ranges. We estimated wolf numbers using radiocollars, standard ttack counts, and information from local trappers and pilots (Boertje *et al*, 1996). Mandatory reporting forms provided information on wolf harvest locations. Regulations allowed wolf hunting during 10 August–30 April and wolf trapping during 15 Octobet–30 April on most of the hetd's annual ranges.

Evaluating herd nutritional status

We used 4 indices to evaluate relative condition/nutritional status of the hetd. First, we estimated pregnancy rates and age of first reproduction during the 1992 through 1997 calving seasons using a radiocollared sample of cows as described above. Sample sizes varied annually from 39–47 cows ≥36 months old and 5–6 cows 24 months old. Second, we annually weighed 14 or 15 female autumn calves and 44–60 newborn calves using a calibtated spring or electronic scale. Third, we estimated the median

Table 2. Timing of mortality of radiocollared calves in rhe Fortymile caribou herd, 1994–1997.

	Radiocollared calves dying by period/Calves radiocollared in May (proportion dying, %)							
Year	May	Jun	Jul	Aug	Sep	Oct	Nov–May	Total
1994	17/50 (34)	9/50 (18)	1/50 (2)	2/50 (4)	0/50 (0)	1/50 (2)	4/50 (8)	34/50 (68)
1995	18/52 (35)	5/52 (10)	1/52 (2)	2/52 (4)	1/52 (2)	1/52 (0)	2/52 (6)	30/52 (58)
1996	17/60 (28)	8/60 (13)	3/60 (5)	1/60 (2)	0/60 (0)	3/60 (5)	5/60 (8)	37/60 (62)
1997	7/55 (13)	3/55 (5)	2/55 (4)	1/55 (2)	1/55 (2)	0/55 (0)	6/55 (11)	20/55 (36)

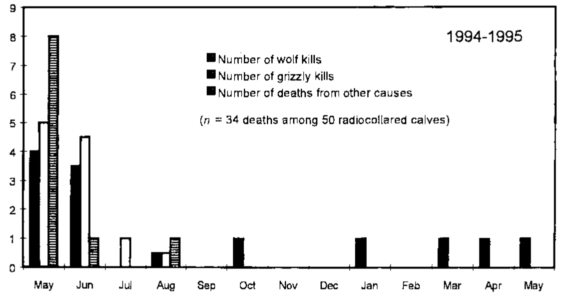

Fig. 2. Frequency distribution of causes of death among 34 radiocollared caribou calves that died from May 1994 through early May 1995, Fortymile caribou herd, Eastcentral Alaska.

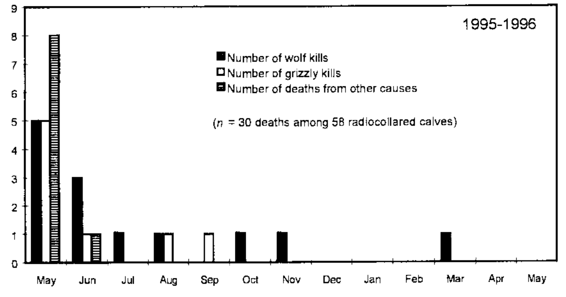

Fig. 3. Frequency distribution of causes of death among 30 radiocollared caribou calves that died from May 1995 through early May 1996, Fortymile caribou herd, Eastcentral Alaska.

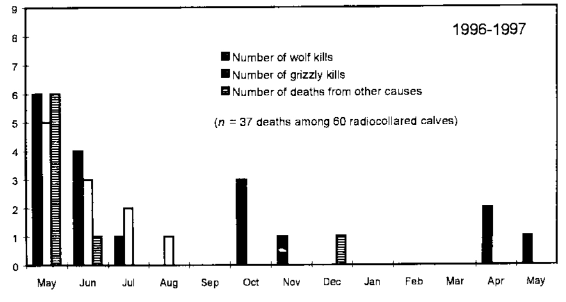

Fig. 4. Frequency distribution of causes of death among 37 radiocollared caribou calves that died from May 1996 through early May 1997, Fortymile caribou herd, Eastcentral Alaska.

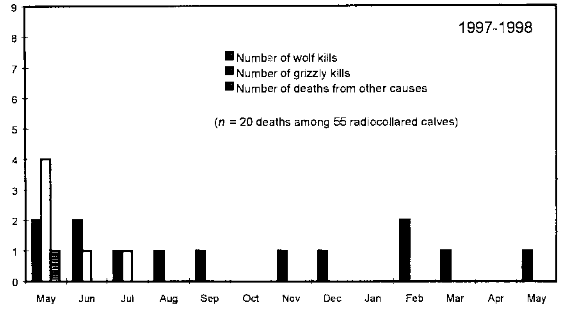

Fig. 5. Frequency distribution of causes of death among 20 radiocollared caribou calves that died from May 1997 through early May 1998, Fortymile caribou herd, Eastcentral Alaska.

calving date during 1992–1997, which is the date by which 50% of the pregnant radiocollared cows had given birth.

Lastly, we estimated the percent mortality of calves during their first 2 days of life. High calf mortality (e.g., 15–25%) during the first 2 days of life has been linked to malnutrition and we evaluated this factor as an index to herd nutritional status (Whitten *et al*, 1992). To detect calf mortality during the first 2 days of life, we observed a sample of 32 to 39 radiocollared, pregnant cows on consecutive days during calving seasons 1992 through 1997. These cows were observed each day until they gave birth and on the first 2 consecutive days after birth. During 1994–1997, we determined the cause of mortality among calves to test the hypothesis that early mortality was attributable to malnutrition.

Evaluating the lichen component of the herd's winter diet to assess range condition

We collected 24 fecal samples from the Fortymile herd winter ranges during January through April 1992–1996. Each sample contained 25 pellets; 1 pellet was collected from each of 25 different piles found afield (Boertje *et al.,* 1985). Samples were analyzed at the Composition Analysis Labotatory in Fort Collins, Colorado, USA.

Results and discussion

Herd numbers and trend

The first systematic estimate of herd numbers occurred in 1920 when several observers counted portions of the Fortymile caribou herd crossing the Steese Highway on a 20-day autumn migration that was 60 miles wide. Murie's (1935) extrapolated estimate in 1920 was a "conservative" 568 000.

The low point fot the herd came during 1973–1975 when the first photocensuses were conducted and only 5740–8610 caribou remained (Valkenburg *et al.,* 1994). Herd numbers increased during the late 1970s and 1980s at annual rates of 7–10% reaching about 23 000 caribou by 1989 (Valkenburg *et al*, 1994).

During this study, photocensuses indicated a fairly stable trend during 1990–1995, with approximately 22 000–23 000 caribou in the hetd, followed by an increase to almost 26 000 by 26 June 1997 (Table 1). The increase rate was 4% between 14 June 1995 and 21 June 1996 and 10% between 21 June 1996 and 26 June 1997. Increases were also predicted by models using 1995–1997 composition, pregnancy, and mortality data (Table 1; Appendices A, B, & C). The Team deemed that initiating and continuing management actions to improve caribou survival during a period of natural growth would be opportune.

Timing, rates, and causes of natural mortality

During the combined calving seasons of 1994–1997, we observed newborn calves during 11–28 May. By the end of June 1994–1996, 40–50% of the calves were dead. Anothet 20% died before reaching the age of 1 yeat (Figs. 2–4; Table 2). No significant differences occurred during these 3 years (chi-square test of proportions, 2 x 3 table, $P=0.56$). This pattern of births and deaths is similar to that found in other Interior Alaskan caribou studies (Adams *et al.*, 1995b; Valkenburg, 1997).

A major change occurred in the 1997 cohort when calf mortality rates declined 38–47% compared with the previous 3 years; this decline was statistically significant (Table 2, chi-square test of proportions, 2 x 2 table, $P=0.0008$). By the end of June 1997 only 18% of the calves were dead and the total annual mortality rate was only 36% (Fig. 5; Table 2). Decreased mortality in the 1997 cohort through September was caused by small declines in all causes of mortality (Table 3). A factot contributing to decreased wolf predation probably included successfully spacing calves between wolf territories in the upper elevations of the Seventymile River (Bergerud & Page, 1987). The herd had not previously concentrated its calving in the upper Seventymile, and we know of no wolf packs that regularly used this area in recent years. Also, frequent snowstorms and cool weather during the 1997 calving season provided mottled fresh snow cover, which allowed caribou cows to more easily hide their newborns and increased the search effort required for predators to find calves (Bergerud & Page, 1987). Calving did not appear more concenttated or dispersed in 1997 compared to previous years.

Causes of death among calves <4 months old were similar among years (Table 3). Wolves and grizzly bears were consistently the major predators. Eagles (*Aquila chrysaetos*), black bears (*Ursus americanus*), and wolverines (*Gulo gulo*) were common minor predators. Relatively few calves died from causes other than predation (Table 3).

Since 1991, wolf predation was the major cause of death among caribou calves 4–12 months old and caribou >12 months old. Of the 32 calves 4–12 months old fot which cause of death was determined (Oct 1991–30 Sep 1997), wolves killed 28 (88%), lynx killed 2 (6%), a wolverine killed 1 (3%), and 1 (3%) died from natural causes other than predation (nonpredation). Of the 30 caribou >12 months old for which cause of death was determined (1 Oct 1991–30 Sep 1997), wolves killed 26 (87%), grizzly bears killed 2 (7%), and 2 (7%) died from nonpredation. Most (84%) of these 62 deaths occurred during the 7 months (Oct–Apr) when snow was on the ground.

Annual wolf predation rates (24–32%) on radiocollared calves (n=50–60) varied little among the 1994–1997 cohorts and will provide the pretreatment data needed to see if reducing wolf numbers in the treatment area can significantly reduce wolf predation. Wolf sterilizations and translocations began during November 1997 and

Table 3. Causes of morrality among radiocollared calves in the Fortymile caribou herd from birth to 30 September 1994–1997.

	1994	1995	1996	1997
Calves collared	50	52	60	55
Deaths[a]	29	27	29	14
Cause of death:				
Wolf	8	10	11	7
Grizzly bear	11	8	11	6
Eagle	3	3	5	0
Black bear	1	4	0	0
Wolverine	1	1	0	1
Nonpredation[b]	5	1	2	0

[a] In addition, wolves killed 5 calves during winter 1994–1995, 3 during winter 1995–1996, 8 during winter 1996–1997, and 6 during winter 1997–1998.

[b] During 1994, 3 calves broke theit legs, 1 died from abandonmenr when irs dam had no distended udder and 1 was suffocated at birth due to its large size (10.5 kg). During 1995, 1 died from a broken leg when trapped in a natural rock pit. During 1996, 1 died from abandonment when its dam had no distended udder, and 1 probably died from an unknown birth defect 48 hours after birth (no milk in stomach but dam present with distended udder).

could partially affect survival of the 1998 cohort. Full treatment of 15 key wolf packs is expected from May 1999 through May 2001, which will provide 2 years during which to test whether wolf predation on calves is significantly reduced (1-tailed test) compared to the 4 pretreatment years (May 1994–May 1998). We will also test for decreasing trends in summer wolf caused mortality. Interpretations of data will depend in part on how caribou are distributed in relation to the treatment area among the various years.

Fairly stable mortality rates among caribou older than 4 months during 1993–1997 indicates other factors must be responsible for the herd's increase in 1996 and 1997 (Table 1). No significant declines in these mortality rates were observed during 1996–1997 when the herd was increasing compared with data from 1993–1995 when the herd was stable (chi-square test of proportions, 2 x 2 table, P=0.90).

We found significantly higher mortality among caribou 4–16 months old compared with older caribou for the yeats 1993–1997 (Table 1, chi-square test of proportions, 2 x 2 table, P=0.007). These data conflict with those of Davis *et al.* (1988) who reported similar mortality rates among >5-month-old calves, yearlings, and adults in the Delta herd.

Elevated mortality from age 4 to 16 months in the 1991 cohort (57%, n=14, Table 1) may have been associated with inadvertent separation of calves from theit dams at collaring (27 Sep–22 Oct). We darted calves and their dams simultaneously in 1991 and only 2 of 14 cow-calf pairs reunited aftet tecovery from drugging. In 1990 and 1992 through 1997, we radiocollared calves but not their dams, and cow-calf pairs consistently reunited. Implications of these data are that human hunting of cows with calves during autumn or early winter may reduce the survival of orphaned calves where wolves are major predators. Seven (88%) of the 8 dead calves were killed by wolves.

Population modeling

We completed three annual models using data on herd size, herd composition, pregnancy, and mortality to illustrate the relative importance of factors affecting the size of the Fortymile caribou herd (Table 4). With certain qualifications, the models can help explain why the photocensus results remained stable or changed among years. For example, if the herd increased, was it because of decreased mortality or increased productivity? These models are sensitive to small, statistically insignificant changes in mottality rates, e.g., when an additional 3 among 50 caribou die and adult mortality rates change from 6% to 12%. Therefore caution should be used when interpreting model output.

The first year's model (11 May 1994–10 May 1995) indicated a fairly stable trend, i.e., the number of births almost equaled the number of deaths (Table 4). This stable trend was consistent with independent late June photocensuses from 1990–1995 (Table 1).

The primary difference in the 1995–1996 photocensus and modeling data was that the herd increased. We counted 900 additional caribou on 21 June 1996 (23 458 caribou) compared to 14 June 1995 (22 558). Much of the photocensus increase probably resulted from the approximately 2000 additional calves born during late May 1996 compated to 1994 and 1995 (Tables 1 & 4). The model indicated about 1000 more adult caribou survived wolf predation compared to the

Table 4. Population modeling outputs for the Fortymile caribou herd, 1994–1995 through 1996–1997. Values are from Appendices A, B, and C.

	Approximate number of adults and yearlings			
Year	Beginning of the year	End of the year	Population trend	Calv born
11 May 1994–10 May 1995	20 000[a]	17 370 + 2360[b] = 19 730	Approximately stable	8 09
11 May 1995–10 May 1996	20 000[a]	18 550 + 3420[b] = 21 970	Increasing slightly	8 39
11 May 1996–10 May 1997	21 000[a]	18 230 + 3840[b] = 22 070	Increasing slightly	10 15

[a] Estimated from results of June photocensus each year (Table 1). Significant numbers of calves (2500–4000) were subrra

[b] Yearlings recruited into population at 12 months of age calculated as numbet of calves born minus number of calves dy

1994–1995 model and about 1000 more calves survived because of slightly reduced nonpredation and grizzly bear predation (Appendices A & B). However, the model inputs which resulted in increased survival were not statistically significant. For example, adult mortality decteased from 12% (6/52) during May 1994–May 1995 to 6% (3/49) during May 1995–May 1996 (Appendices A & B); these differences are not significant (chi-square test of proportions, 2 x 2 table, $P=0.34$).

The 1996–1997 photocensus and modeling data also indicated the herd was increasing. We counted about 2 500 additional caribou on 27 June 1997 (25 912) compared to 21 June 1996 (23 458). The most likely causes of this increase were the recruitment of additional calves born during May 1996 (Table 4) and improved calf survival in May and June 1997 (see Timing, Rates, and Causes of Natural Mortality, Table 2), not changes in annual survival rates in the 1996–1997 model (Tables 1–2). Calf survival was significantly higher during May and June 1997 compared to the previous three springs (Table 2; chi-square test of proportions, 2 x 2 test, $P=0.0003$). Calf survival rates in the 1996–1997 model were not significantly different from rates in the previous models (Table 2; chi-square test of proportions, 2 x 2 table, $P=0.89$); neither did survival rates of caribou older than calves differ significantly (Appendices A, B, & C; chi-squate test of proportions, 2 x 2 table, $P=0.46$).

Caribou harvest

To increase social acceptance of the management plan, the Fortymile Team chose to reduce the annual harvest to 150 bulls for 5 years beginning in 1996. We illustrated the relatively minor role that harvest has tecently had on herd dynamics in Table 4. Harvests have been intentionally held low since 1973 to encourage herd growth (Valkenburg et al., 1994). Reducing harvests from 200–500 bulls (≤2% of the herd, 1990–1995) to 150 bulls (<1% bulls, 1996–2000) will not result in the 5% to 10% annual tates of hetd increase desired by the Fortymile Team. Estimated total annual harvest avetaged 2.8% of the midsummer herd size during the 6 years before 1990. In 1990 harvest was intentionally reduced because natural mortality increased and calf:cow ratios declined (Table 1).

Following two hunting seasons with a quota of 150 bulls, we have observed no increase in the bull:cow ratio (Table 1). No significant increases in bull:cow ratios are expected duting the next 3 years. For example, bull:cow ratios in the Fortymile herd ($\bar{x}=43$ bulls:100 cows, range=36–50, 1985–1997, Table 1) are not reduced by harvest compared with ratios from the only Interior Alaska herd with no harvest in recent decades ($\bar{x}=43$ bulls:100 cows, range=29–56 in the Denali herd, 1985–1997).

Wolf harvest

The Fortymile Catibou Calf Protection Program, a group of private citizens, paid $400 per wolf from a large area (33 200 km^2) including most of the Fortymile herd's range beginning winter 1995–1996 and continuing through winter 1996–1997. This $400 approximately doubled the market value of pelts and was provided to stimulate increased wolf harvest with the goal of incteasing the Fortymile herd and associated moose and sheep (*Ovis dalli*) populations.

To evaluate the effect of the Caribou Calf Protection Program on wolves and caribou, we compiled estimates of wolf densities and harvest rates from within the herd's respective annual ranges for 3 years prior to the program and during the 2 years of the program (Table 5). We analyzed wolf harvest rates over the herd's respective annual ranges because caribou used different areas each year, especially during winters. Most of the wolf harvest occurred on caribou wintering areas. We detected no substantial reductions in the autumn wolf densities duting this program, although a slight decline was detected following

Total initial calves and older caribou killed by: (%)

Wolves	Grizzly bears	Other predators	Hunters	Nonpre dation	All factots
190 (15)	2010 (7)	840 (3)	330 (1)	990 (4)	8360 (30)
210 (11)	1410 (5)	1330 (5)	225 (1)	240 (1)	6415 (23)
340 (17)	2055 (7)	1020 (3)	150 (<1)	515 (2)	9080 (29)

he photocensus to derive a prior May precalving population estimate.

Table 5. Estimated autumn wolf numbers and harvest in the respective annual ranges of the Fortymile caribou herd, 1992–1996.

	Column				
	A	B	C	D	E
Winter	Area of annual caribou range (1000 km²)	Number of wolf packs preying on the herd (number of border packs)[a]	Estimated autumn wolf numbers in annual caribou range[b]	Wolf harvest in and adjacent to respective range	Estimated percent wolf harvest (Columns D/C x 100)
1992–1993	29.1	32 (7)	187	54	29
1993–1994	23.1	26 (6)	156	49	31
1994–1995	30.4	35 (7)	186	40	22
1995–1996	27.7	33 (7)	220[b]	126[c]	57[c]
1996–1997	35.0	37 (5)	239	68[c]	28[c]

[a] Border packs were packs that ranged only about 50% in the annual caribou range.
[b] Autumn wolf numbers are from the respective annual ranges of the Fortymile herd for the years beginning 1 Oct. We included only 50% of the wolves in the border packs, except in 1995–1996 when large numbers of wolves were harvested along the border. Wolves in 1995–1996 ranged in about 31 000 km². To account for single wolves, we added 10% to the number of wolves estimated to be in the annual range.
[c] Caribou Calf Protection Program provided a private incentive to increase harvest.

winter 1995–1996 when 57% of the wolves were harvested (Table 5). Without substantial teductions in autumn wolf densities, annual wolf predation on caribou is not expected to decline significantly.

Sustained wolf harvest rates exceeding about 28% of the autumn wolf population are expected to result in wolf population declines (Fuller, 1989; Gasaway *et al.,* 1992). However, significant increases in moose and caribou numbers have been reported only after maintaining spring wolf densities 69–85% below initial autumn wolf numbers for several years (Larsen & Ward, 1995; Boertje *et al.,* 1996). In contrast, wolf densities in the respective annual ranges of the Fortymile hetd were reduced only 19–28% by harvest during winters 1992–1993 through 1996–1997, except during winter 1995–1996 (Table 5).

Sustained high harvest rates are required to keep wolf populations below levels found in systems with little or no harvest, because wolves have high reproductive and immigration rates (Larsen & Ward, 1995; Boertje *et al.,* 1996). Recent autumn densities of 7–8 wolves/1000 km² in this study were similar to estimates prior to the ptivate incentive program, when ttapping pressure was less intense (Table 5). In Denali National Park and Preserve, where little wolf harvest occutred and prey densities were similar to those in the Fortymile herd's range, Meier *et al.* (1995) reported autumn densities of 5–10 wolves/1000 km² during 1986–1992. Average autumn densities of 8 wolves/1000 km² were reported in 13 Alaska and Yukon study areas where wolves were lightly harvested and prey densities were similar to those in the Fortymile herd's range (Gasaway *et al.,* 1992).

Herd nutritional. indices, weather, and related herd performance

We studied indices to nutritional status, weather data, and herd productivity and survival for several reasons. First, comparisons with similar data from other herds allowed us to evaluate the relative nutritional status of the Fortymile herd. Second, nutritional data lent insights into what weather factors could be important to herd performance. Third, we wanted to identify which nutritional indices may be useful in predicting herd performance.

We found consistent evidence for moderate to high nutritional status in the Fortymile herd during this study when indices wete compared with other Alaskan herds (Whitten *et al.,* 1992; Valkenburg, 1997). However, more data are needed during a natural decline and increase in the Fortymile herd to describe the potential lower and upper level of nutritional indices in the Fortymile ecosystem. For example, we found no evidence of pregnancy in 32 radiocollared 2-year-olds during this study. Pregnant 2-year-old caribou are rarely found in Alaska and their calves rarely survive, but pregnancy in 2-year-olds signifies extremely good nutritional status (Davis *et al.,* 1991; Valkenburg, 1997).

The single evidence for malnutrition during this study was the low pregnancy rate during 1993 following the abnormally short growing season of 1992. However, this single evidence fot malnutrition resulted in no strong decline in herd numbers, as occurred in the Delta and Denali herds (Table 1; Boertje *et al.,* 1996). Many adult cows (≥3 years old) apparently did not gain sufficient fat to breed in autumn 1992. The pregnancy rate in 1993 was low in the Fortymile herd (68%; Table 1), the Delta herd (30%), the Nelchina herd (66%), and the Chisana hetd (50%; Valkenburg, 1993). Pregnancy rates fot caribou are commonly ≥82% (Table 1; Bergerud, 1980). Only 5 (42%) of twelve 3-year-olds produced calves in the Fortymile herd in 1993, compared with 5 (83%) of 6 in 1994, 5 (71%) of 7 in 1995, 9 (100%) of 9 in 1996, and 6 (100%) of 6 in 1997. Only 126 snow-free days occurred in Fairbanks in 1992 compared with 160 to 199 days during the previous 19 years (Boertje *et al.,* 1996). Snowmelt was several weeks late during spring 1992, and snowfall was several weeks early in autumn 1992.

Data from pregnancy rates probably provide indices to the previous spring/summer/autumn condition, similat to data on autumn calf weights. Data on pregnancy rates indicate caribou nutritional status was poor in autumn 1992, excellent in autumn 1995, and average in autumns 1991, 1993, 1994, and 1996 (Table 1). Autumn calf weights have been relatively high and stable compared with nutritionally stressed herds (Table 6; Valkenburg, 1997). Autumn calves reached relatively high weights in 1992 despite the short growing season. Only during 1997 were weights significantly higher than all other years (P=0.02 in comparing cumulative yeats, ANOVA, and P=0.001–0.056 when comparing individual years, Student's t-test).

Birthweights and calving dates probably provide indices to winter and spring conditions. Low birthweights and delayed calving are thought to indicate malnutrition (Espmark, 1980; Reimers *et al.,* 1983; Skogland, 1985; Adams *et al.,* 1995b). Fortymile birthweights during this study wete relatively high and stable compared with nutritionally stressed herds (Table 7; Valkenburg, 1997). Birthweights indicated spring nutritional status improved significantly during 1995–1997 compared to 1994 (Table 7). Unlike data from the Denali herd, an increase in birthweights was not observed when calf mortality declined in 1997 (Tables 2 & 7; Adams *et al.,* 1995b). Median calving dates indicate spring nutritional status may have improved beginning in 1994, e.g., median calving dates were 23 May in 1992 (n=25) and 22 May in 1993 (n=24) compared with 18 May in 1994 (n=32), 1996 (n=37), and 1997 (n=39) and 20 May (n=28) in 1995.

Lastly, we examined the rates (1992–1997) and causes (1994–1997) of mortality among calves during their first 2 days of life to test whether perinatal mortality in the Fortymile herd is caused largely by nutrition-related factors, as concluded by studies of the Porcupine herd (Whitten *et al.,* 1992). We found no convincing support fot this hypothesis in the Fortymile herd. Instead, predation was the major cause of death among calves ≤2 days old, e.g., in 17 (74%) of 23 cases of observing radiocollared cows or calves. Also, rates of perinatal mortality were highly variable among years and not highest in 1993 when nutritional status was low. Perinatal mortality rates observed among offspring of collared cows were 3% (n=30) in 1992, 14% (n=28) in 1993, 22% (n=32) in 1994, 7% (n=28) in 1995, 21% (n=38) in 1996, and 3% (n=35) in 1997. In conclusion, we do not recommend mortality rates among young Fortymile calves be used as an index to hetd nutritional status. The data is difficult and expensive to collect and does not appear to be correlated with nutritional status.

In contrast, we will continue to collect data on pregnancy rates, weights of calves, and calving dates to evaluate the varying role of nutrition during the period of reducing predation. The effects of nutrition and predation on a herd's performance are clearly intertwined (Boertje *et al.,* 1996).

Because we saw no strong decline in the Fortymile herd during 1992 when nutritional status was poor, we conclude that poor nutritional status was not as strong a factor affecting caribou

Table 6. Ranked mean weights (kg) with standard error of the mean of autumn calf caribou in 11 Alaskan herds of various size and density.

Herd	Year	$\bar{x}$ weight (kg)	$s_{\bar{x}}$	n	Herd size in 1993[a]	Herd multiyear density per km^{2}[a]
Western Arctic	1994	32.4	1.3	15	450 000	1.5
	1995	36.8	1.2	9		
	1992	40.4	1.8	13		
Northern Alaska Peninsula	1995	44.7	1.6	10	18 000	0.5
	1996	46.0	2.4	10		
	1997	48.3	2.1	10		
Nelchina	1996	48.3	2.1	10	40 361	0.5
	1995	53.5	1.5	15		
	1997	55.5	1.8	10		
Chisana	1990	51.7	1.8	13	850	<0.1
Fortymile	1990	52.8	1.1	14	22 000	0.4
	1991	53.9	1.4	14		
	1994	54.5	1.2	14		
	1996	54.7	1.4	14		
	1992	55.1	1.7	14		
	1993	56.1	0.9	15		
	1995	56.7	1.1	15		
	1997	59.3	1.3	15		
Delta	1992	54.6	1.4	14	3 661	0.5
	1993	55.6	1.4	11		
	1996	55.7	1.4	14		
	1991	57.9	1.2	14		
	1997	58.2	1.0	20		
	1995	59.5	1.3	13		
	1994	59.6	1.3	15		
Macomb	1996	58.4	2.6	8	500	0.1
Wolf Mtn	1995	59.6	2.1	8	650	<0.1
White Mtns	1991	58.5	2.1	9	1 000	0.1
	1995	60.6	2.1	6		
	1997	61.6	1.1	6		
Ray Mtn	1994	60.9	1.3	20	700	<0.1
Galena Mtn	1994	65.6	1.3	9	275	<0.1
	1993	66.5	3.2	4		

[a] Herd sizes and multiyeat densities from Valkenburg *et al.* (1996) for 1993.

numbers in the Fortymile herd as in the Delta and Denali herds (Boertje *et al.,* 1996). A contributing factor may be that weather patterns are more continental in the Fortymile herd's range.

Herd diseases

Potential exposure of the Fortymile herd to 10 ungulate diseases has been monitored since 1980 using blood sera collected from immobilized caribou ≥4 months old. Similar data have been collected from other herds in Alaska and the Yukon (Zarnke, 1996). Few documented cases exist where infectious diseases have had a detectable effect on caribou herds in Alaska. Brucellosis in arctic caribou herds is a notable exception (Valkenburg *et al*, 1996b; Zarnke, 1996). From 1980–1995, 159 sera samples have been collected from Fortymile hetd caribou. There was no evidence of exposure to *Brucella suis* IV in any of these samples.

Range condition

Range condition appeared excellent during wintets 1991–1992 through 1995–1996, as evidenced by high proportions ($\bar{x}$=80%) of lichen fragments in

Table 7. Average newborn caribou weights from 6 Alaskan herds.

Herd and year	Males			Females		
	Weight (kg)	$s_{\bar{x}}$ [a]	n	Weight (kgs)	$s_{\bar{x}}$ [a]	n
Porcupine 1984	7.30	0.22	33	6.70	0.18	23
Porcupine 1983	7.40	0.19	24	6.60	0.16	28
Porcupine 1985	7.70	0.23	27	7.30	0.20	26
Nelchina 1996	8.26	0.24	23	7.19	0.19	17
Nelchina 1997	8.43	0.18	30	7.89	0.23	30
Fortymile 1994[b]	7.71	0.20	22	7.55	0.27	22
Fortymile 1997	8.52	0.25	24	7.97	0.21	32
Fortymile 1996	8.54	0.24	26	8.09	0.17	32
Fortymile 1995	8.65	0.16	24	7.94	0.19	25
Delta 1997	8.35	0.18	40	7.98	0.21	35
Delta 1996	8.39	0.23	22	7.40	0.19	28
Delta 1995	8.72	0.29	26	8.31	0.24	19
Mentasta 1994[c]	8.83	0.21	18	8.09	0.19	23
Mentasta 1993[c]	8.90	0.23	15	7.91	0.20	23
Denali 1984–1987[d]	9.00	0.11	67	7.80	0.11	60

a With standard errors of about 0.2 kg, a difference in means of 0.6 kgs would be significant at the P=0.05 level (Student's 2-tailed t-test).

b Fortymile birthweights of males (P=0.001, t=3.36) and females (P=0.075, t=1.80) increased significantly during 1995–1997 compared with 1994.

c Data from Jenkins (1996).

d Denali data is corrected for calf age; uncorrected weights would be 0.3–0.5 kg higher (Adams *et al.,* 1995a).

caribou fecal samples (Table 8). Samples were collected from several different wintering areas (Fig. 6). Boertje (1981) and Boertje *et al.* (1985) provided data showing the usefulness of fecal samples in evaluating use of lichens on winter ranges. Lichens are slower growing than vascular plants and ate a highly preferred and highly digestible winter forage, in contrast to mosses and evergreen shrubs (Boertje, 1990). Fecal samples from overgrazed winter ranges elsewhere in Alaska contained reduced proportions of lichens (30–40%) and higher proportions of mosses (30–60%) or evergreen shrubs (30%) compared to values observed in the Fortymile herd's range (Table 8; Boertje *et al.,* 1985; Valkenburg, 1994).

Conclusions

The Fortymile herd clearly has the potential to grow. The herd currently uses <30% of its historic range, its multiyear density is about 500 caribou/1000 km^2, and nutrition is not a strong limiting factor. Predicting trends in caribou numbers is problematic. We know that a variety of factors can cause a surge or drop in numbers, that stability is seldom long tetm, and that rapid declines can occur from the synergistic effects of adverse weather and increased predation (Boertje *et al.,* 1996). Also, we know that continental Alaskan caribou herds have commonly remained at multiyear densities of ≤500 caribou/1000 km^2 during the last 2 decades largely because of predation (Bergerud, 1980; Valkenburg *et al.,* 1996a). Exceptions were found where strong predator control and favorable weather occurred and where predation is lessened by a natural lack of alternative prey for wolves (particulatly on seasonal calving areas).

Assuring achievement of time-specific objectives for increased Fortymile caribou numbers will depend on actions that substantially reduce ptedation, presumably combined with favorable weather. Novel, experimental approaches to reducing predation have been proposed and we are well prepared to test the effectiveness of these approaches.

Table 8. Proportions of discerned plant fragments (mean % ± standard error of the mean) in 24 fecal samples collected from Fortymile caribou during January–April 1992 rhrough 1996. Collection sites are depicted in Fig. 6.

Plant genus or group	1992 n=6	1993 n=7	1994 n=1	1995 n=6	1996 n=4	All years n=24
Lichens	72 ± 9	81 ± 4	80	84 ± 3	86 ± 4	80 ± 3
Equisetum	7 ± 6	3 ± 1	6	8 ± 3	6 ± 2	6 ± 2
Mosses	9 ± 3	7 ± 2	4	1 ± <1	1 ± 1	5 ± 1
Ledum	7 ± 2	5 ± 1	5	3 ± 1	4 ± 1	5 ± 1
Graminoids	1 ± <1	1 ± <1	4	2 ± 1	2 ± 1	2 ± 1
Forbs	3 ± 2					1 ± 1
Picea	2 ± <1	2 ± <1	<1	1 ± <1	1 ± <1	1 ± <1
Dryas	1 ± 1					<1
Salix		1 ± <1		<1	<1	<1

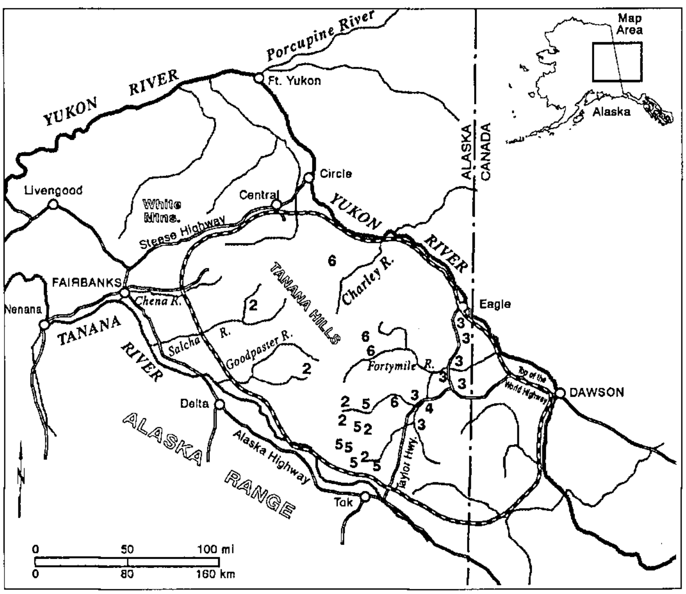

Fig. 6. Locations where caribou fecal samples were collecred during Jan.–Apr. 1992 (2), 1993 (3), 1994 (4), 1995 (5), and 1996 (6).

Reducing predation is a value-based socioeconomic and political decision beyond the scope of this teport. Ecological and biological issues ate mote easily addressed. For example, sustainable harvest of a caribou herd is ecologically sound compared to dependency on alternative livestock and agricultural industries. Past studies have shown wolf reductions can be biologically effective and sound, i.e., 1) caribou herds can grow rapidly following large reductions in wolf numbers and 2) wolf numbers can recover within a few years (Larsen & Ward, 1995; Boertje *et al.,* 1996).

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Appendices

APPENDIX A. Values and calculations used to model caribou population dynamics, Fortymile caribou herd, 15 May 1994–14 May 1995.

Estimated parametets and calculations	Observed or calculated values
Cows ≥24 months old in May 1994 = percent cows in herd in October 1993 when randomly mixed (0.57) x estimated hetd size in early May 1994 (20000)	11400
Cows 24 months old in May 1994 = percent calves in herd in October 1992 (0.17) x estimated herd size in early May 1993 (20000) x survival rate from 12 to 24 months old (0.90) x proportion of females (0.5)	1530
Cows ≥36 months old in May 1994 = (11400–1530)	9870
Calves produced in May 1994 = (9870 x 0.82)	8090
Calves dying by 14 May 1995 = (8090 x 39/55)	5740
Number and cause of calf deaths, 15 May 1994–14 May 1995 (n=34 deaths from known causes):	
Wolf (0.382 x 5740)	2190
Grizzly bears (0.324 x 5740)	1860
Other predators (0.147 x 5740)	840
Nonpredation (0.147 x 5740)	840
Nonhunting deaths among caribou ≥12 months old from 15 May 1994–14 May 1995 = (20000) (6 ÷ 52)	2310
Number and cause of nonhunting deaths among these 2310 caribou (30 adult and yearling death sites were examined from 1 Oct 1991–1 Oct 1997):	
Wolf (0.867 x 2310)	2000
Nonpredation (0.067 x 2310)	150
Grizzly bear (0.067 x 2310)	150
Annual harvest of adults and yearlings May 1994–May 1995	330
Estimated herd size 15 May 1994 (counted 22104 on 1 July 1994 with some calves included in photos)	20000
Estimated herd size 14 May 1995 = (20000 + 8090 - 5740 - 2310 - 330) rounded to nearest 100	19700
Conclusion: Herd trend approximately stable, consistent with photocensus results	

APPENDIX B. Values and calculations used to model caribou population dynamics, Fortymile caribou herd, 15 May 1995–14 May 1996.

Estimated parameters and calculations	Observed or calculated values
Cows ≥24 months old in May 1995 = percent cows in herd in Octobet 1994 when randomly mixed (0.57) x estimated herd size in early May 1994 (20000)	11400
Cows 24 months old in May 1995 = percent calves in herd in October 1993 (0.17) x estimated herd size in early May 1994 (20000) x survival rate from 12 to 24 months old (0.90) x proportion of females (0.5)	1530
Cows ≥36 months old in May 1995 = (11400–1530)	9870
Calves produced in May 1995 = (9870 x 0.85)	8390
Calves dying by 14 May 1996 = (8390 x 32/54)	4970
Number and cause of calf deaths, 15 May 1995–14 May 1996 (*n*=30 deaths from known causes):	
Wolf (0.433 x 4970)	2150
Grizzly bears (0.267 x 4970)	1330
Other predators (0.267 x 4970)	1330
Nonpredation (0.033 x 4970)	160
Nonhunting deaths among caribou ≥12 months old from 15 May 1995–14 May 1996 = (20000) (3 ÷ 49)	1220
Number and cause of nonhunting deaths among these 1220 caribou (30 adult and yearling death sites were examined from 1 Oct 1991–1 Oct 1997):	
Wolf (0.87 x 1220)	1060
Nonpredation (0.07 x 1220)	80
Grizzly bear (0.07 x 1220)	80
Annual harvest of adults and yearlings May 1995–May 1996	225
Estimated herd size 15 May 1995 (counted 22558 on 14 June 1995 with some calves included in photos)	20000
Estimated hetd size 14 May 1996 = (20000 + 8390 - 4970 - 1220 - 225) rounded to nearest 100	22000
Conclusion: Herd trend approximately stable, consistent with photocensus results	

APPENDIX C. Values and calculations used to model caribou population dynamics, Fortymile caribou herd, 15 May 1996–14 May 1997.

Estimated parameters and calculations	Observed or calculated values
Cows ≥24 months old in May 1996 = percent cows in herd in Octobet 1995 when randomly mixed (0.57) x estimated herd size in early May 1996 (21000)	11970
Cows 24 months old in May 1996 = percent calves in herd in October 1994 (0.16) x estimated herd size in early May 1995 (21000) x survival rate from 12 to 24 months old (0.90) x proportion of females (0.5)	1510
Cows ≥36 months old in May 1996 = (11970–1510)	10460
Calves produced in May 1996 = (10460 x 0.97)	10150
Calves dying by 14 May 1996 = (10150 x 38/61)	6320
Number and cause of calf deaths, 15 May 1996–14 May 1997 (*n*=37 deaths from known causes)	
Wolf (0.486 x 6320)	3070
Grizzly bears (0.297 x 6320)	1880
Other predators (0.162 x 6320)	1020
Nonpredation (0.054 x 6320)	340
Nonhunting deaths among caribou ≥12 months old from 15 May 1996–14 May 1997 = (21000) (8 ÷ 64)	2620
Number and cause of nonhunting deaths among these 2620 caribou (30 adult and yearling death sites were examined from 1 Oct 1991–1 Oct 1997)	
Wolf (0.867 x 2620)	2270
Nonpredation (0.067 x 2620)	175
Grizzly bear (0.067 x 2620)	175
Annual harvest of adults and yearlings May 1996–May 1997	150
Estimated herd size 15 May 1996 (counted 23458 on 21 June 1996 with some calves included in photos)	21000
Herd size 14 May 1996 (21000 + 10150 - 6320 - 2620 - 150) rounded to nearest 100	22000
Conclusion: Herd trend increasing, consistent with photocensus results	

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Status of endangered and threatened caribou on Canada's arctic islands

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Abstract: Caribou (*Rangifer tarandus*) on rhe Canadian Arctic Islands occur as several populations which are nationally classified as either endangered or threatened. On the western High Arctic (Queen Elizabeth) Islands, Peary caribou (*R. t. pearyi*) declined to an estimated 1100 caribou in 1997. This is the lowest recorded abundance since the firsr aerial survey in 1961 when a high of ca. 24 363 caribou was estimated on those islands. Peary caribou abundance on the eastern Queen Elizabeth Islands is almost unknown. On the southern Arctic Islands, thtee caribou populations declined by 95-98% between 1973 and 1994 but out information is unclear about the numerical trends for the two other populations. Diagnosis of factors driving the declines is complicated by incomplete information but also because the agents driving the declines vary among rhe Arctic's different climatic regions. The available evidence indicates that severe winrers caused Peary caribou die-offs on the western Queen Elizabeth Islands. On Banks Island, harvesting together with unfavourable snow/ice condirions in some years accelerated the decline. On northwestern Victoria Island, harvesting apparently explains the decline. The role of wolf predation is unknown on Banks and northwest Victoria islands, although wolf sightings increased during the caribou declines. Reasons for the virtual disappearance of arctic-island caribou on Prince of Wales and Somerset islands are uncertain. Recovery acrions have started with Inuit and Inuvialuit reducing their harvesting but it is too soon to evaluate the effect of those changes. Recovery of Peary caribou on the western Queen Elizabeth Islands is uncertain if the current trends toward warmer temperarures and higher snowfall persist.

Key words: declines, population status, *Rangifer tarandus, R. t. pearyi,* tecovery.

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Introduction

In 1991, the Committee on the Status of Endangered Wildlife in Canada classified caribou *Rangifer tarandus* on both eastern and western Queen Elizabeth Islands (Fig. 1) and on Banks Island as "Endangeted" and those on Victoria, Prince of Wales, and Somerset islands and the Boothia Peninsula as "threatened" (Miller, 1990b). The rationale fot the endangered status was the steep population declines during the 1970s and no discernible ovetall recovery in the eariy 1980s. The designation of thteatened was assigned to populations whose harvest appeared high relative to incomplete infotmation on population size.

By 1998, the two Endangered populations of *R. t. pearyi* on the western Queen Elizabeth Islands have further declined and the endangeted caribou on Banks Island also appear to have declined further in the late 1990s. The threatened population on Prince of Wales and Somerset islands has almost disappeared, and the threatened northwestern Victoria Island population had further declined but has, perhaps, now started to increase. The status is unknown fot the endangered caribou on the eastern Queen Elizabeth Islands and the threatened caribou on southern and east-central Victoria Island and the Boothia Peninsula.

Our paper describes the status of the different populations and summarises information on factors that drove the declines and options for recovery. We

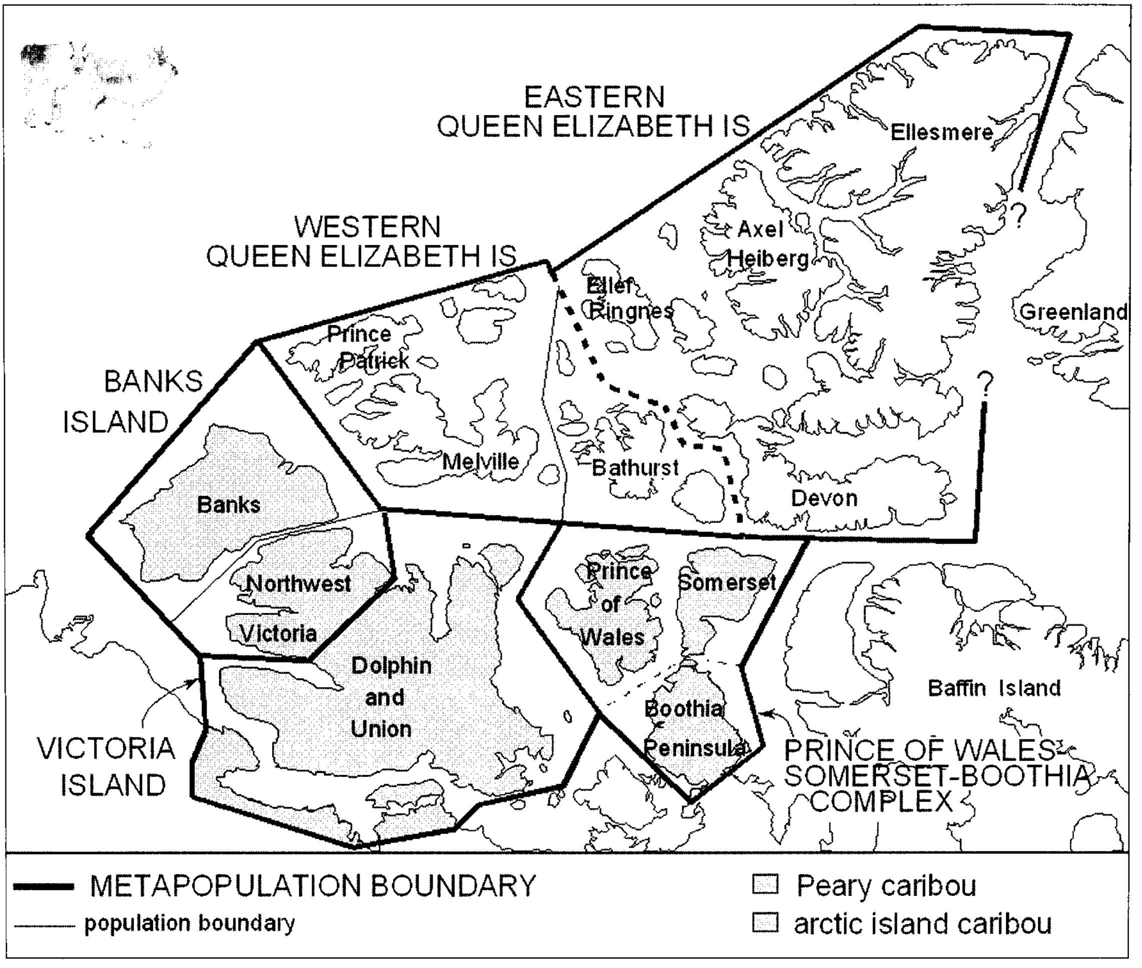

Fig. 1. Currently recognized [or established] population boundaries for Peary caribou and arctic-island caribou and their assumed metapopulation units, Canadian Arctic Archipelago, excluding the Baffin Island region and the islands in Foxe Basin and Hudson Bay.

first describe the regional diversity in caribou and the distribution and abundance of the different populations on the Arctic Islands (in this papet, Arctic Islands do not include the Baffin Island region or the islands in Foxe Basin and Hudson Bay). We discuss factors causing the declines and reason that severe winters, characterized by deep snow and freezing rain have been associated with die-offs and low productivity especially on the western Queen Elizabeth Islands. The role of hunting is based on comparing known harvests to caribou numbers but information on other factors proposed as causing declines is sparse: wolf (*Canis lupus*) predation, possible competition with muskoxen (*Ovibos moschatus*), interactions between caribou themselves, weather, the forage supply, and other human activities. We discuss management and recovery while acknowledging that this is no simple task given limitations in the state of knowledge about the ecology of caribou on the Arctic Islands and socio-economic constraints on options for recovery. We conclude with the brief assessment of the outlook for caribou on the Arctic Islands and the need to take a precautionary approach to their management.

Taxonomy and populations

Caribou on the Canadian Arctic Islands are diverse in appearance and size (Manning, 1960; Banfield, 1961; Manning & Macpherson, 1961; Thomas & Everson, 1982; Gunn & Fournier, 1996), suggesting adaptation to the Arctic's regionally different climatic and vegetation zones. The High Arctic (Queen Elizabeth Islands) and Banks, Victoria, Prince of Wales and Sometset Islands encompass five climatic regions (Maxwell, 1981) with different plant growing seasons, diversity and biomass (Edlund & Alt, 1989).

Caribou on the Arctic Islands share physical characteristics but vary in the expression across north-south and east-west clines. Those characteristics held in common include: relatively broad and short skulls, broad hooves (telative to body size), grey antler velvet, light-coloured coats, whitish underparts and absence of a pronounced flank stripe (Banfield, 1961). Those features ate most conspicuous among caribou on the Queen Elizabeth Islands although caribou on Banks and northwest Victoria islands exhibit those features more than caribou on south and east Victoria Island and to the east on Prince of Wales and Somerset islands and the Boothia Peninsula.

Currently, we recognise that diversity by defining 'Peary caribou' as those on the Queen Elizabeth Islands (Miller, 1990b: north of ca. 74°N latitude - the Queen Elizabeth Islands). We follow Miller's (1990b) definition of caribou on the southern Arctic Islands (Banks, Victoria, Prince of Wales and Somerset islands, plus some of those caribou on the Boothia Peninsula) as "atctic-island caribou".

Mitochondrial DNA sequencing (J. Eger, pers. comm.) indicates that arctic-island caribou are not intergrades between barren-ground caribou (*R. t. groenlandicus*) and Peary caribou, but are more likely the ancestral stock for Peary caribou. Given this interpretation, Peaty caribou would have evolved from barren-ground caribou as they sptead north with Wisconsin glacial retreat. The extreme arctic environment imposes intense selection, resulting in the rapid appearance of local adaptations. Previously, Manning (1960) and Banfield (1961) concluded that Peary caribou had evolved in high arctic refugia and that arctic-island caribou were the results of invading barren-ground caribou interbreeding with Peary caribou on the southern Arctic Islands.

We tentatively define seven populations (herds) based mostly on calving distribution (Fig. 1) although the definitions are based on varying levels of information. The land areas used or ice/water bodies crossed by the populations provide the basis fot their names. Seasonal abundance, calving distribution and track surveys were used to define populations on Banks, western Queen Elizabeth Islands and Prince of Wales and Somerset islands. Discrete distributions of satellite- and radio-collated caribou both during calving and rutting defined two populations on Victoria Island and two populations on Boothia Peninsula (one of which is a barren-ground caribou population). Population size and structute in the eastern Queen Elizabeth Islands is unknown.

Distribution and abundance

Peary caribou and arctic-island caribou occur on most Canadian Arctic Islands (except Baffin Island and its satellite islands, and islands in Foxe Basin and Hudson Bay). The seasonal and annual use of smaller islands may depend on densities of catibou population(s) on adjacent larger islands, seasonal migration patterns, and/or existing environmental conditions.

Historic accounts, Inuit knowledge, and aerial surveys since the 1960s, reveal fluctuations in caribou abundance, although the timing and intensity of those fluctuations vaty between and among regions. Aerial surveys, which began as recently as the 1960s, were irregular in time and atea covered, with variable levels of coverage. This hampers our ability to critically evaluate population estimates and identify trends in size (when available we report those population estimates as the mean ± one standatd error and those estimates include calves except when indicated otherwise).

Western Queen Elizabeth Islands

The western Queen Elizabeth Islands include the major islands of Melville, Bathurst and Ptince Patrick and their satellite islands (98 000 km^2). The all-time high was 24 363 caribou estimated in 1961 (Tener, 1963). The 1100 Peary caribou estimated there in 1997 (Gunn & Dragon, in prep.) is the lowest abundance tecorded since 1974 when 2666 caribou were estimated (Miller, 1990b). Bathurst and its satellite islands have been surveyed most frequently and caribou numbers have gone through two declines and one recovery. In 1961, Tener (1963) estimated there were 3608 caribou within the Bathurst Island complex but the islands were not surveyed again until 1973 and in 1974 when Millet *et al.* (1977) estimated 797 ± 174 and 266 ± 150, respectively. Twenty yeats later in 1994 Miller (1997b) estimated 3037 caribou on Bathurst and its satellite islands but then the population collapsed and in 1997, Gunn & Dragon (in prep.) estimated 76 ± 25 caribou.

Eastern Queen Elizabeth Islands

The eastern Queen Elizabeth Islands (317 000 km^2) includes the major islands of Ellesmere, Devon, Axel Heiberg (which are 60% glaciers and high mountains) and the telatively low-lying islands of Ellef Ringnes, Amund Ringnes, Cornwall, Graham, King Christian and North Kent. The only essentially complete survey of these islands was in 1961, when Tenet (1963) estimated 1482 caribou, but coverage was extremely low (<5%). Subsequently, three surveys have partially covered a few of these islands but survey areas, methods and timing varied considerably. Nonetheless, all of those surveys revealed low caribou densities (Riewe, 1973; Case & Ellsworth, 1991; Gauthier, 1996). In the 1970s, hunters from Grise Fiord reported a decline on southern Ellesmere Island (Riewe, 1973) but, during the mid 1990s, hunters report caribou returning to areas where they had formally been absent (S. Akeeagok, pers. comm.). In the 1990s, caribou surveys flown over northetn Ellesmere Island have also revealed extremely low densities. Based on June and August aerial surveys in the mid 1990s, there may be only 50-100 Peary caribou (0.1-0.3 caribou per 100 km^{-2}) within the 37 775 km^2 Ellesmete Island National Park Reserve (R. Wissink, pers. comm.).

Banks Island

On Banks Island, elders reported few caribou in the 1950s, but increasing numbers during the 1960s (Nagy *et al.,* in prep.). Results of eight island-wide surveys between 1972 and 1994 indicated a decline from 12 098 in 1972 (Urquhart, 1973) to 897 ± 151 in 1991 (Nagy *et al.,* 1996) and 558 ± 76 caribou in 1998 (J. Nagy, pers. comm.).

We believe that the clear statistical separation (P <0.05) between the estimated number of 1+ yr-old caribou on Banks Island in 1991 and 1992 vs. 1998 indicates a real decline in the size of the Banks Island caribou population between 1991 and 1998 (based on data obtained from Nagy *et al.,* 1996; J. Nagy, pers. comm.).

The 1994 estimate is neither significantly (P >0.05) lower than the 1991 and 1992 estimate, nor significantly higher (P>0.05) than the 1998 estimate (1991 and 1992, Nagy *et al*, 1996; 1994, 709 ± 128 1+ yt-old caribou and 1998, 436 ± 71 1+ yr-old caribou, J. Nagy, pers. comm.). When the 1998 survey is compared to the pooled estimate for 1991-94, however, there is a significant separation (P<0.05) between the early 1990s and 1998 (equations derived for combining independent estimates from a single population: cf. Gasaway *et al*, 1986). The nonsignificant gradient caused by the 1994 estimate tends to mask the decline in number of caribou on Banks Island. Alternatively, we regressed the four population estimates from 1991 to 1998 on year, weighting each estimate by the invetse of its variance to teflect the relative accuracy of the estimates. This analysis indicated a significant non-zero slope (P=0.026) of -77.9 animals per year. Thus, both methods indicate that the apparent continuing decline in the number of caribou on Banks Island between 1991 and 1998 is real.

Northwest Victoria Island

On northwest Victoria Island, elders reported few caribou in the 1950s, but increasing numbers during the 1960s and 1970s (Nagy *et al*, in prep.). Surveys between 1980 and 1993 indicated a decline from 4500 in 1980 to 2600 in 1987, and 100 in 1993 (Gunn, in press). During a survey in June 1994, only four caribou were observed on northwest Victoria Island (Nishi & Buckland, unpubl. data). The most tecent July 1998 survey estimate of 633 ± 81 (J. Nagy, pers comm.), may indicate that caribou on northwest Victoria Island have started to recover. However, this conclusion is uncertain because the estimate likely includes caribou from the Dolphin and Union herd as the two herds have adjacent summer ranges (Gunn & Fournier, in press). Therefore, it is tenuous to attribute the observed rate of increase entirely to births exceeding deaths. This is especially true as, even when we start with 100 caribou in 1993 or 1994 and assume no 1+ yr-old mortality, the required rate of annual increase (r) would far exceed the accepted maximum of 0.3 for the species (1993 to 1998, r = 0.446; and 1994 to 1998, r = 0.586). Only subsequent survey results and studies of marked caribou will shed light on this matter.

Dolphin and Union herd

Caribou abundance on southern and east-central Victotia Island (Dolphin and Union Herd) has fluctuated from high numbers in the eatly 1900s, to almost disappearing in the 1920s (Manning, 1960), and then increasing numbers during the 1970s and 1980s (Gunn, 1990). The first estimate was 7900 ± 1100 caribou in August 1980 (Jakimchuk & Carruthers, 1980), and a second estimate of 14 500 ± 1000 caribou was made in June 1994 (Nishi &

Buckland, unpubl. data) but neither survey covered the entire summer range. In October 1997, however, 27 800 ± 2400 caribou were estimated on their rutting area along the southern coast of Victoria Island (Nishi & Gunn, unpubl. data). Expansion of the winter range and resumption of a traditional migration (Gunn *et al*. 1997), together with recent survey data suggest that caribou have increased since 1980. However, the extent of hunting and accidental drownings during fall migration while the straits are freezing over are unknown but give rise to community concerns and reported annual rates of harvest are high in relation to the estimated population size.

Prince of Wales and Somerset Islands
The inter-island population of Prince of Wales and Somerset islands was considered to be relatively stable between 1974 and 1980 when 1+yr-old caribou were estimated to number 4540 in 1974, 3766 in 1975 and 5022 in 1980 (Fischer & Duncan, 1976; Gunn & Miller, 1983). By the late 1980s and early 1990s, hunters had reported seeing fewer caribou and more wolves on those two islands. A subsequent aerial survey in summer 1995 (Gunn & Dragon, 1998) confirmed that the caribou on those two islands had essentially disappeared. A follow-up survey in April-May 1996 confirmed the virtual absence of caribou in late winter (Miller, 1997a).

Boothia Peninsula
Inuit reported that caribou on Boothia Peninsula increased after the 1950s. Aerial surveys in 1985 and 1995 indicated that caribou numbers varied nonsignificantly from an estimated 4831 ± 543 in 1985 to 6658 ± 1728 1+yr-old caribou in 1995 (Gunn & Ashevak, 1990; Gunn & Dragon, 1998). However, interpretation of the estimates is confounded by the northward movement of barren-ground caribou onto the Boothia Peninsula (A. Gunn, unpubl. data). There are two calving areas on the northern Boothia Peninsula, one in the northwest used by arctic-island caribou and one in the northeast used by barren-ground caribou (A. Gunn, unpubl. data). The presence of both kinds of caribou on the Boothia Peninsula seriously complicates any evaluation of the status of arctic-island caribou on Boothia Peninsula.

Causes of declines
Information on factors causing declines is sparse because detection of declines must be after-the-fact and documentation of causes or contributing factors is often impossible and always too late. Diagnosis of the causes of declines has focused on the most conspicuous factors affecting caribou survival, *i.e.*, winter die-offs and hunting.

Winter weather
Most information on winter-die-offs is from the western Queen Elizabeth Islands. The climate is sufficiently severe that plants and herbivores are at the extreme edge of their range and weather has relatively intense effects. Caribou throughout that entire region experienced a ca. 50% decline over the 1973/74 winter-spring period and caribou within the Bathurst Island complex declined by *ca.* 68% (Miller *et al.*, 1977). Following the winter of 1996/97, Gunn & Dragon (in prep.) documented another major regional die-off throughout the western Queen Elizabeth Islands.

The most detailed information on the effects of severe winters is from the Bathurst Island complex where a 9-year project documented a series of favourable winters followed by a run of three severe winters (Miller, 1997b; Miller, 1998; Gunn & Dragon, in prep.). The 3037 caribou estimated on Bathurst and its satellite islands declined by *ca.* 30% in 1994/95. Widespread deep snow and icing from freezing rain in early winter and then springtime ground fast ice that restricted forage availability appears to be the sole cause of the decline. The following two severe winters caused further declines at the rates of 78% in 1995/96 and 83% in 1996/97. Overall, the estimated number of caribou within the Bathurst Island complex declined by 97% from summer 1994 to summer 1997. The time required for any recovery will be affected by at least three factors. The first is severe to near total losses of calf production and yearling recruitment in at least, 1995, 1996, and 1997. The second complication is the time lag in the numerical response of the associated wolf population. The third is the favourability of near future weather and the time interval to the next major die-off.

Since weather records began in the late 1940s, the heaviest total snowfalls in the western Queen Elizabeth Islands were in the three consecutive winters, 1994/95-1996/97 when high to extremely high rates of caribou deaths were recorded (Miller, 1997b; Miller, 1998; Gunn & Dragon, in prep.). Deep, hard-packed, windblown snow along with ice in the snow cover and ground fast ice eithet prevented the caribou from getting to the vegetation and/or forced them to expend too much enetgy in finding forage and, thus, the caribou died from extreme undernutrition (malnutrition).

The decline in Peary caribou on Bathurst Island is documented from changes in population estimates and counts of caribou carcasses. However, some hunters doubt the survey results because they encountered caribou in areas not typically used by the animals. Instead, they suggest that caribou moved away rather than died. Environmentally-forced movements occur as individual caribou seek forage elsewhere when snow and ice make foraging impossible or extremely difficult on their usual ranges (Miller, 1990a). Desperation movements are also known from huntet's reports for Banks Island caribou in the early 1950s (McEwen, 1955) and for Bathurst Island caribou in 1973-74, 1995 and 1996 (Miller *et al.,* 1977; Miller, 1998). At least for Bathurst Island, the proportion of caribou leaving Bathutst and its satellite islands is relatively small as the estimated number of carcasses explains most of the decline of estimated caribou numbers. Also satellite telemetry within the Bathurst Island complex (1993-97) showed that only one cow among six collared animals (5 cows and 1 bull) moved a relatively long distance beyond her known traditional tange in response to apparent unfavourable range-wide forage unavailability - and all six animals died (Miller, 1998; Miller, unpubl. data).

The absence of any information on caribou die-offs in the eastern Queen Elizabeth Islands may be a lack of detection and teporting more than of fact. Also, at the extremely low densities that caribou occur at in the eastern Queen Elizabeth Islands, even proportionally large declines would still involve relatively few individuals in areas rarely travelled. A die-off could easily have gone undetected. Elsewhere, die-offs have been recorded for Banks Island during severe winters in the 1950s (McEwen, 1955; Manning & Macpherson, 1958), 1970s (Morrison, 1978) and 1980s (McLean & Fraser, 1992) and marked calf crop reductions in the early 1990s (J. Nagy, pers comm.). But the influence of those die-offs on population trend was indistinguishable from other factors, and the proportions that died, while significant, were not apparently as severe as recorded on the western Queen Elizabeth Islands.

Hunting

On the southern Arctic Islands, the influence of othet factors confounds the effect of weather on population dynamics. Hunting was a factot in the declines for at least two populations on the southern Arctic Islands, especially, if not solely in the final stages of the declines (Nagy *et al.,* 1996; Gunn, in prep.). The harvest remained high while the populations declined on Banks and northwest Victoria islands. Thetefore, while weather caused caribou die-offs in some years on Banks Island, the overall decline was accelerated and prolonged by hunting (and possibly predation in the later stages of the decline) on at least Banks and northwestern Victotia islands.

Caribou were hunted on Prince of Wales and Somerset islands up to and including the time when hunters tepotted finding only a few caribou. But the effect of hunting on the near disappearance of caribou is unknown as harvest levels are not available and the last two population estimates were 15 years apart. Prince of Wales Island and western Somerset Island ate in the same climatic region as Bathurst Island. However, in summer 1995, we saw no carcasses which suggests that the caribou had disappeared before the 1994-95 severe winter.

There is no reason to believe that hunting has played an important tole in the major die-offs of Peary caribou on the western Queen Elizabeth Islands. Although no die-offs are reported for caribou on the eastern Queen Elizabeth Islands, Riewe (1973) suggested that caribou had declined locally in the Grise Fiord area due to over-harvesting.

Wolf predation

Predation by wolves could accelerate caribou declines, especially in the final stages of those declines when caribou populations are small. Predation could also prevent or temporally retard recovery of remnant caribou populations. Essentially no information exists for wolves on the Canadian Arctic Islands especially on ptedation rates and prey selection. We do not know whether wolves select caribou relative to availability and or in preference to smaller or larger prey (arctic hares, *Lepus arcticus,* and muskoxen, *Ovibos moschatus: cf.* Potvin *et al.* (1988) regarding ungulate selection by size among mainland wolves).

Wolf survival on the Arctic Islands is undoubtedly strongly tied to ungulate prey populations - both caribou and muskoxen (Miller, 1995; Miller & Reintjes, 1995) but, regional diversity across the Arctic Islands should introduce caution into extrapolating predation rates and wolf diet between or among regions. On islands where muskoxen are more abundant than caribou (e.g., Ellesmere), or areas where caribou are absent (e.g., North and East Greenland, Marquard-Petersen, 1998), muskoxen are the major prey item in the wolf's diet. Field examination of wolf scats within the Bathurst Island complex where caribou were relatively abundant to muskoxen and where both species recently have experienced major die-offs suggests that caribou and muskoxen were utilized in proportion to their availability, particularly when fed on as carrion (F. L. Miller, pers. observ.; A. Gunn & F. L. Miller, pers. observ.). It is apparent that wolves occur and den on some western Queen Elizabeth Islands where only caribou were abundant enough to support wolves year-round (e.g., Cameron Island: F. L. Miller, pers. observ.). Incidental observations between 1968 and 1978 on Bathutst Island, where both caribou and muskoxen occur showed that wolves routinely kill caribou and a single wolf had no problem killing an adult caribou or muskoxen. D. Gray (unpubl. data) described thtee successful attacks including a single wolf killing a cow; three unsuccessful attacks and five suspected wolf kills, all in an area where muskoxen far outnumbet caribou.

Densities and distributions of arctic hares are higher and more continuous on the mountainous eastern Queen Elizabeth Islands than on the western Queen Elizabeth Islands (F. L. Miller, pers. observ.). Also, arctic hate populations periodically experience lows and cyclic-like 'crashes,' so they are undependable in all years, even as secondary prey. With declines in both caribou and muskoxen, wolf predation will become mote important in the dynamics of those local ungulate populations.

Interspecific and intraspecific competition for forage

Fluctuating abundance of herbivores often raises the questions of whethet and how interspecific and intraspecific competition for forage influence population trends. Interspecific competition, usually with muskoxen, has often been implied but not demonstrated as having a role in affecting a caribou decline or preventing their recovery. Although caribou declines on Banks, northwest Victoria, Prince of Wales and Somerset islands coincided with increases in muskox numbers, caribou increases and decreases on the western Queen Elizabeth Islands and southern Victoria Island changed in synchrony with muskox numbers.

Much of the concern about caribou and muskox relationships originated from Banks Island in the early 1970s where the high coverage of herbaceous tundta and rolling terrain is particularly favourable muskox habitat. Muskoxen on Banks Island rapidly increased between 1973 and 1994 and muskoxen outnumbered caribou on average by about 44 to 1 in 1992 and about 80 to 1 in 1994 (extrapolated from Nagy *et al.,* 1996). The most recent aerial survey in July 1998 indicates that muskoxen on Banks Island have declined (J. Nagy, pets. comm.), however, the mean ratio of muskoxen to caribou has actually widened to about 101 to 1.

Although diet and habitat use is mostly dissimilar between caribou and muskoxen (e.g., Kevan, 1974; Parker & Ross, 1976; Wilkinson *et al.,* 1976; Miller *et al.,* 1977; Parker, 1978; Thomas & Edmonds, 1984), recent work by Lartet & Nagy (1997) shows that both ungulates consume willow (*Salix* spp.) and legumes. Thus, under high muskox densities or difficult foraging conditions (i.e., deep snow and/ot widespread icing), relationships may change and diet or habitat use could ovetlap.

Our ability to interpret interspecific relationships is hampered by a basic lack of understanding on telationships between summer weather, plant growth and how the hetbivores themselves interact with their forage. However, some information suggests that, at least for muskoxen, the relationship between grazing and plant growth depends on the plant species as well as grazing intensity (Raillard, 1992; Mulder & Harmsen, 1995; Smith, 1996). Almost nothing is known about the functional or numerical relationships between caribou and their forage let alone the effects of caribou on their forage.

Winter survival depends partly on winter foraging but is strongly influenced by the fat and protein teserves accumulated during the previous summer (Adamczewski *et al.,* 1993). We, however, know little about the extent to which caribou can compensate during the summer following nutritional stress during the previous wintet although compensatory growth is tecorded for other cervids (e.g., Suttie & Webster, 1995). Pregnancy rates depend on cows attaining sufficient body reserves by the end of autumn, which is influenced by the quality and quantity of summer food (Thomas, 1982).

Quantitative information on range conditions before, during and after population declines is fragmentary but it is bolstered by empirical observations. Studies are underway on Bathurst and Banks islands but they occur after-the-fact of significant caribou declines. In summer 1961, when Peary caribou numbers were high on the western Queen Elizabeth Islands, initial calf production and early calf survival was high. In summer 1973, before the 1973/74 winter die-off, calf production and early survival was also moderately good on the western Queen Elizabeth Islands. Most tecently, in the Bathurst Island complex, annual survival of 1+ yr-old caribou, initial calf production and early calf survival were all high in the year preceding the 1994/95-1996/97 winter-spring die-offs. Those favourable population dynamics for both Peary caribou and muskoxen immediately prior to the major die-offs of both species adds further support to our position that range deterioration or destruction (quality and/or quantity) did not cause or contribute to those declines.

The conspicuous factots of winter-die-offs and hunting may mask or interact with other factots. A diagnosis of a factor causing a decline is supported, but not confirmed, when amelioration or reversal of that factor is followed by recovery. However, to assume that the factors causing a decline and recovery are necessarily symmetrical is simplistic. Ecological influences on populations are rarely simple and can change over time (Holmes, 1995) and we acknowledge possible incompleteness in out diagnosis of factors causing declines for some geographic areas. We note, for example, that although thete is no current evidence for the effect of parasites such as gastro-intestinal nematodes, they are prevalent in the Dolphin and Union herd which is the only population examined for parasites (Gunn *et al*, 1991) and the nematodes depress appetite in Svalbard reindeer (Arneberg *et al.*, 1996).

Management and recovery

Peary caribou and arctic-island caribou are currently the management responsibility of the Government of the Northwest Territories which will divide in April 1999 into Nunavut and the Northwest Territories. In Nunavut, the government will have ultimate responsibility for wildlife management while the Nunavut Wildlife Management Board has responsibility for co-management, access to wildlife and ensuring that Inuit are effectively involved in wildlife management. On the western Arctic Islands, the Inuvialuit Game Council has responsibility for co-management together with the Northwest Territorial Government, which has ultimate responsibility.

Recovety actions will require the support of local people, especially from those whose lives are directly affected, and that support will not be forthcoming without their involvement in recovery planning. To this end, information on population status and factors affecting caribou have been presented and discussed at community meetings. Also, the Conservation Breeding Specialist Group (SSG/IUCN) facilitated a workshop in March 1998 to bring together co-management boards, community tepresentatives and biologists to exchange views on the declines and tecovery of caribou (Gunn *et al.*, 1998). More consultation is planned to draft implementation plans which will be part of the National Recovery Strategy produced by the Recovery of Nationally Endangeted Wildlife, Peary caribou and arctic-island Caribou Recovery Team.

The national recovery strategy's goal is to prevent extinctions and to maintain and enhance populations of Peary caribou and arctic-island caribou. The choice of activities is relatively limited as the effect of weather cannot be ameliorated, and it is not feasible on a range-wide basis to offset forage unavailability by supplementary feeding (e.g, Miller & Reintjes, 1993). The most immediate and manageable tecovety prescription is to reduce caribou death. The first action is to teduce hunting and ensure that alternate caribou sources are available as replacement meat.

Recovery actions have started with hunters taking voluntary measures to restrict their hunting. On Bathurst Island, in 1975, Inuit banned caribou hunting aftet the 1973-74 winter die-off (Freeman, 1975). In 1989, hunting for up to 25 bulls was allowed but halted in 1996 after the die-off in 1995/96. On Ellesmere Island, Inuit from Grise Fiord halted caribou hunting near their community for 10 years from 1975 to 1985 (Ferguson, 1987). More recently on Banks Island, in 1991, the Hunters' and Trappers' Committee of Sachs Harbour established an annual quota of 30 male caribou which was increased in 1992 to 36. In 1993, the Olokhaktomiut Huntets' and Trappers' Committee (Holman) agreed not to hunt caribou from northwest Victoria Island. The Government of the Northwest Territories has assisted communities in acquiring caribou from other areas as replacement meat and has increased muskox quotas to encourage the use of teadily assessable muskox populations.

If declines continue, and wolf predation has been demonstrated to be a factor, then the next action to further reduce caribou deaths could be to decrease predation. There is justification for acting without additional information, as a satisfactory level of detection is unlikely and remnant caribou populations likely would perish before evidence is obtained and corrective action is taken (whether there is an adequate number of muskoxen to support the wolves or whethet there is not). If wolf removal by translocating or hunting wolves were to be undertaken, wolves would be reduced only on those islands designated as having priority for caribou conservation. The high arctic wolf (*C. l. arctos*) warrants protection at the regional level outside of 'caribou priority areas' to help assure its persistence in the Canadian High Arctic.

Longer-term recovery actions relate to habitat and ensuting that caribou have sufficient forage. If competition with muskoxen is demonstrated to cause caribou declines or impede recoveries, accelerated muskox harvesting is an option. Habitat protection through land use regulations up to protected areas including national parks will also add a degree of security to the persistence of caribou.

Caribou as a cold desert herbivore may have similar population dynamics to a hot desert herbivore, the red kangaroo (*Macropus rufus*) whose long-term aperiodic fluctuations in population size are a mathematical consequence of unpredictable short-tetm fluctuations in weather (Caughley & Gunn, 1993). Increasing and decreasing ttends are intrinsic to the system and do not necessarily reflect special and persistent causes. If this is the case fot Peary and arctic-island caribou, then long-term management would need to ensure that hunting does not amplify natural fluctuations. That is, in the absence of human-caused climate change which cause extremes beyond those experienced by natural variation in the weather. In particular, populations that have reached a low level would not be hunted or hunted at a low rate until recovery was well established.

If, howevet, global warming (whethet a natural or human-caused change) is both possible and likely, it will influence the magnitude of and interactions between or among factots influencing caribou numbers (for example, warmer, wetter summers may increase parasite infectivity). Weather trends in the western and central Arctic are toward warmer temperatures and heavier snowfall, which are consistent with predictions for global warming (Houghton *et al.,* 1995; Maxwell, 1997).

Increased severity of winters and frequency of deep, hard-packed, windblown snow and/or heavy icing conditions is an obvious starting point for the likelihood of a cascade of changes as plants, caribou and other herbivores adjust. Those changes will be felt most on the edges of caribou distribution and where the effects of global warming are predicted to be the strongest - the western Arctic (Maxwell, 1997). Global climate change could impose some symmetry on population changes which is why we find the declines of three of the five western and central populations during the 1980s and 1990s a cause for concern. The near disappearance of caribou from Prince of Wales and Somerset islands is a strong reminder against complacency.

We suggest that Peary caribou and arctic-island caribou will be vulnerable to any persistent perturbations in their ecology. The declines of the Banks Island population and the northwest Victoria Island population, even if cessation of hunting initiates some recovery, leaves those two populations relatively small and thus vulnerable to extreme environmental changes and/or predation. The effect of environmental severity is the most marked on the western Queen Elizabeth Islands and those caribou are now at a historic low. The populations on central Victoria Island and on the Boothia Peninsula ate still numbered in the thousands and may be stable or possibly increasing. The abundance of Peary caribou in the eastern Queen Elizabeth Islands is unknown and we suspect it to be telatively low given the climate and terrain.

Management of endangered and threatened caribou populations on Canada's Arctic Islands requires implementation of tecovery actions despite gaps in our knowledge and uncertainties in diagnoses of declines. Given reduced abundance of caribou in the northwestern and western climatic regions, if population declines continue or even if theit status is unknown, we must seriously weigh the risks of inaction. Although predictions fot ecological responses to a changing climate are hedged with uncertainties and we caution against making generalities among populations, we suggest that precautionary actions such as translocation of caribou within the Arctic Islands or captive breeding be considered as potential recovery actions

- these actions requite considerable public consultation.

Ptecautionary approaches have been recommended for management of the high-latitude marine mammal ecosystem (Tynan & Demaster, 1997). The argument for the precautionary approach is strengthened for the terrestrial ecosystem by the possibility that environmental changes are underway, and by the time we have determined how wildlife populations will respond, they will already be doing so. The changes will likely exceed anything experienced over the last 400 years and thus, the past will be an insecure guide to the future.

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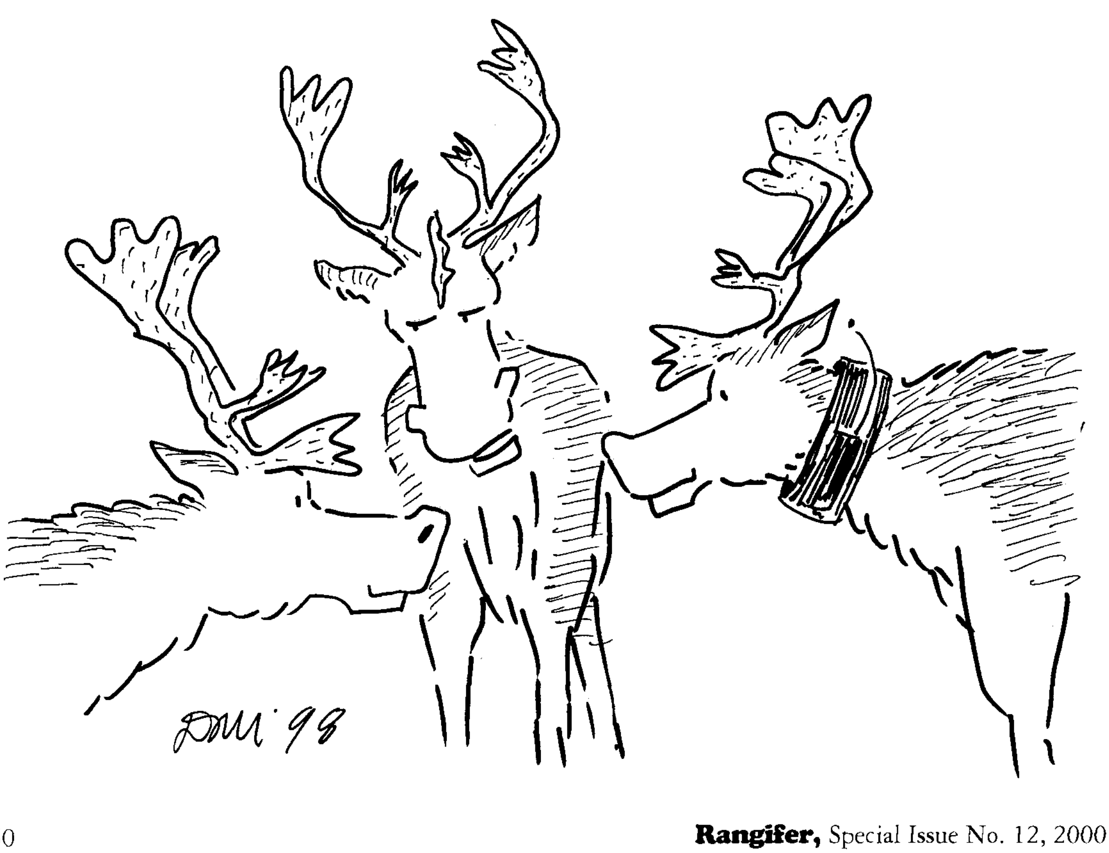
SAY SOMETHING DIRTY INTO HIS RADIOCOLLAR



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Predation rate by wolves on the Porcupine caribou herd

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Abstract: Large migratory caribou (*Rangifer tarandus*) herds in the Arctic tend to be cyclic, and population trends are mainly driven by changes in forage or weather events, not by predation. We estimated daily kill rate by wolves on adult caribou in winter, then constructed a time and space dependent model to estimate annual wolf (*Canis lupus*) predation rate (P_{annual}) on adult Porcupine caribou. Our model adjusts predation seasonally depending on caribou distribution: $P_{annual} = \Sigma K_{daily} * W * A_p(2) * D_p$.

In our model we assumed that wolves killed adult caribou at a constant rate (K_{daily}, 0.08 caribou wolf^{-1} day^{-1}) based on our studies and elsewhere; that wolf density (W) doubled to 6 wolves 1000 km$^{2-1}$ on all seasonal ranges; and that the average area occupied by the Porcupine caribou herd (PCH) in eight seasonal life cycle periods (D_p) was two times greater than the atea described by the outer boundaries of telemetry data (A_p /1000 km^2). Results from our model projected that wolves kill about 7600 adult caribou each year, regardless of herd size. The model estimated that wolves removed 5.8 to 7.4% of adult caribou as rhe herd declined in the 1990s.

Our predation rate model supports the hypothesis of Bergerud that spacing away by caribou is an effective anti-predatory strategy that greatly teduces wolf predation on adult caribou in the spring and summer.

Key words: *Canis lupus*, kill rate, *Rangifer tarandus*, Yukon.

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Introduction

Migratory barren-ground caribou (*Rangifer tarandus*) herds show wide population fluctuations that have been explained by changes in forage, climate, ptedation and harvest (as reviewed in Klein, 1991). Various researchers have pointed out the difficulty of separating interactions of forage-climate-ptedation when trying to determine the cause of change in caribou abundance (Gauthier & Theberge, 1986; Thomas, 1995; Adams *et al.*, 1995; Bergerud, 1996; National Research Council, 1997). The effects of wolf (*Canis lupus*) ptedation on migratory barren-ground caribou were poorly understood in the past, mainly because arctic wolves were migratory and difficult to follow (Kuyt, 1972; Stephenson & James, 1982). Recent studies in arctic Alaska (Dale *et al.*, 1994; Ballard *et al.*, 1997) and Canada (P. Clarkson, Government of the Northwest Territories, unpubl.; R. Hayes, unpubl.) provide new data about arctic wolf movements, range use and their killing rates on caribou. These data wete required their to develop quantitative models for estimating predation rates on migratory caribou herds.

In this paper, we present data on winter kill rate by wolves on adult caribou when Porcupine numbers were high. We construct a simple ptedation rate model that includes constants for wolf density and kill rate that are applied to changing seasonal range use and densities of caribou. We discuss why predation by wolves is not the main force limiting the size of the Porcupine herd in the 1990s.

Study area

We conducted our predation rate research in 1989 in a 14 450 km^2 study area in the Northern Richardson Mountains. Predation studies that winter were part of a latger study of wolf ecology conducted between 1987 and 1993 in the northern Yukon (R. Hayes, unpubl.).

Our study area straddled the northern boundary of the Yukon and Northwest Territories (NWT). The main study area included the Northern

Richardson Mountains and the eastern part of the Yukon Coastal Plain. The study area was bounded by the Blow and Bell Rivers to the West, the MacKenzie Delta to the East, the Rat River to the South, and the Arctic Coast to the North. The study atea included two communities in the NWT, Aklavik (population 801) and Fort MacPherson (878, Statistics Canada 1996).

We studied winter kill rate across 3 ecoregions (Oswald & Senyk, 1977): the Northern Mountains, the Coastal Plain, and Berry Creek. We have paraphrased descriptions of physiography and vegetation from Oswald and Senyk (1977). Most of the northern Yukon was a glacial refugia that now lies within the zone of continuous permafrost. The Northern Mountains Ecoregion includes the Richardson Mountains where elevations commonly exceed 1500 m above sea level (asl). Most of the Coastal Plain Ecoregion lies below 150 m asl. The eastern part of the Yukon Coastal Plain include four watersheds: the Peel, Big Fish, and Blow Rivers and Rapid Creek. The Richardson Mountains are drained by the Willow, Rat, Fish and Bell Rivers.

The Berry Creek Ecoregion forms the southwestern flank of the study atea, and ranges from flat to gently rolling terrain with uplands below 600 m asl, and valleys below 300 m asl. The area is drained by the Bell, Porcupine, Eagle and Driftwood Rivers.

Most of the study area is open tree-less tundra, except along protected valleys whete there are isolated stands of black sptuce (*Picea mariana*), white spruce (*Picea glauca*) and balsam poplar (*Populus balsamifera*). The main vegetation is sedge (*Carex* sp.) and cottongrass (*Eriophorum* sp.) tussock tundra. Dwarf birch (*Betula* sp.), willow (*Salix* sp.) and alder (*Alnus* sp.) are found on warmer sites. Cooler sites support ericaecious shrubs, willows and various forbs. Riparian spruce and balsam poplar forests are found on the Bell, Driftwood and Porcupine Rivers. Shrub birch and willow dominate most openings and the forest understory. Sedge and cottongrass tussocks dominate most poorly drained open areas.

Four ungulate species inhabit the study area: caribou, moose (*Alces alces*), Dall sheep (*Ovis dalli*) and muskoxen (*Ovibus moschatus*). The PCH increased from 135 000 caribou in 1983 to 178 000 in 1989; an annual finite rate of increase of 1.048 (λ). Between 1989 and 1992 the herd declined to about 160 000 caribou (λ= 0.965, Fancy *et al*, 1994). The PCH traditionally calves on or near the Arctic National Wildlife Refuge in northeastern Alaska, then spends the post-calving and summer periods along the Yukon Coastal Plain. The herd then migrates to various traditional wintering areas in the Richardson Mountains, Eagle Plains, Ogilivie Mountains and southern Brooks Range in Alaska. During the winter 1988-89, a large of number of Porcupine caribou winteted in out study area.

Moose density is low and most moose winter in the limited riparian forests along the Bell River (Smits, 1991). Few moose wintered in the north slope drainages, where we conducted most of predation studies. In the same area, Barichello *et al.* (1987) counted about 900 sheep in 1986. C. Smits (Yukon Fish and Wildl. Br., unpubl.) counted 157 muskoxen on the Yukon Coastal Plain in 1993, mainly to the west of our study area.

Other large predators in the study area include brown bear (*Ursus arctos*) (Nagy, 1990), black bear (*Ursus americanus*) in the taiga, lynx (*Lynx canadensis*) and wolverine (*Gulo gulo*). Arctic fox (*Alopex lagopus innuitus*) are restricted to coastal areas (Youngman, 1975). Ravens (*Corvus corax*) are the main scavengers that compete with wolves at kills.

Materials and methods

We used radiotelemetry techniques (Mech, 1974) to study predation behaviour of wolves. After we first located a wolf pack by fixed-wing aircraft, we dispatched a helicoptet (Bell 206B) and immobilized wolf pack members with Capchur (Palmer Chemical and Equip. Co., Douglasville, Ga.) equipment. Most wolves received a dose of Zoletil (A. H. Robins) at 8 mg/kg, based on an estimated average wolf weight of 40 kg. We attached conventional VHF radio-collars on wolves (Telonics, Mesa, Arizona).

We studied kill rates by monitoring the daily activities of seven radio-collared packs from 23 March to 16 April 1989 from a Maule LR7 aircraft. We defined pack size as the mean number of wolves seen in the period (Messier, 1994; Dale *et al*, 1994; 1995; Hayes *et al*, 2000). We defined kill rate as the number of caribou killed per wolf per day. The total biomass (kg) of caribou killed was used to measure consumption rates of wolves. Based on data from Skoog (1968) we estimated the live weights of adult caribou: male 107 kg, female 79 kg and unknown caribou 86 kg. We assumed the consumable biomass was 75% of caribou live weight (Ballard *et al*, 1987; 1997).

Each day, we located six wolf packs (2-6 wolves) once in the morning (9:00-12:00h). We located the

Table 1. Killing rates by wolves on caribou in our study, March and April 1989.

Pack name	Pack size	Period (days)	No. wolf days	No. of caribou killed	Total kg. killed	No. caribou killed/wolf/ day	Kg. caribou killed/wolf/ day	Kg. caribou consumed/ wolf/day
Blow River	12	25	300	9	776	0.03	2.59	1.94
Bell River	2	7	14	3	274	0.21	19.57	14.68
Blow R. 450	3	6	18	2	195	0.11	10.83	8.13
Rat River	6	25	150	4	406	0.03	2.71	2.03
Rat River II	3	24	72	1	109	0.01	1.51	1.14
Trail River	3	14	42	2	195	0.05	4.64	3.48
Two Ocean	2	19	38	2	172	0.05	4.53	3.39

12 member Blow River pack twice a day, in the morning and evening (18:00 to 22:00 h). We compared kill rate for morning-only sightings of Blow River wolves, and for the combined motning and evening to test for temporal bias in our ability to detect caribou kills by locating othet packs once daily.

Most packs traveled in the north slope drainages where snow conditions were heavily windblown in 1989. Wolves and their prey carcasses were difficult to see because of the contrasting mosaic of open ground and snow fields. Snow was usually too wind-packed to backtrack wolves to detetmine their activities between location points. We located radio-collared wolves, then systematically searched for any kills in a 2-3 km^2 area, until we eithet found kills or we were confident wolves had not made a kill nearby.

We estimated annual *predation rate* as the proportion of adult Porcupine caribou killed by wolves. To determine the rate of wolf predation on the Porcupine herd we needed a model that was based on reasonable ecological assumptions about wolves and caribou. From wolf surveys in the northern Yukon (R. Hayes *et al*, unpubl.) and in other parts of the PCH range (Stephenson, 1994; Carrol, 1994), we estimated a mean density of about 3 wolves/ 1000 km^2, giving a population of 725 wolves in the entire range of the herd. Not all wolves have caribou available to them each year, and the numbet must vary with the area caribou occupy during different phases of their annual life cycle (*e.g.,* spring migration, calving, winter). This means that we cannot estimate predation rate by simply applying a fixed kill daily rate to the entire wolf population. To account for changing distributions of caribou and wolves, both in space and time, we constructed the model for estimating annual predation rate (P_{annual}):

$$P_{annual} = \Sigma K_{daily} * W * A_p(2) * D_p.$$

We assumed that wolves killed adult caribou at a constant rate (K_{daily}); that wolf density (W) doubled to 6 wolves per 1000 km^2 on all seasonal ranges; and that the average area occupied by the PCH each yeat in eight seasonal life cycle periods (D_p, see Table 2) was twice as latge as the average area described by the outer boundaries of satellite telemetry data (A_p /1000 km^2; Int. Porcupine Caribou Board 1993).

Results

Kill rate by wolves

We followed the daily activities of seven wolf packs for 17.1 ± 3.1 (standard error of the mean) days (Table 1). Traveling pack size was 4.4 ± 1.4, ranging from 2 to 12 wolves per pack. We found 23 wolf-killed caribou and we examined 13 carcasses in situ. All were adults (8M, 5F). The mean age of killed catibou was 6.1 ± 0.7 years-old. The lowest kill rate was for wolves in the Rat River II pack (Table 1) which scavenged from many hunter kills in the area. After excluding this pack, we estimated the wolf kill rate was 0.08 ± 0.03 caribou per day per wolf; or 7.5 ± 2.7 kg of caribou killed per wolf per day. Wolves consumed 5.6 ± 2.0 kg caribou each day in winter.

We did not find a difference in the numbet of kills seen for morning-only sightings of Blow River wolves compared to the combined motning and evening sightings (n=9 kills, 0.36 caribou per pack per day). We conclude that twice daily locations did not improve our ability to detect kills made by study packs.

Predation rate by wolves

Based on a daily kill rate of 0.08 adult caribou (K_{daily}), our model projected that wolves killed 7600 adult catibou from the Porcupine herd each year. About 84% of the adults were killed during fall and

Table 2. Variables and values used in modeling annual wolf predarion rare on Porcupine caribou herd. Values for D_p and A_p were provided by Inr. Porcupine Caribou Board (1993).

Caribou life cycle Period	D_p No. of Days	Mean Area[1]	A_p Area of Available Caribou[1]	W Wolf Density[2]	K_{daily} Daily Kill Rate by Wolves on Caribou
1. Late Winter	120	25.9	51.8	6	0.08
2. Spring	62	27.4	54.8	6	0.08
3. Calving	11	8.8	17.6	6	0.08
4. Post Calving	22	7.5	15	6	0.08
5. Early Summer	16	3.4	6.8	6	0.08
6. Mid Summer	22	5.99	11.98	6	0.08
7. Late Summer and Fall Migration	62	12.8	25.6	6	0.08
8. Rut and Late Fall	50	37.1	74.2	6	0.08

[1] in 1000 km^2 units.
[2] number of wolves per 1000 km^2.

winter (Table 2, Fig. 1) when caribou use the largest areas, allowing more wolves to concentrate on fall and winter range. The remaining 16% of adults were taken in spring and fall when the herd's range is substantially compressed, and their availability to wolves is lowest (Table 2, Fig. 1).

Because our predation model does not depend on herd size, we applied it to Porcupine census data in 1992, 1994 and 1998. Each year the herd was censused with photo counts in July (D. Russell, unpubl.). The percent calves was annually estimated in March (D. Cooley, Yukon Fish and Wildl. Br., unpubl.). Our model estimated that wolves removed 5.8% of adults in 1992 when herd size was 160 000; 6.3% in 1994 when herd size was 152 000; and 7.4% when herd size fell to 129 000 in 1998.

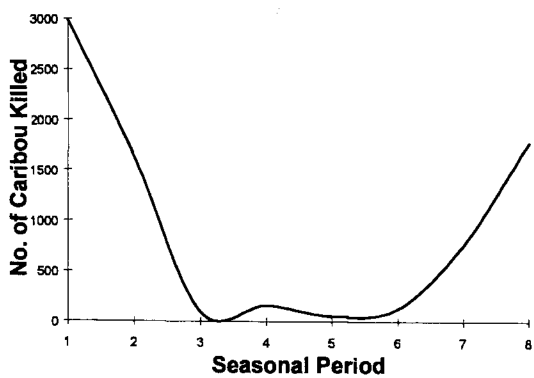

Fig. 1. Seasonal predation rate by wolves on PCH based on model. Seasonal periods correspond with numbers shown on Table 2.

Discussion

Kill rate by wolves

The daily kill rate of our study wolves was similar to caribou-killing wolves in Alaska (0.08 caribou per wolf per day, Dale *et al.,* 1994) and Northwest Territories (0.05 caribou, P. Clarkson, unpubl.), although out pack kill rates were more variable. We studied wolf kill rate in mainly small packs of 2-3 wolves (Table 1). Hayes *et al.* (2000) found wolves in small packs had much wider variation in kill rate of moose compared to larger packs, which could also explain our caribou predation data.

The mean daily consumption rate was 4.9 kg of caribou per wolf, above the range of 1.7 to 4.0 kg required for survival (Mech, 1977; Thurber & Peterson, 1993) and above the 3.2 kg required for reproduction (Mech, 1977). Similar consumption rates were recorded for arctic wolves in northwestern Alaska (5.3 kg of moose and caribou, Ballard *et al.,* 1997) and NWT (4.4 kg, P. Clarkson, unpubl.).

Previous estimates of wolf consumption rate are probably higher than actual, because biologists usually assumed that wolves eat all available biomass of their kills (Carbyn, 1983; Messier & Crete, 1985; Ballard *et al.,* 1987; Fuller, 1989; Hayes *et al.,* 1991; Thurber & Peterson, 1993; Dale *et al.,* 1995). Hayes *et al.* (2000) adjusted kill rates to account for raven scavenging, estimating that ravens can remove up to half of consumable moose biomass from small wolf packs (2-3 wolves). Five of our study packs were small and we commonly saw ravens at caribou kills. However, we agree with Ballard *et al.* (1997) who estimated that wolves lost less of their caribou kills to tavens because wolves can consume caribou carcasses more rapidly than they can consume moose - leaving less caribou biomass for scavengers.

By back-tracking wolf trails, Dale *et al.* (1994) increased their estimate of kill rate because wolves killed then left the caribou carcasses before the next radio location. Hayes *et al.* (2000) underestimated kill rate by wolves on woodland catibou by locating packs once daily, and recommended back-tracking whenever possible. Clarkson and Liepens (unpubl. data) believed that arctic wolves remained close to their kills in order to protect them from other migratoty packs, therefore, back-tracking was not useful in tundra areas. Without backtracking we recorded a similar kill rate as Dale *et al.* (1994) did with backtracking. We had the advantage of studying small migratory packs that traveled in open tundra areas, which probably remained near kills for defense purposes (P. Clarkson, unpubl. data). Increasing our observation rate to each morning and evening did not increase our ability to detect caribou kills made by a pack of 12 wolves. Despite the windblown conditions, we teasonably estimated kill rate of our study packs on Porcupine caribou winter range.

Predation rate model

We verified our model assumptions by looking at caribou and wolf studies elsewhere. Our study, Dale *et al.* (1994) and P. Clarkson (unpubl.) reported kill rates of 0.05-0.08 caribou wolf^{-1} day^{-1}. Thus, we believe that substantial changes to the value for variable K_{daily} are not justified. Out study, Patker (1973), Kuyt (1972), Thomas (1995) and Clarkson & Liepins (unpubl.) all found a two-fold increase in wolf density on winter range. We had substantial telemetry data to evaluate seasonal PCH distribution for over twenty years. Thus, we could not justify increasing the areas of available caribou more than two-fold. Our model does not incorporate changing vulnerability to predation, which Mech *et al.* (1998) found was an important function of wolf predation rate on the Denali caribou herd.

We next examined how our predation rate fit current knowledge of Porcupine caribou ecology. Fancy *et al.* (1994) found mean adult mortality rate for ≥3-year-old caribou was 15% for females and 17% for males. Using our 1992 wolf predation rate estimate of 5.8%, our model projects that wolves were responsible for about 1/3 of the adult mortality in the early 1990s.

Accotding to Fancy *et al.* (1994) and Walsh *et al.* (1995) the growth of the PCH is most sensitive to the survival rates of females three years and older, followed by production and survival rates of calves. Fancy *et al.* (1994) speculated that the decline of the PCH after 1989 was related to a combination of low parturition rate of ≥3-year-old females in 1991, and lowered calf survival in March 1992. Using stochastic modeling, Walsh *et al.* (1995) showed that a survival rate decline of about 3% among adult females or 4% among calves could be enough to cause the Porcupine herd to decline. Our model projects that wolves would have to nearly double their predation rate to account for an additional 3% decline in adult female survival.

Using different predation rate models, Dale *et al.* (1994) and Ballard *et al.* (1997) also determined that predation by wolves was not the main factor limiting catibou in northwestern Alaska. Ballard *et al.* (1997) estimated that wolves annually removed about 6-7% of the Western Arctic caribou herd.

Predation by wolves is an important factor limiting smaller caribou herds in Canada and Alaska (Gasaway *et al*, 1983; Bergerud & Elliot, 1986; Edmonds, 1988; Seip, 1992; Hayes & Gunson, 1995; Mech *et al*, 1998). Cutrent knowledge suggests wolf predation acts in a depensatory fashion (i.e., it increases as herd size declined) where caribou are secondary prey to wolves that rely primarily on moose. Wolf predation does not appear to be the main cause of population change for large migratory caribou herds in the arctic (Messier, 1995; Crete & Huot, 1993; Thomas, 1995). Large migratory caribou herds tend to be cyclic, and previous population trends have been linked to changes in forage or weather events (Crete & Huot, 1993; Fancy *et al*, 1994; Messier, 1995).

The low effect of predation by wolves is supported by the hypothesis of Bergerud (1974), who has argued that the migratory behavior of caribou evolved as a predator-avoidance strategy. Bergerud (1992) believes that migratory caribou calve on small remote areas to 'space away' from predators. By doing so, they can flood a large number of young in a small area where the per capita risk to being killed by any predator is lowest.

Our model does not estimate predation rate on calves, howevet, it does supports that 'spacing away' is also an effective anti-predatory strategy of adult caribou (Bergerud, 1974; 1992; Thomas, 1995). In late spring and summer, Porcupine caribou concentrate on the coastal plain of Alaska and Yukon, whete they occupy the smallest seasonal tange, thereby reducing their exposure to predators (Table 2). Adult wolves are limited in their ability to travel there due to their requirement to feed pups at dens (Thomas, 1995; R. Hayes, unpubl. data).

Ftyxell *et al.* (1988) developed a similar time-space dependent model for estimating African lion (*Panthera leo*) predation rate on migratory wildebeeste (*Connochaetes taurinus*) that supports the 'spacing-away' advantage. They concluded that large migratory wildebeeste herds could not be regulated by lions, mainly because lions could not maintain contact with herds year-round, reducing annual predation rate.

We believe that the variables of our model are useful at various Porcupine caribou herd sizes because: 1) the area that caribou used seasonally was similar in the 1970s when the herd was about 100 000 caribou (Le Resche, 1975); and 2) as the herd declines we should not expect a strong density-dependent change in the wolf functional response (Dale *et al.,* 1994). Thus, wolf kill rate should remain constant. Also, taiga wolves can readily switch to low density moose prey to survive (Ballard *et al.,* 1997) reducing the negative effect of declining caribou abundance on wolf numerical response.

Data quality

Although our estimate of mean daily kill rate was similar to other studies, it was bounded by a wide standatd error. This could be because the sample size of packs was small, or the kill rate was undetestimated for some packs due to terrain or weather constraints.

We acknowledge some shortcomings with our predation rate model. Although the model fits current indices of the PCH, components of the model need furthet validation. First, we assumed that K_{daily} in the summer period was the same as for winter. Wolves are reported to surplus kill neonatal and adult caribou (Miller *et al.,* 1983; 1988; C. Gardner, Alaska Dep. Fish and Game, pers. comm.). The effect of wolf predation rate on changing calf recruitment rates of the Porcupine herd remains unknown, and we did not include this important population process in our model.

Second, the estimates of the area that caribou occupy seasonally are based on radiotelemetry locations. There is a declining gradient outward from these areas where low density caribou will still be available to wolves. We estimated caribou-available areas to be twice the areas described by caribou telemetry, but the area might be even larger. However, we needed to increase the caribou available area in our model by five-fold before wolves took 10% or more of the adults. Thitd, arctic wolves show strong preference for caribou, and wolves probably continue to search for caribou even when caribou appear to be absent (P. Clarkson, pers. comm.). If PCH wolves behave this way, then our estimates of seasonal predation rates could also be low.

Nevertheless, our results are consistent with othet arctic wolf studies that found a uniquely migratory behaviour among wolves associated with barren-ground caribou, naturally low wolf densities, a preference for caribou prey, and moderate daily kill rates by wolves. The model we present is based on detailed knowledge of a dynamic seasonal range use pattetn by Porcupine caribou that was available only after decades of radiotelemetry studies. Future predation research should be conducted to investigate whethet the assumptions of our model hold in this period of declined herd size.

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Genetic relationships of three Yukon caribou herds determined by DNA typing

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Abstract: In this paper we examine genetic relationships of caribou (*Rangifer tarandus caribou*) in the Aishihik, Chisana, and Wolf Lake hetds in the Yukon using DNA fingerprinting. The assignment test used in this analysis showed that the caribou herds were distinct. This finding is consistent with movement data from radio-collared caribou which demonstrares home range fidelity. We found a high level of heterozygosity and a genetic basis for population boundaries. DNA fingerprinting may provide an effective means to compare ecological and genetic relationships.

Key words: DNA fingerprinting, home range, microsatellite, woodland caribou.

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Introduction

Comprehensive studies of caribou (*Rangifer tarandus caribou*) have been ongoing in the Yukon since 1980. The objective of these studies is to inventory all herds by identifying each population's total and seasonal ranges, secure reliable population size estimates, and monitor population trends using sex/age composition count surveys. From 1980 to 1998, 178 population counts were conducted on 17 of 22 herds, and 289 relocation flights were flown to provide relocation contacts for 485 radio-collared caribou (Farnell *et al.,* 1998). Since 1995, whole blood samples were collected from 228 caribou captured and handled for radio-telemetry studies of 13 herds. These samples allow the opportunity to examine the genetic relationships between herds.

Over the past 18 years, the data on movements have shown that caribou have strong fidelity to discrete home ranges (Fig. 1) (Farnell & Russell, 1984; Farnell & MacDonald, 1988; 1989; 1990; Farnell *et al.,* 1991; 1996; 1998; Kuzyk & Farnell, in prep). Caribou herds in the Yukon conform to typical patterns of distribution fot woodland/mountain caribou, being highly dispersed during summer and clumped during winter. On the basis of these observations wildlife managers in Yukon have defined a caribou herd as those caribou sharing a common winter range (Farnell & Russell, 1984). Historic and present day distributions of migratory caribou are known to periodically overlap with sedentaty caribou herds during winter (Boertje & Gardner, 1996; Fancy *et al.* 1994). Despite frequent overlap, radio-collared individuals have strong herd fidelity (Farnell & Russell, 1984). Consequently, caribou herds are managed as discrete populations. The geographic boundaries established from surveys have facilitated management planning on a herd basis but genetic telationships of these populations remain to be established.

Within this management framework there is concern for the viability of small caribou populations. There may be a genetic basement number below which a population cannot persist for very long because of the effects of inbreeding and loss of heterozygosity (Grumbine, 1992). This could reduce reproduction and survival capabilities of individuals and lead to extinction at the population (i.e. herd) level from demographic, environmental, and/or catastrophic uncertainties. To test this prediction, it is necessary to determine whether there is gene flow between adjacent populations or genetic variation within small populations.

The use of DNA fingerprinting using microsatellite loci allows measurement of variation within and among populations and can distinguish sepatate populations at the genetic level (Kushny *et al.,* 1996; Paetkau *et al.,* 1995). This could improve our understanding of potential recent and historical

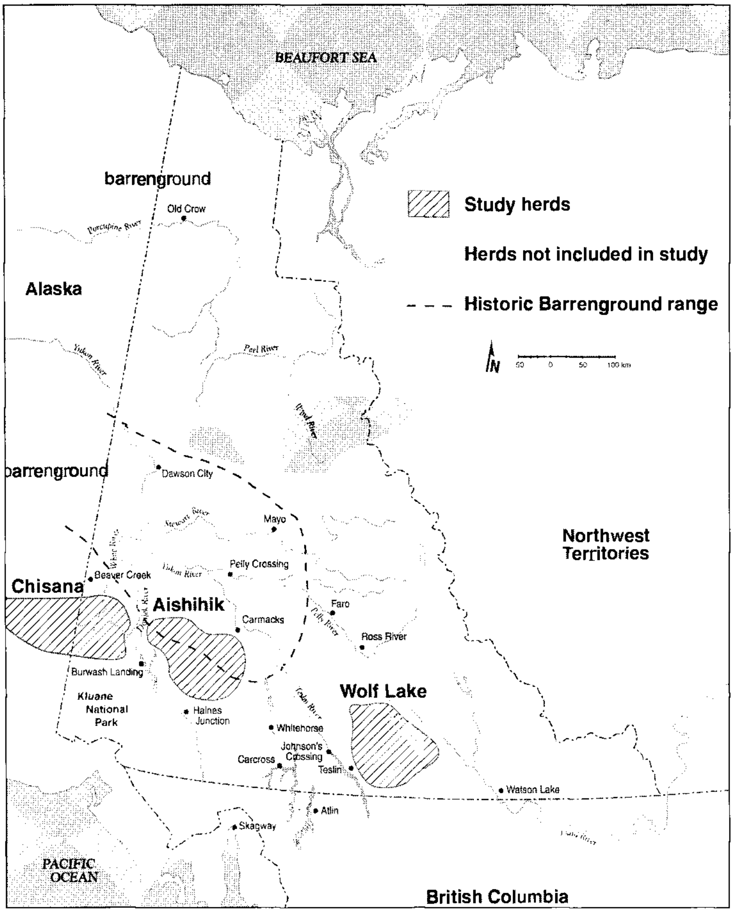

Fig. 1. Geographic distribution of barrenground and woodland caribou herds in Yukon as determined from inventory studies carried out between 1980 and 1998.

migrations between populations and therefore test our conceptual framework of population identity. DNA fingerprinting could furthermore provide a measure of individual herd heterozygosity and therefore provide insight into herd genetic variation and determination of minimum viable population sizes.

We describe the use of microsatellite markers to describe the genetic telationship between three woodland catibou herds that show varying degrees of geographic separation and population trends. Sample sizes were as follows: Aishihik (n=32), Chisana (n=22), Wolf Lake (n=31). All three study herds are located in southern Yukon, and their boundaries do not overlap (Fig. 1). No movement between hetds has been documented, but there are other caribou herds located between them. The herds exhibited a variety of population trends. The Aishihik herd increased at r=0.12 (from 750 in 1993 to 1200 in 1997), the Chisana herd declined at r=-0.14 (from 2000 in 1989 to 500 in 1997), and the Wolf Lake herd remained relatively stable at r=0.03 (from 1200 in 1993 to 1400 in 1998) (data on file).

Materials and methods

Whole blood samples (approximately 10ml) were collected from caribou when they were radio-collared. The red blood cells were lysed by repeated washings with 1 X ACK (0.155 M NH_4Cl, 10 mM $KHCO_3$, 1 mM EDTA, pH 7.4). DNA was isolated from white blood cells using the QIAamp Blood protocol (QIAGEN Inc.). Each DNA sample was amplified at six microsatellite loci (RT6, RT7, RT9, RT13, RT24, and RT27; Wilson *et al.,* 1997) using the polymerase chain reaction (PCR) . PCR conditions for a Perkin-Elmer 9600 thermal cyclet were 1 min at 94 °C, followed by three cycles of 30 s at 94 °C, 20 s at 54 °C and 5 s at 72 °C, followed by 33 cycles of 15 s at 94 °C, 20 s at 54 °C and 1 s at 72 °C, and then 30 s at 72 °C. One primer from each pair was fluorescently labelled. Allele sizes for each locus were determined by analysis of the PCR products after polyacrylamide gel electrophoresis on a model 373A Automated Sequencer (PE Biosystems), using "Genescan™ 2.0.2" and "Genotyper® 2.0" software.

The identified genotypes were used to measure the genetic diversity within herds and, subsequently, the relationships among herds. The genetic diversity within a herd was measured by the number of alleles per locus, the degree of heterozygosity, and the probability of identity. Heterozygosity is the proportion of a population exhibiting two different alleles at a given locus. The probability of identity is the probability that two randomly chosen individuals are genetically identical. Heterozygosity (H) and probability of identity at a single locus (P_{id}) were calculated by the following formulae:

$H = 1-\sum p_i^2$ and $P_{id} = \sum p_i^4 + \sum\sum(2p_ip_j)^2$, respectively, where p_i and p_j are the frequencies of the i^{th} and j^{th} allele. The probability of identity over all loci is the product of the probabilities of identity at each locus.

Genetic distances between herds were calculated by D_{LR} (as described by Paetkau *et al.,* 1997). In addition, an assignment test, which assigns each individual to the herd in which its genotype is most likely to occur, was performed to determine the distinctness of each herd. These data were then compared to herd home range boundaries determined from radio-collar movement data. The method for these calculations is available at the following website:
http://www.biology.ualberta.ca/jbrzusto/Doh.html.

Results

The measures of genetic diversity show that each herd exhibited a high degree of variation (Table 1). The number of alleles per locus ranged from 7.5 to 9.3. For the hetds examined, heterozygosities ranged from approximately 74% to 82%. The probabilities of identity range from three in 10 million to one in 100 million.

Table 1. Measures of genetic diversity: heterozygosity, probability of identity and mean number of alleles per locus for three Yukon caribou herds.

Caribou Herd	Sample Size	Mean Number of Alleles	Hetero-zygosity %	Probability of Identity
Aishihik	32	7.50	74.1	3.8×10^{-7}
Chisana	22	8.00	81.6	1.1×10^{-8}
Wolf Lake	29	9.33	82.3	1.4×10^{-8}

Discussion

The genetic distances calculated by D_{LR} mean that, based on their genotypes, caribou from one population ate that many times more likely to belong to their own population than to the other population. The genetic distances between the three caribou herds ranged from 2.2 to 3.2 (Table 2).

The genetic distances between the three herds were quite similar, despite their different geographic separation. The shottest genetic distance was between Chisana and Wolf Lake, which ate the two most geographically distant herds. These results suggest that geographic distance between herds does not influence genetic relationships.

The results of the assignment test show that the three caribou herds are virtually distinct (Fig. 2). That is, almost all of the caribou assign to their respective herds; an average of only 8% of individuals were not assignable to their herds. Assignment tests have shown similar results in other species (Wasser & Strobeck, 1998).

The caribou that do not assign to the expected populations could be migrants or offspring of migrants. An alternative explanation may be that, originally, these herds were all related and they are not yet completely differentiated. Analysis of these samples at an increased number of loci may resolve this issue. Analyses of additional samples from the herds examined and from additional hetds from the same area may provide a better understanding of caribou population structure in Yukon.

Conclusion

These data show that there is a genetic basis for population boundaries defined from seasonal movement data for adjacent and separate caribou herds, and so far justifies our management framework. Future sampling will provide more rigor to this analysis by examining genetic variability and possible patterns of gene flow between populations located at closer geographical proximity to each other.

At its present population level and trend the Chisana herd has a high level of heterozygosity and is presently not likely to be threatened by the detrimental effects of inbreeding (subject to lowered reproduction and survival as a result of lowered genetic variation). Further monitoring of genetic variability in the Chisana herd over time and increased sampling of other small caribou herds (<200 individuals) could provide insight into the potential level at which a genetic basement population may occur.

DNA fingerprinting using microsatellite analysis is an effective means of comparing ecological and genetic perspectives. These results constitute the first step needed to advance our understanding to the broadet implications of genetic structure of cari-

Table 2. Genetic distances between three Yukon caribou herds.

	Aishihik	Chisana	Wolf Lake
Aishihik	0		
Chisana	2.9	0	
Wolf Lake	3.2	2.2	0

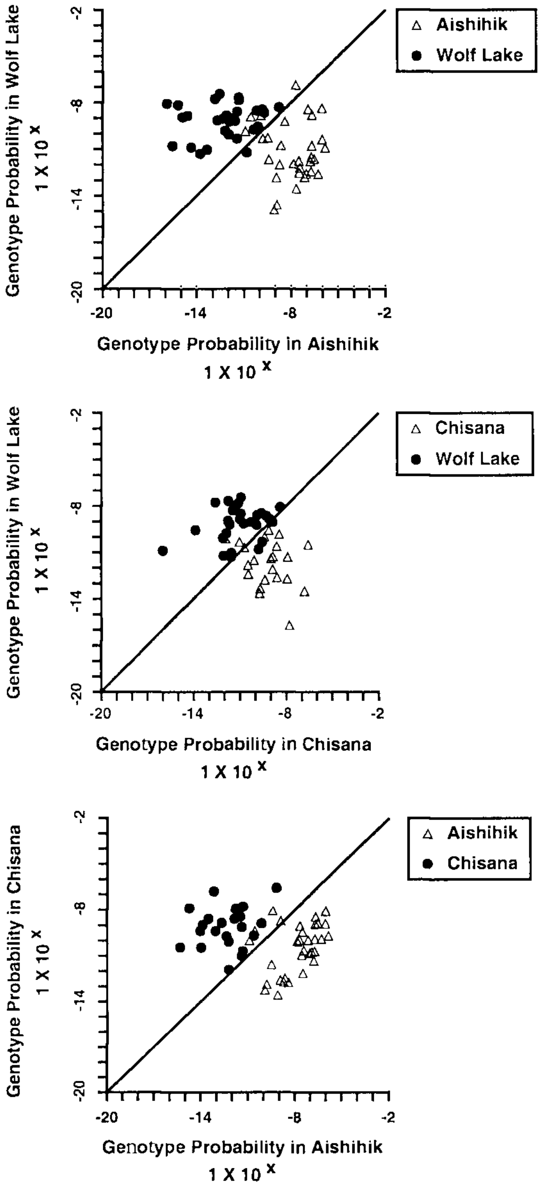

Fig. 2. Results of assignment tests fot pairwise comparisons of each of three caribou herds. (An individual occurring on the diagonal has an equal probability of occurring in each population).

bou herds. With more data it may be possible to identify a "population of origin" for caribou samples.

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Reproductive performance of female Alaskan caribou

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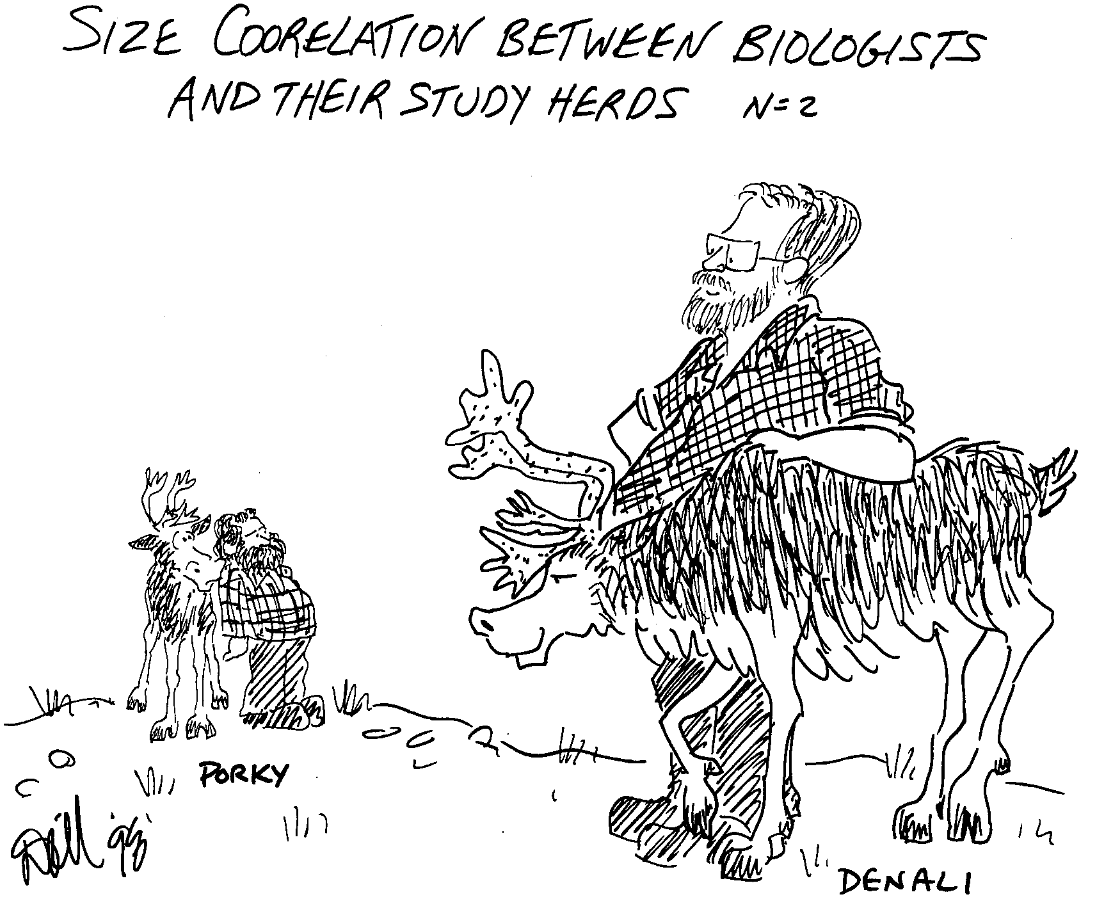
Abstract: We examined the reproductive performance of female barrenground caribou (*Rangifer tarandus*), in relation to age, physical condition and reproductive experience for 9 consecutive years (1987-95) at Denali National Park, Alaska, during a period of wide variation in winter snowfall. Caribou in Denali differed from othet populations whete reproductive performance has been investigated in that they occut at low densities ($\leq$0.3/km^2) and experience high losses of young to ptedation. Average annual natality rates increased from 27% for 2-year-olds ro 100% for 7 year-olds, remained high for 7-13-year-olds (98%), then declined for females $\geq$14. Females $\geq$2 years old that failed to reproduce were primarily sexually immature (76%). Reproductive pauses of sexually mature females were rare (6%) and occurred predominantly to young (3-6 years old) and old ($\geq$14 years old) females. Natality incteased significanrly ($P<0.05$) wirh body mass of 10-month-old females weighed 6 months prior to the autumn breeding season, and of females >1 year old weighed during autumn (late September-early November). Natality fot 2-, 3-, 4-, and 6-year-olds declined significantly with increasing late winter snowfall (February-May) during the winter prior to breeding. Because influences of weather on productivity were limited to young age-classes and adverse weather also decreased recruitment, population productivity was affected more by changes in population age-structure, than by age-specific producrivity.



Abstract: The Eight North American Caribou Workshop, Whitehorse, Canada, 20-24 April, 1998.

Sex, age, and condition of wolf-killed caribou

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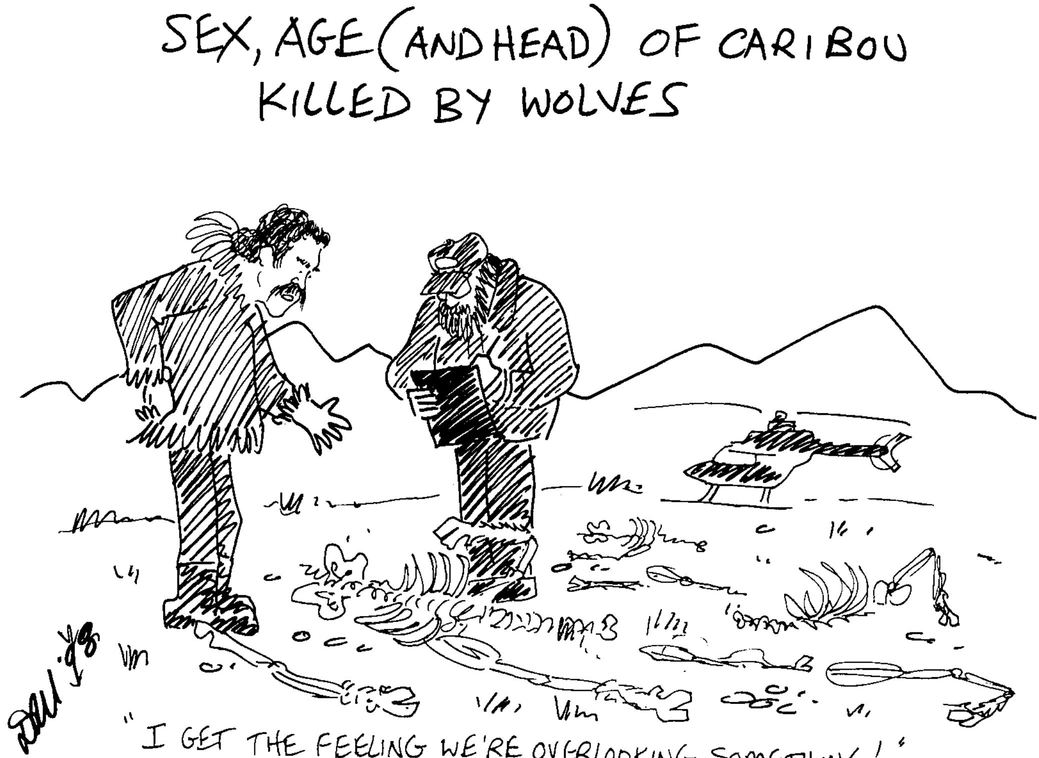
Abstract: We compare rhe sex, age, and condition of caribou killed by wolves with caribou killed by hunters, and estimates of herd composition. These comparisons provide insight into selectivity and predarion characteristics of wolves on barren-ground caribou. We investigated 205 kills after wolves had left the kill site and examined 65 hunter killed caribou. Of 124 known-sex kills, males comprised 45% of caribou killed by wolves. Ageclass could be determined for 171 caribou kills, of which calves comprised 17% of wolf-killed caribou. Herd composition surveys indicated available proportions of 57% cows, 14% calves, and 29% bulls. Although confidence intervals were wide, selection by wolves for calves and adult males was suggested. Sex of wolf-kills did not vary by season (March *vs.* November) in this study, although the test was weak due to small sample sizes. Hunters killed primarily adult females and the huntet kill may therefore reasonably approximate the availability of full-grown (>3) adult females. Wolves killed proportionally more old (ages ≥8) caribou than in the hunter-killed sample (2X2 Chi-square=6.58, P=0.010). While the old vs. young categorization is arbitrary, chi-square analyses were still significant if the cut off age was moved one year in either direction. This pattern of selectivity is consistent with that reported for other species. The comparison of physical characteristics by cause of death was limited to adult females because sample sizes for bulls and calves were insufficient. Sample sizes for wolf-killed adult females ranged from 10-12 resulring in low power of statistical comparisons. Only mean diastema length varied significantly by cause of death (P=0.031). However, means for all parameters were consistently lower for wolf-killed caribou suggesting increased vulnerability of small individuals to wolves. Trends were identical fot full-grown females (>3 years of age). Wolf-killed adult female caribou had significantly lowet marrow fat ($\bar{x}$=67%, s=0.319, n=12) than hunter-killed adult females ($\bar{x}$=90%, s=0.048, n=52). Three of rhe wolf-kills had very low marrow fat (<25%) that likely had a strong influence on means. None of the 52 hunter-killed adult females had less than 30% marrow fat. Sample sizes are small and controls only roughly reflect availability. Nonetheless, this analysis suggests that selectivity by wolves among caribou sex and age classes is similar to that shown for other ungulates.



The Western Arctic caribou herd: current status and management issues

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Abstract: As of July 1996, the Western Arctic herd numbered approximately 463 000 caribou (*Rangifer tarandus*). This herd last peaked at 243 000 caribou in 1970, then declined to about 75 000 by 1976. From 1976 to 1990, this herd grew approximately 13% annually. Since 1990, growth has been about 2% annually. Annual indices of recruitment and adult cow mortality collected since the eatly 1980s appear consistent with this population trend. Since 1990, annual subsistence and sport harvests have been roughly 20 000 and 1000-3000 caribou, respectively. Biological issues currently facing the Western Arctic herd include: 1) body condition and its relationship to instances of severe, localized fall and winter mortality; 2) potential effects of disease and environmental contamination on caribou and people who subsist on them; and 3) potential range deterioration. Social issues include: 1) mutual trust and exchange of information between managers and users; 2) diverse, complex and sometimes competing demands among subsistence users, sporr hunters, commercial operators and nonconsumptive users of Western Arctic caribou; 3) expansion of caribou into reindeer ranges; 4) conflicts with muskoxen management; and 5) antlet sales and a proposed commercial harvest of caribou for meat. Technical issues center on monitoring a population this large over irs expansive range. The political issue of dual state-federal management of wildlife in Alaska overlays all biological and social considerations. Comanagement is cutrently being explored to meld biological, social and political aspects of managing the Western Arctic herd.

Effects of recent climate warming on caribou habitat and calf survival

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Abstract: Recent investigarions of global climare change have focused on temperature, gas and nutrient flux, and vegetation, microbial, and invertebrate response. Potential effects of climate change on tetrestrial vertebrates have been the subject of much speculation, but quantitative assessment has been limited by the lack of long term habitat and population data. As the dominant large herbivore in arctic regions, migratory barren-ground caribou (*Rangifer tarandus granti*) are likely to respond to global climatic changes that affect temporal and spatial variability of their forage resources. The Normalized Difference Vegetation Index (NDVI) derived from the Advanced Very High Resolution Radiometet (AVHRR) on board National Oceanic and Atmospheric Administration (NOAA) polar orbiting satellites offers the opportunity to assess large scale habitat conditions for caribou and other vertebrates during the growing season. Here we present a predictive equation relating early survival of caribou calves and NDVI at calving and the post-calving rate of increase in NDVI during 1985-1996. Because small changes (~5%) in survival of caribou calves can determine whether a population grows or declines, the relationship between calf survival and vegetation biomass and rate of vegetation growth may be used to predict effects of habitat restriction on caribou populations.

Responses of the Aishihik caribou herd to reduced wolf predation and harvest restrictions: an adaptive management experiment in the Yukon

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Abstract: Since 1992, we have studied population responses of woodland caribou (*Rangifer tarandus caribou*) moose (*Alces alces*) and Dall sheep (*Ovis dalli*) to a reducrion of wolf (*Canis lupis*) numbers and harvest testrictions in the Aishihik area of southwest Yukon. We annually reduced wolf numbers in a 20 000 km^2 area to about 20% of the original population. Caribou hunting was closed from 1991 to present. Four caribou population parameters are being srudied in both treated and untreated herds: calf recruitment, adult sex composition, population size and adult survival. Calf recruitment and adult sex composition are being compared in the treated Aishihik herd against three untreated woodland caribou herds of similar size in the southern Yukon and along the Alaska border. Population rates of change and adult survival are being compared between the Aishihik herd and the Wolf Lake herd, an intensively studied untreated herd. We are testing for differences in the rare of increase berween these two herd sizes during rhe past five years using stratified random quadrat survey techniques. We are also testing for differences in adult survival rates using samples of 82 radio-tagged caribou in the Aishihik herd and 72 in the Wolf Lake herd. We believe that wildlife biologists can learn from manipulations of wolf-prey systems by resring hypotheses using an experimenral design approach. Large scale wolf-ungulate experiments are inherently confounded by problems wirh treatment interspersion, pseudoreplication error and orher spatial constraints. We are attempting to solve these problems using a deductive statistical approach that best explains the nature of woodland caribou responses to wolf predation and harvest treatments.

Estrous synchronization and early pregnancy

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Abstract: Previously, in a subsample of wild Porcupine caribou, blood samples collected at approximately 20-41 days post breeding, were postitive for Pregnancy Specific Protein B (PSPB) but had baseline progesterone levels. This same group of females were also in very poor body condition leading to the interpretation that the cows conceived but underwent early embryonic loss (Russell *et al.*, 1998. *J. Wildl. Manage.*, in press.). The objective of this study was to validate the use of combined progestetone and PSPB as an indicator of early embryonic loss and to characterize the behavior of PSPB protein in caribou/reindeer plasma. We report here the preliminary progesterone results. At the Large Animal Research Station, UAF, 7 caribou and 7 reindeer were adminisrered prosraglandin 5 days after antler cleaning, to synchronize estrus, and again 7 weeks later to abort the embryo. After the first injection the cows were penned with bulls for 5 days. Blood samples were collected twice weekly for 11 weeks from these cows and from 5 non-bred, non-injected control cows (3 reindeer, 2 caribou) . All blood was assayed for progesterone. Two of 7 reindeer and 5 of 7 caribou became pregnant. The remaining 7 animals failed to come into first estrus prior to harem formation. The non-bted reindeer underwent a small short cycle followed by 2-3 regular 21 day esttous cycles. In all pregnant animals, progesterone remained elevated, declining immediately to baseline (0.5 ng/ml) upon prostaglandin injection. All these cows returned to estrus. Prostaglandin is an effective luteolysin in *Rangifer* when a corpus lureum is present. The failure to synchronize estrus in 7 females appears to be a consequence of late onset of estrus activity. We know that rising estradiol is responsible for antler cleaning in female *Rangifer.* However, the association of antler cleaning with onset of estrus was variable in this study. The late onset of estrus may be a consequence of keeping the females separated from bulls.

Surviving in the north – a conceptual model of reproductive strategies in arctic caribou

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Abstract: Arctic and sub-arctic *Rangifer* populations have evolved in an environment characterized by long, cold winrers and short growing seasons. Available resources, such as digestible nitrogen, are limited in time and space. Post parturient females must balance the requirement to replenish protein and fat reserves depleted during the winter with producing sufficient high quality milk to ensure over winter survival of her calf. This trade-off manifests itself in the allocation of energy above maintenance and activity, the partitioning of protein and fat deposition and the timing of weaning. From sequential captures of over 200 individual caribou between 1992 and 1994, the authors developed a conceptual model to evaluate implications of resource allocation to population dynamics in *Rangifer. Post-natal weaning* occurs when plant biomass during the first week in June, and rate of plant growrh over rhe next thtee weeks, are insufficient to maintain growth rates in the calf (see Griffith *et al.,* this meeting). Upon weaning the calf dies. The cow increases in body weight and potential pregnancy (Gerhart *et al ,* 1997. *J. Zool.* 242: 17-30) and bitth rate (Cameron & Ver Hoef, 1994. *J. Wildl. Manage.* 58: 674-679). *Summer weaning,* from our observations, occurs when cow protein reserves fail to be replenished. The most likely cause is accidental injury or disease in the cow as we consider nitrogen availability not limiting in the summer range of the Porcupine caribou herd (PCH). Upon weaning the calf dies. An increase in pregnancy rate is likely for the cow. *Early-autumn weaning* occurs when the fat reserves of the cow are below a specified threshold primarily due to a combination of the factors lisred above and a particularly bad insect year. The survival rate of the calf declines and the age of first reproduction of the calf is likely advanced. For the cow this strategy increases her chance of pregnancy and enhances her survival through winter. *Extended lactation* is common in rhe PCH (Gerhart *et al ,* 1997. *Ibid*) and is associated with low far reserves in rhe calf at or abour early winter. As a consequence, the cow suffers reduced probability of pregnancy due to "lactational infertility" but increases the survival of her calf. Weaning is assumed for the following spring-summer. *Normal weaning,* which is initiated during rhe rut, results in high pregnancy rates for rhe cow. In this latter case both cow and calf have healthy levels of fat and protein reserves. The implication of these strategies is discussed in relation to industrial developmenr and climare change, a porential challenge to Rangifer herds throughout the circumpolar north.

Session two

Co-Management

The Eight North American Caribou Workshop,
Whitehorse, Yukon, Canada,
20–24 April, 1998.

Ecological role of hunting in population dynamics and its implications for co-management of the Porcupine caribou herd

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Abstract: At a present population size of 160 000 animals, the Porcupine caribou herd has been subjected to an annual harvest rate of 2% for the past couple of decades. We modeled potential sensitivity of herd population dynamics to hunting and used that telation as a basis for a herd monitoring system. Maximum number of adult cows that could be harvested without causing a subsequent decline in herd size was calculated as a function of total number of adult cows in the herd and recruitment of calves to yearling age-class. Maximum cow harvest, therefore, is a threshold above which hunting has destabilizing effects on herd dynamics. Actual harvest in relation to theoretical maximum harvest provides a basis for prediction of herd sensitivity to hunting. Maximum harvest is a linear function of recruitment. Herd dynamics are especially sensitive to low recruitment, however, when combined with low hetd size. The two relations involving recruitment and herd size provide the basis for predicring herd dynamics and sensitivity to hunting. Herd size is best estimated by aerial census, while an index of recruitment can be predicted by monitoring autumn body condition of adult females. Body condition can be estimated on the basis of a few simple metrics measured by hunters in the field. The hunters' data on body composition, combined with aerial census dara on herd size, provide a useful tool for managers and co-management boards to devise policies and regulations to manage the herd. The population model and monitoring system can opetate on the Internet and be accessible to all users in villages within the range of the Porcupine caribou herd.

Key words: Alaska, caribou, monitoring system, Northwest Territories, population model, *Rangifer tarandus,* Yukon.

Rangifer, Special Issue No. 12, 71–78

Introduction

"Co-management" systems for managing human exploitation of common-property natural resources are becoming increasingly popular in rural and remote regions of the wotld (Betkes *et al.,* 1991, Pinketton, 1994). They are based on the assumption that user-groups involved in management decisions are more likely to comply with harvest limitations than if limitations ate simply dictated by a governmental authority. Voluntary compliance with regulations is especially important in remote regions whete legal enforcement is logistically or administratively difficult. Co-management systems, therefore, hold prospect for much of the world's underdeveloped regions. They also offer potential for reducing political conflicts over natural resource management in developed regions where perceptions of needs differ between local residents and geographically distant administtators.

Klein & Kruse (1996; Klein *et al.,* 1999) recently studied effectiveness of co-management in application to caribou (*Rangifer tarandus*) harvest systems. They compared user (rural hunters) and manager (government agencies) perceptions of management effectiveness in two contrasting systems: the Beverly and Qamanirjuaq caribou herds in Canada, compared with the Western Arctic caribou herd in Alaska. The Canadian herds were managed by a co-management board comprised of 8 users and 5 government managers, while the Alaskan herd was managed by a state board of game with no direct decision-making by users. Although government managers were found to be more sensitive and responsive to user concerns in the co-management system than in the state-controlled system, the surprising finding was that co-management did not increase the likelihood that users would cooperate with management decisions. The principal conclusion was that co-management boards, alone, cannot substitute for frequent and continued interaction between managers and users at the village level. Users need to understand the rationale for management decisions and be part of the information system that leads to those decisions.

The Porcupine caribou herd is a migratory herd that calves on the arctic coastal plain of northeastern Alaska and winters in the subarctic taiga of northwestern Canada. It is subject to management by both jurisdictions, therefore, but its remote location makes it mostly harvested by local, rural hunters in the Alaskan villages of Kaktovik, Arctic Village, Venetie, and Fort Yukon, and the Canadian villages of Old Crow (Yukon), and Fort McPherson and Aklavik (Northwest Territories). The International Porcupine Caribou Board coordinates international issues that affect the herd. A co-management system is employed by Canada's Porcupine Caribou Management Board. There is much interaction between the Gwich'in native villagers on both sides of the international border.

The United States Man and the Biosphere Program took an interest in the Porcupine caribou herd's co-management system in 1996 as an example of co-management harvest systems and their implications for achieving sustainable human society and natural environments in rural areas of the North. Our charge was to investigate the role of hunting in herd dynamics of the caribou and to develop a monitoring system that would provide both historical trend data and prediction of herd sensitivity to hunting.

We expected on the basis of ecological theory that the role of hunting in herd dynamics is not constant or a simple matter of number of animals harvested (Van Ballenberghe & Ballard, 1994; Pascual & Hilborn, 1995). It is critical to the success of any co-management system to understand when effects of hunting may be most important and when they may be relatively unimportant. Furthermore, both users and managers alike should understand dynamic relations. The co-management board needs to know the answers to the following questions: "(1) How big is the herd?; (2) Is it threatened?; (3) Is it healthy?" (Urquhart, 1996). Also, users must be involved in frequent participation with managers in the monitoring and prediction system (Klein & Kruse, 1996). Our goal, therefore, was to develop an analytical system with the following features: (1) is both relatively simple and understandable, (2) requires data input from both users and managers in different but complementary ways, and (3) provides a basis for both monitoring key population factors over time and predicting herd sensitivity to hunting at any given time. Simplicity and practicality come at some expense of technical complexity and precision. We sought to find an appropriate balance that would yield meaningful and useful results.

Materials and methods

Rationale

Recent modeling analyses of the Porcupine caribou herd have revealed adult-female survival and recruitment (calf production and survival) to be the two most sensitive factors affecting the herd's population dynamics (Fancy *et al.*, 1994; Walsh *et al.*, 1995). Recent theoretical analysis of sustainability of harvested populations in fluctuating environments has shown that "threshold harvesting" is most often the optimal strategy for balancing yield against risk of population depletion (Lande *et al.*, 1997). We, therefore, sought an analytical framework that would predict a harvest threshold based on adult-female survival and recruitment rate, where effects of hunting would be considered significant versus insignificant in relation to the herd's size and stability.

We considered harvest threshold to be the maximum number of adult-female caribou that can be harvested (N_{max}) without causing a reduction in number of adult females the subsequent year. N_{max} is a function of total number of adult females in the herd (N_f) and average recruitment of female calves to the yearling age-class (number of spring calves)/(number of non-calves in the population). Thus, N_f times recruitment, minus non-hunting mortality, equals 'harvestable surplus' (N_{max}) of production. Our concept of threshold entails 4 major, simplifying assumptions: (1) Under all harvest scenarios, there will always be sufficient adult males to ensure timely breeding of all estrous females. (2) There is no evidence of density-dependent limitation of the population; thus, survival and recruitment ate independent of population density. (3) Location of harvest (e.g., Village A *vs.* Village B) doesn't matter; analysis is based on the entire herd rather than geographic segments. (4) Timing of harvest is not important, except in the case of productive cows killed before autumn while still nutsing a calf; hunting of such cows must be treated as a teduction in both adult population and calf recruitment.

We also assumed that only in rare cases are there sufficient data to model a population in its detailed demographics of sex- and age-specific survival and recruitment. A practical, useful model fot co-management must be based on data that can be obtained routinely under normal operating budgets and normal amounts of time and effort. We focused on two variables for predicting N_{max}: (1) number of adult females (age ≥2 years) in the population, and (2) percentage body fat of adult females in autumn, which we used as an index of recruitment of calves to the yearling age-class. Number of adult females can be estimated from aerial surveys conducted every three years by government managets. Recruitment of calves to the yearling age-class, rather than recruitment of females to the adult age-class, is a simplification based on an assumed 50:50 sex ratio of calves at birth, equal survival of males and females to age 3 years, and high survival (relative to adults) of 1- and 2-year-olds (Fancy *et al.,* 1994).

Although tecruitment is a critical factor, it is very difficult to measure. It is the product of calf production (parturition), early calf survival (to first autumn), and over-wintet calf survival. Walsh *et al.* (1995) estimated that sampling efforts would have to be double the efforts of 1994 to detect a 10 percent change in survival for the Porcupine herd. Conception, parturition, and early calf survival, however, are highly correlated with maternal body condition at time of breeding in fall (Thorne *et al.,* 1976; Verme 1977; Cameron *et al.,* 1993; Russell *et al.,* 1998). Females that are in good body condition (high body fat) have high conception rates, low early embryonic loss, and high perinatal survival of their calves (thus high parturition rates). Female caribou exhibit an array of reproductive strategies in association with body condition. Productive females normally wean their calves in late September. However, if females are not adequately replenishing protein and fat reserves in summer, they can wean calves eatly, resulting in summer mortality of calves. If female fat reserves are low in early September, calves are weaned and the calves' over-winter survival is reduced. If calf fat reserves in autumn are low, cows extend lactation and the probability of pregnancy is reduced through lactational infertility (Gerhart *et al.,* 1997; Russell *et al.,* 1998).

Indices of adult-female body fat in autumn can be relatively easily measured by hunters (Chan-McLeod *et al.,* 1995). Therefore, we used adult-female body fat in autumn as our predictor, or surrogate variable, for recruitment in calculating N_{max}. Its measurement by hunters complements the measure of total population size by government managers. In our model, linkage between autumn fat and recruitment is through time allocated to lactation. Low autumn fat values are associated with a low percentage of normal weaners and a high percentage of early weaners and extended lactators (Gethart *et al.,* 1997).

Modeling and analysis

We used a simulation model developed for the Porcupine caribou herd (Kremsater, 1991; Russell, 1991; White, 1991) to genetate the following relations: (1) recruitment of calves to yearling age-class as a function of adult-female body fat (percentage of live body weight) in the preceding fall; (2) N_{max} as a function of N_f and recruitment of calves to yearling age-class; and (3) N_{max} as a function of N_f and adult-female body fat in the preceding fall. The model is a deterministic model based on many years of study of the Porcupine caribou herd. It calculates body condition and growth rates of individual animals as a function of food resources and energy expenditures in its ENERGY submodel. It calculates population demographics and dynamics as a function of energy balance and body condition of individual animals in its POPULATION submodel. The model has been developed specifically for the Porcupine caribou herd and incorporates average values of all variables for that herd and its habitat. Therefore, model predictions for our harvest-threshold relations are for best-approximation, "average" conditions. The model is the core of an ongoing research program and so will be subject to refinement for years to come. Harvest-threshold relations can always be recalculated, however, aftet future changes in the model.

Relation between recruitment of calves to yeatling-age class as a function of adult-female body fat in the preceding fall was generated by varying adult-female body fat, throughout its range of reasonable values, as an input variable in the POPULATION submodel, and calculating resultant recruitment the following year (calves to age 12 months). Relations between N_{max} and N_f, N_{max} and recruitment, and N_{max} and both N_f and recruitment wete generated, similarly, by varying each of the independent variables throughout its range of reasonable values and calculating the resultant value of N_{max}. Harvest thteshold relation of N_{max} as a function of N_f and adult-female body fat was calculated by substituting the relation for recruitment as a function of female body fat into the relation fot N_{max} as a function of N_f and tecruitment.

Results

Recruitment of calves to yearling age-class was a linear function of adult-female body fat in the preceding fall (Fig. 1a). N_{max} increased linearly with N_f (Fig. 1b) and curvilinearly with both fall fat weight (Fig. 1c) and recruitment (Fig. 1d). The combined response surface (Fig. 2a) indicates that when a havestable surplus exists (i.e., $N_{max}>0$) N_{max} is lowest at low population levels combined with low rates of recruitment. The population would be most sensitive to hunting when in this area of the response surface.

The harvest threshold relation of N_{max} as a function of N_f and adult-female body fat (Fig. 2b) looks very similar to the response surface of Fig. 2a. However, with adult-female body fat substituted fot recruitment, N_{max} now can be calculated as a function of two variables that can be monitored routinely and effectively. The relations are the same as for recruitment: Hunting is most likely to have significant, destabilizing consequences when the population level is low and, especially, when adult females are, on average, in poor body condition (low body fat). Hunting is most likely to be relatively insignificant in reducing the herd when the

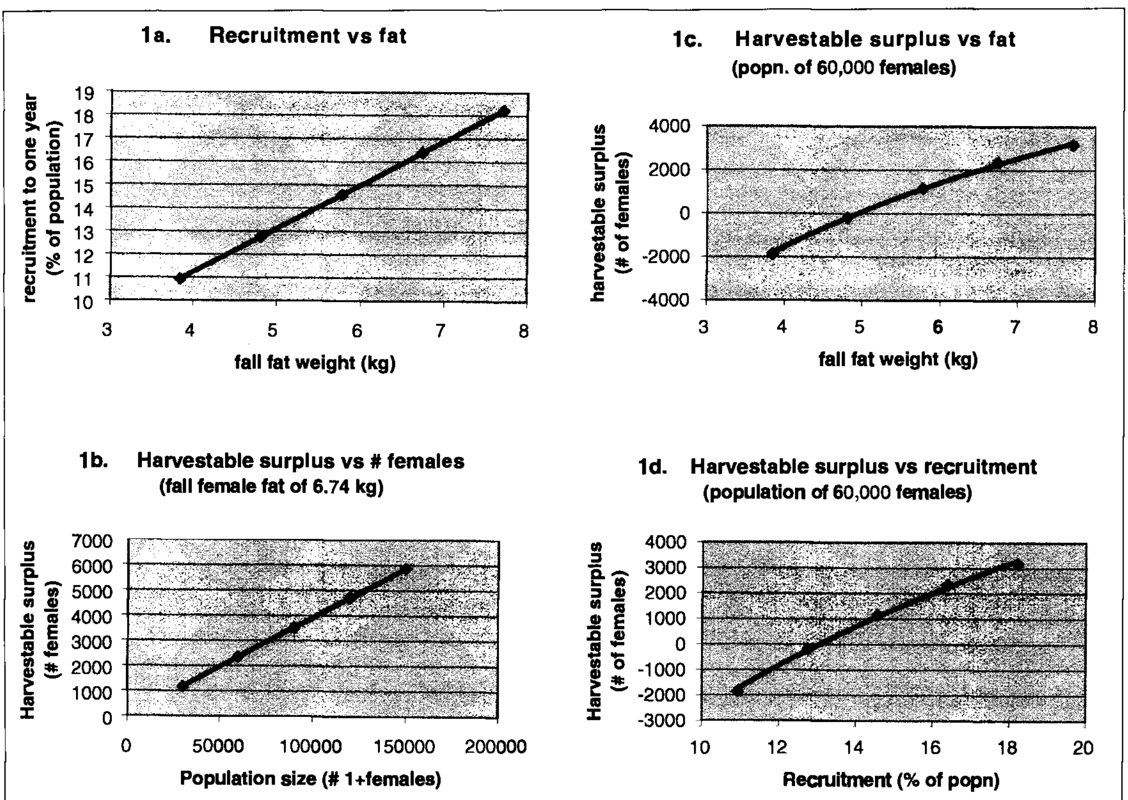

Fig. 1. Modelled relarionships berween recruitment tate (%) and fall fat weight (1a), harvestable surplus and number of females in population (1b), harvestable surplus and fall fat weight of females (1c) and harvestable surplus and recruitment rate (1d).

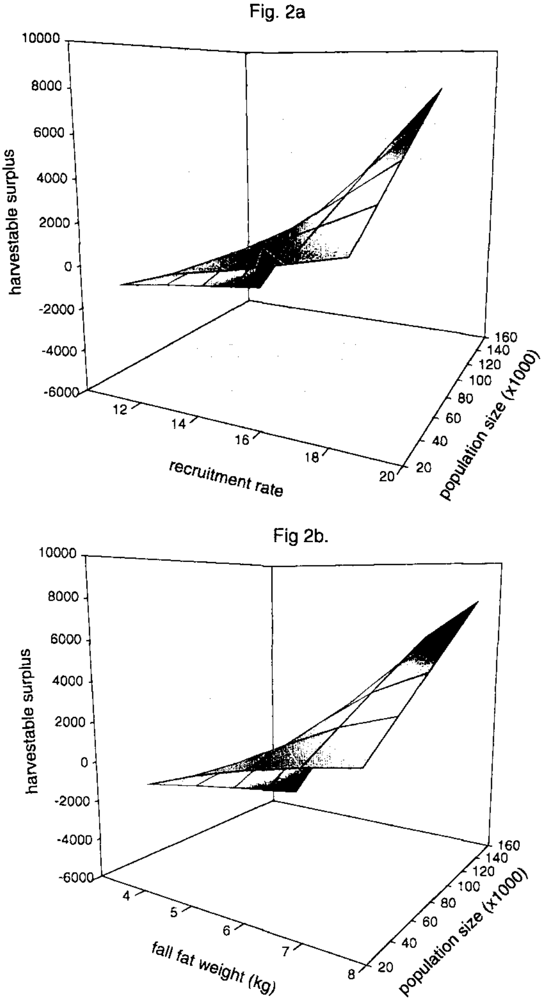

Fig. 2. Modelled response surface relating harvestable surplus and female population size to recruitment (2a) and fall fat levels (2b).

population level is high and adult females are in good body condition (high body fat). The situation of low population level and high body fat would occur when the herd is recovering rapidly from low population levels (e.g., a catastrophic winter die-off). Reduced hunting pressure at such a time would be expected to petmit the herd to increase more rapidly than under higher hunting pressure, and relative effects of hunting would be lessened (with higher N_f) in the neat future. Conversely, the situation of high population level with low body fat would signal that the herd is in a precarious state - possibly a case of having exceeded the carrying capacity (i.e., a state of density-dependent population limitation) or a case of environmental change in habitat reducing its quality for caribou. This situation is complicated, because the appropriate harvest-management sttategy could be very different, depending on the cause(s) of the poor body condition.

Since body fat monitoring ofı the Porcupine caribou herd was initiated in the mid 1980s, average autumn body fat has been about 6.8 kg (unpubl.). From Fig. 2b and assuming an average female population size for the Porcupine herd of 60 000 animals, we determine the average annual harvestable surplus for the hetd would be 2000 females. Average annual harvest of the Porcupine herd during the last decade has been about 2800 animals with about 50% (1400) being adult females (Porcupine Caribou Management Board, 1998). The theoretical maximum hatvest was never exceeded during this period.

Discussion

Implications

The harvest threshold relation of N_{max} is a highly simplified concept, calculated from a deterministic simulation model for average conditions. N_{max} should never be regarded as a precise, absolute number. Both adult survival and recruitment actually vaty substantially from year-to-year (Fancy *et al.,* 1994), and average conditions seldom prevail. Nevertheless, the shape of the N_{max} response surface is instructive in undetstanding the dynamics of herd sensitivity to hunting. Actual harvest in relation to N_{max} provides an index of potential magnitude of effect of hunting during any given year. It is very difficult to restrict hunting, howevet, especially where subsistence needs are great. Thus, co-management of caribou does not react on an annual basis to new data; it reacts to major trends over periods of years (Urquhart, 1996). However, for it to react appropriately at all, it needs ptactical information (data) and practical guidelines. Periodic monitoring of number of adult females in the population and annual body condition in autumn, combined with herd harvest data and the harvest threshold relation of N_{max}, will provide insightful data for identifying trends and understanding their significance.

One practical implication of instituting such a monitoring system is that hunter attention is immediately focused on importance of the productive component of the population (adult females) and importance of recruitment to the population (calf production and survival). Implications of harvest sex- and age-ratios, therefore, clearly favor harvest of adult bulls during any time of potential herd sensitivity to hunting. This has significant educational value. Furthermore, times of increased sensitivity can be anticipated through the relation of actual (or projected) harvest to N_{max}.

Hunters are always limited in their ability to judge total herd size, because each can see only a small part of it. They, therefore, need to rely on government managers for aerial census data. Government managers, on the other hand, need to rely on hunters for body-fat data. The system encourages (indeed, requires) frequent, meaningful interaction between users and managers working in concert to monitor size and health of the herd and predict its relative sensitivity to hunting. Value of the monitoring system increases with time, because (1) time is required to see real trends through apparent annual variations, (2) time is required to increase familiarity and instill confidence in both the system and cooperation between users and managers, and (3) time is required to build a data base that provides historic perspective and credibility.

"Good times" of increasing herd size and minor or insignificant effects of hunting, such as have prevailed for the past couple decades in the Porcupine herd (Fancy *et al.,* 1994), are easy times for co-management. Management decisions then have little consequence on herd dynamics, so contention is relatively low. However, during periods of population decline, management decisions will be contentious. The test of co-management effectiveness for the Porcupine caribou herd is yet to come. The sooner a monitoring system can be implemented, the better it will be in developing historical perspective and familiarity with users and managers.

Limitations

The harvest threshold relation of N_{max} will prove to be inadequately simple under circumstances that diverge from its underlying, fundamental assumptions. One example is the case where non-human predation of the population increases significantly, such as might be the case under suddenly low population levels (after a major herd decline). This would be a violation of the assumed "average" conditions that went into calculating N_{max} production surplus, where non-hunting mortality has exceeded average conditions. In such a case, increased predation must be considered as additive to hunter harvest. In other words, for a given N_{max}, hunter harvest must be reduced by increased non-human predation on a one-for-one basis. The harvest threshold relation still would be useful, but interpretation of N_{max} in terms of hunter harvest would require additional biological consideration to account for effects of increased predation. It also would require additional kinds of data to quantify the increase in predation.

Another, possibly more likely, complication would arise if the population enters a period of density-dependent population limitation, such as when overgrazing has reduced supply of food. The combination of high population density and low body fat would be the same as for the situation of sudden environmental change (not density-dependent) in reduced habitat quality for the herd. In the first case, hunting of adult females and calves should be increased (even though the N_{max} relation would indicate the opposite), because the objective would be to intentionally reduce population level of the herd. In the second case, the preferred management decision might be to protect females and calves until more is learned about the cause of loss of body condition. In either case, however, additional biological consideration and additional kinds of data would be required beyond the simple N_{max} harvest threshold relation. In both cases, historic perspective from an established monitoring system would be invaluable.

Implementation

Implementation requires that managers and users agree on need and value of a monitoring system. It also requires faithful adherence to data collection. Data requirements are the following: (1) periodic aerial census of population levels, specifically number of adult females; (2) annual sampling of adult-female body-fat indices from a sufficient number of animals for reliable estimate of population mean; and (3) annual tracking of hunter harvest. Hunter harvest data, however, are not required for monitoring size and health of the herd; they merely provide historic perspective and basis for evaluating harvest in relation to herd size and health in any given year. The co-management board would benefit from harvest data in any deliberations about need to change harvest numbers or composition.

Hunters cannot estimate total body fat of caribou directly. Rather, they must measure indices of body fat, which then can be used to calculate body fat. Three relatively simple indices can be obtained from hunter-killed animals without any need to destroy meat or ensure special handling procedures: (1) chest girth, measured with a tape measure, (2) backfat thickness, measured with a ruler, and (3) femur marrow-fat weight or percentage, measured in the laboratory from the femur bone saved by the hunter (Chan-McLeod *et al.,* 1995). All measures should be made in autumn, preferably September or early October. Backfat thickness is a good ptedictot when body fat exceeds 8%, while femur marrow fat is a good predictor for body-fat levels <9%. Large sample sizes can be obtained by hunters, thereby yielding a relatively ptecise estimate of the population mean. A starting point for this sort of sampling might be along the Dempster Highway, where hundreds of cows usually are taken by huntets in October each year.

Communication between managers and hunters and between villages is crucial to the successful implementation of any monitoring system to be used in co-management. Data must be easily updated and readily available to all interested parties. That requirement has been virtually impossible until recently. With the advent of the internet, it has now become a relatively simple mattet to provide a website whete data can be input and/or viewed from any village or government agency at any time. Most villages within the range of the Porcupine caribou herd currently have intetnet access, and plans exist to expand service to all villages. Usets may share information about current location and movements of the caribou herd. Data may be input and managed in any way preferred by usets, managers, and the co-management board. Results of analysis of the data, along with the historic data base (or trend summary) may be readily available and viewed by anyone at any time. Political considerations about what data any particular village is willing to share with the "outside" are probably the greatest obstacles remaining. Such nontechnical issues need to be worked out among users and the co-management board.

Implementation of a relatively simple yet effective monitoting system should bring users and managers together in a mutually beneficial telationship of understanding and managing their caribou herd. With increased familiarity and trust in the system, the co-management board is most likely to be able to succeed in recognizing any need for change in management strategies and for accomplishing such change through voluntary participation of temote users. This is a first step along that path.

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A case study of the Carcross herd in the southern Yukon

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Abstract: The Carcross caribou herd is a small herd of 450 woodland caribou (*Rangifer tarandus caribou*), which ranges in the most densely populated area of rhe Yukon. In response to concetns about the herd's declining numbers, a community-based plan was developed in 1992 to recover the herd. As a result of the plan, Yukon hunting of the herd was stopped by regulations and voluntary compliance by First Nations. However, land use pressures on the winter range and migrarion corridors continue to threaten this hetd. While the caribou are relatively undisturbed on alpine summer ranges, deep snow forces them into the populated lowlands for the critical winter period. Every year during spring and fall seasonal migrations, caribou are killed in vehicle collisions on highways that bisect the winter range. Land alienation by agriculture, cottage lot and residential development continue to displace caribou. Mining, forestry and unregulated fuelwood cutting can displace and distutb catibou on the winter range, and expand the network of roads and trails. Acrivities such as snowmobiling, ATV use, skiing, dogmushing and biking follow quickly with new access. The cumulative impacts of these activities reduces the 'effective' wintet range and stresses caribou when their energy needs are most critical. Living with the Carcross caribou herd will continue to require dedicated efforts by many individuals and governments.

Human impacts on the Porcupine caribou herd

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Abstract: The Porcupine Caribou Management Board is directed by the communities that rely on the Porcupine caribou herd to promote the conservation and protection of the caribou and its habitat. This task is enormous as the herd ranges over two nations, one state, two terrirories, five First Nations land claims areas, a wildlife refuge, two national parks, and several protected areas. The formation of the Canadian Porcupine Caribou Management Board and the International Porcupine Caribou Management Board are the results of efforts to place renewable resource management in the hands of the Notthern people. The Porcupine Caribou Management Board's eight members have equal narive and government representation.

The Porcupine caribou herd is the foundation of the culture of the native peoples who depend on the herd. Their lifestyles combine the use of the caribou with the water, the land, the language, and the culture. Caribou are not only a vital food source but a way of life. The native peoples of the North have a vested interest in the continuance of the herd for future generations. The core calving ground of the herd is in the Arctic National Wildlife Refuge on Alaska's north coast. While the herd migrates over vast regions of northern Canada and Alaska, the migrarion parrerns of the herd dictate that the continued success of the now 160 000 strong herd depends on at least 50% of the cows calving in this nutrient rich area on Alaska's coastal plain. Unfortunately, politics and oil development threaten the calving grounds and therefore, the existence of the herd.

The poster, which depicts the calving grounds on Alaska's northetn coast, is a composite of several individual frames. It has become the signature poster for the lobby efforrs to permanently protect the calving grounds. The Board, along with native organizations and environmental groups, has for many years acrively lobbied for permanent prorecrion of this vital area. To date, the Refuge has still not been given permanent protection. Migtation, industrial development, and politics are a volatile mix.

Behaviour and human disturbance

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Abstract: The Porcupine caribou herd is an ancient relarive that the Gwitchin people have relied on for food for thousands of years. They have lived in harmony with the caribou since time immemorial. With the rapid increase of technology and roads the caribou certainly feel the effects of human disturbances. Where there is human activity, othet life forms will always be affected. Many factors come into play depending on the type of species, it's resiliency, and its role in nature. The building of the Dempster Highway has affecred the caribou. Although their have been few road kills, increased traffic has resulted in an increased morrality rare. Overzealous hunters also have grearer access to the caribou that cross at points on the Dempster. Earlier studies and First Nation's observations indicate that the catibou are hesitant about crossing rhe highway where hunting has occurred. Alrhough the herd is healrhy there is one major human threar ro their survival. Oil development in the crucial '1002' calving grounds in Alaska could seriously harm the herd. Disturbance to the cows who calve in the Refuge could disrupt theit calving patterns causing a decline in herd numbers. The Porcupine Caribou Management Board in cooperation with First Narion governments and environmental groups has been actively lobbying for permanenr protection of the Refuge for over ten years. So far we have been very successful however, it is very important that the U.S. Congress protect the Arctic National Wildlife Refuge from any development. In order for them to do that it is vety important that Canada do its part in protecting the caribou. They need to seriously reconsider re-opening the oil-caps in the wintering grounds of the Porcupine caribou herd. Another human disturbance factor are aircraft that fly low over caribou. They become alarmed resulting in panic and confusion. In panic, the calves have become separated ftom their mothers. This has tesulted in more dearhs due ro starvation and predators. Caribou are also vulnerable ro the noises of snow machines. There has been a lot of monitoring of the herd since the 1950s. Biologists have monitored Porcupine caribou body condirion year after yeat. The calves have been studied for their mortality rates. Radio collars have been used to track the caribou over the years. We, as First Nations people hold tremendous amounts of knowledge pertaining to the caribou as well as the migration routes of the herd.

Learning with locals to model a future

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Abstract: Native communities of the North American Arctic increasingly expect that research endeavors will address community concerns and incorporare local knowledge inro research processes. While many researchers acknowledge these expectations as valid, research methods which serve to meet these objectives are currently underdeveloped. This paper presents the method used by academic researchers and native community members in a collaborative research project. The National Science Foundation's Arcric Community Sustainability Project is a four-year, interdisciplinary study which, in part, seeks to advance our understanding of how local knowledge and science can work in tandem to address applied research questions. Of concern in the Sustainability study is how possible future changes (short- and long-term climate change, the implications of 1002 gas and oil development, and shifts in levels and types of tourism and non-local hunting) may affect life in Porcupine caribou user communities of Canada and the United States. Consequences of possible changes on Porcupine caribou herd are a central focus of the study. An objective of the project is to combine local knowledge with multi-disciplinary scientific inquiry to model driving causal factors in order for researchers and locals to discuss better the implications of possible futures. Locals of Old Crow, Aklavik, Fort McPherson, and Arctic Village participate in focus group research and complete a mapping exercise to document current-day hunting patterns and prompt local hunters' discussions about ecological conditions affecting caribou movements and distribution. An iterative process of multiple small-group interviews is used in each community in which locals and researchers together generate and refine qualitative proposirions about environmental conditions affecting caribou and hunting success. Findings of former studies (e.g., harvest data, GIS displayed harvest locations, biological data, and socio-economic data on household and community sharing) are presented to groups of hunters to prompt their interprerations of data. Propositions address a range of topics and are later to be used with researcher's findings in the development of a project synthesis model which projects change.

Potential value of reindeer to caribou in a co-management system

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Abstract: A privarely owned herd of several thousand reindeer is managed in an open herding system in the western Arctic. This herd interfaces with the Bluenose caribou herd, to which it could become an asset. Firsrly, the reindeer are monitored annually for infectious diseases including parasites, and therefore they have potential value as sentinel animals for the early detection of diseases which may be introduced into the region from time to time. Secondly, the herd will be developed for meat production which could be used by local consumers to take the pressure off rhe caribou population in times of natural decline. Thirdly, gentled reindeer will introduce visitors to *Rangifer* and their place in the tundra biome, raising awareness of the nature of Arctic ecosystems. Principles of co-managemenr will be applied through continuing consultation with other entrepreneurs and with all the people with whom we share the use of the land.

The mystery of the Clear Creek caribou herd

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Abstract: The Nacho Nyak Dun (NND) First Nation, the Mayo District Renewable Resources Council (MDRRC) and the Government of Yukon are equal partners in the Integtated Wildlife Management Plan for the NND Tradirional Territory. The objective of the plan is to coordinate the management of wildlife within the Traditional Territoty. The plan details the cutrent status, concerns and solutions under selecred ropics. One issue that arose during the planning process was that caribou in the Clear Creek area might be a separate herd from Hart Rivet caribou, as they are currently managed. If Clear Creek caribou are separate from Harr River, rhey should be managed as a small herd. If herd size is small, reported plus unreported harvest in the past has probably exceeded the sustainable limit. Woodland caribou herds in the Wernecke Mountains were defined following a caribou inventory in 1989, when seasonal caribou ranges were delineated using radio collar locations from 32 caribou. In order to determine if the Cleat Creek caribou are a separate herd from rhe Hart River caribou, the 1989 survey is being reviewed, employing both traditional knowledge of caribou range use, and wildlife survey techniques. During the summer of 1995, 17 long term Mayo residents were interviewed. This historical informarion revealed that caribou have been seen in the Clear Creek area for many years, and during all seasons of rhe year. During the winter of 1997-98, the MDRRC conducted more interviews. Clear Creek caribou were reported to use an area between the McQuesten River and the Klondike Rivet, south of the delineated Hart River herd range. A 4-year inventory project was started in October of 1997. The project will determine whether Clear Creek caribou are separate from the Hart River herd, whether range use of caribou in Clear Creek overlaps with Hart River caribou range, and will determine the herd size and composition of both herds in order to assess safe harvesting levels. Eight radio collars were deployed in the Clear Creek area in October 1997. Three telemetry flights during the winter of 1997-98 found that these cows had not moved to the usual Hart River herd winter range. Twenty-two more radio collars were deployed in March 1998. Blood samples were taken from the collared animals to be analyzed in conjunction with a Yukon wide caribou DNA sequencing project. DNA sequencing results will determine how related the 2 caribou populations are. Body measurements were taken to confirm local observations that Clear Creek caribou are of larger body size than Hart River caribou. In March 1998, snow depth and density measurements were taken to relate to caribou range use. Fecal samples were collected in March 1998 and will be archived. Over the remaining period in the 4-year inventory, five telemetry flights will be flown per year to locate the 30 collared caribou and determine range use. In 1999 a census will be conducted to calculate allowable harvest levels. As well, local knowledge will continue to be summarized to enhance the understanding of these two caribou populations, and cement the use of traditional knowledge in the realm of wildlife management practices.

Session three

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Seasonal distribution and population parameters of woodland caribou in central Manitoba: implications for forestry practices

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Abstract: Woodland caribou (*Rangifer tarandus caribou*) in the boreal forest are believed threatened by human encroachment and associated disturbances such as resource exploration and extraction. We radiocollared and monitored fifteen female woodland caribou in central Manitoba, from 1995 to 1997, to obtain informarion on their population range, seasonal distribution and movements in relation to forestry concerns. The population ranged over 4 600 km^2 within a large peatland system and concentrared their activities in two areas for both the summer and winrer seasons. Females were relatively more solitary during the summer and exhibited fidelity to specific calving and summering areas averaging 83.4 km^2. Individual wintering locations varied between years and among individuals. Post-rut and pre-calving mixed-sex aggregarions occurred on rhe southern portion of the herds range. Caribou from the northern part of the range utilized a traditional travel corridor moving as far as 65 km to access the aggregation areas and their summer or winter ranges. Adult survival during the study period averaged 0.90 (95% CI, 0.80-1.00). Survival of rhe 1995 cohort appeared to be high as indicated by the 0.65:1 calf-cow ratio, and 30 ± 7% calf composition of observed caribou in the autumn of 1995. The annual rate of change (λ) of 1.19 (95% CI, 1.02-1.36) from January to November of 1995 indicated that the population was increasing at that time.

Key words: logging, peatlands, *Rangifer tarandus*, survival.

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Introduction

Factors responsible for the decline of woodland caribou in North America include habitat loss and increases in hunting and predation (Bergerud, 1974). Industrial activities such as forestry and petroleum development have the potential to contribute to this decline by altering caribou habitat, and increasing access for both humans and predatots into caribou range (Edmonds, 1988; Cumming, 1992; Rettie & Messier, 1998).

Post logging succession in the boreal forest creates habitats that are favourable for moose (*Alces alces*), and subsequently may result in higher moose densities (McNicol & Gilbert, 1980; Thompson & Vukelich, 1981). The associated increase in predators such as wolves (*Canis lupus*) in these areas not only compromise spacing-away strategies used by caribou to minimize encounters with such ptedators, but may result in higher caribou mortality (Seip, 1992; Stuart-Smith *et al.,* 1997; Rettie & Messier, 1998). This increased risk of encounters with predators can be especially important during the calving and wintering periods when some caribou herds may be more vulnerable to predation (Betgerud *et al.,* 1984; Gautier & Theberge, 1986). The development of logging roads not only has the potential to affect caribou movement and distribution, but the greater access into caribou ranges may increase hunting pressure (Johnson, 1985; Benoit, 1996). Though the full effect of forestry on woodland caribou is still unknown, studies have indicated that in areas whete logging occurs caribou are usually displaced from part or the entirety of their former range (Darby & Duquette, 1986; Cumming & Beange, 1987; Chubbs *et al.,* 1993). Through careful management it may be possible for woodland caribou and forestry to coexist, and already there are many plans attempting to integrate caribou needs and forestry practices (Ministère des Forêts *et al*, 1991; Cichowski & Banner, 1993; Cumming & Beange, 1993; Armleder & Stevenson, 1994). Such mitigating actions, howevet, can only be drawn up and acted upon if there first exists baseline infotmation on general caribou ecology from the areas of concern.

The forest industry is rapidly expanding in Manitoba and the projected increase in logging in the boreal forest has raised concerns about local caribou herds. Woodland caribou numbers in the province were estimated at >4000 in 1957 but current estimates indicate that the population has declined 50% since that time, with the most noticeable losses documented at the southern portion of theit range (Johnson, 1993). Licensed hunting of woodland caribou in Manitoba was closed between 1947 and 1967, then re-opened with testrictions until it was again closed in 1992 (Johnson, 1993). Subsistence hunting of caribou continues but most animals are harvested opportunistically. As the bulk of studies concerning woodland caribou have concentrated on herds in the south-east portion of the province (Stardom, 1975; Darby & Pruitt, 1984; Schaefer & Pruitt, 1991), little information exists from which to formulate any forest management decisions in the context of catibou ecology for central Manitoba.

The main objective of this study was to provide resource managers with information on the population parameters, seasonal distribution, and associated movements of woodland caribou in central Manitoba.

Study area

The 8300 km^2 study area was located in the vicinity of the town of Wabowden (55°55'N; 98°37'W) in central Manitoba (Fig. 1). The area straddles the Boreal Shield and Boreal Plain ecozones (Ecological Sttatification Working Group, 1995). The elevation ranges from 200 m above sea level in the north to 260 m in the south-east with major lakes and rivers oriented south-west to notth-east, draining into the Hudson Bay. The climate is continental with mean daily temperatures of 16 °C in July and -25 °C in January. Annual precipitation averages 536 mm, of which 34% is in the form of snow (200 cm) lasting typically from October until April. Lakes and rivers normally freeze up in mid November and are totally ice free by mid May (Environment Canada, 1998).

In the north, uplands are dominated by black spruce (*Picea mariana*), jack pine (*Pinus banksiana*) and trembling aspen (*Populus tremuloides*). Subdominant species include white spruce (*Picea glauca*), birch (*Betula papyrifera*), and balsam poplar (*Populus balsamifera*). Lowlands are comprised of dense, wet black spruce stands, black spruce and tamarack (*Larix larcinia*) peatlands, and open peatlands dominated by sedge (*Carex* spp.) and dwarf birch (*Betula glandulifera*). The southern portion of the study area is almost exclusively treed peatlands with lesser amounts of wet black sptuce stands and some interspersion of jack pine and black spruce uplands. Moose, wolves, black bears (*Ursus americanus*), and lynx (*Lynx canadensis*) are common in the region while wolverine (*Gulo gulo*) sightings have been infrequent.

The study area is dissected by two main highways, a number of seasonal and all weather logging roads, a railway line and many seismic cut lines. Nickel mining occurred in the area from 1970 to 1975, and mineral exploration is still continuing. Logging of major pulpwood species began in the early 1970s on a relatively small scale and has been rapidly expanding since 1989, with greater increases slated in the futute. A full histoty of forestry in the area is detailed elsewhere (REPAP Manitoba Inc., 1996). Owing to the efforts of fire suppression, relatively few large burns have occurred in the region. Approximately 570 km^2 are of recent fire origin, located in the southern portion of the study area, with the majority stemming from either of the two large fire seasons of 1989 or 1995.

Materials and methods

Capture and radio-tracking

Fifteen female caribou were captuted (10 in January 1995, 5 in February 1996) using shoulder-held netguns fired from a helicopter, and manually restrained. Animals were fitted with radio collars (151 Mhz, Lotek Engineering Inc., Newmarket, Ont.) and subsequently located using fixed-wing aircraft and helicopters equipped with directional two-element antennae. Radio-tracking flights wete conducted from 25 January 1995 to 30 June 1997 with an attempted 3-4 week schedule. A more intense flying schedule (4-7 day intervals) was implemented during the calving and early winter season. Seasons wete selected based on caribou ecology and snow cover, and were defined as winter (1 December to 29 February), late winter/spring (1 March to 30 April), calving/summer (1 May to 15 September), and autumn (16 Septembet to 30

November). Caribou locations were either recorded directly from an onboard Global Positioning System (GPS) unit or plotted on topographic maps (1:250 000 or 1:50 000) and later converted to UTM co-ordinates. During relocation flights, information concerning age (adult or calf), sex, and group size were recorded whenever possible. Sex was determined by the presence or absence of a vulval patch and antlet development during the rut. The minimum population size was determined as the maximum numbet of caribou observed during any one flight over each year. Calf:cow and adult (individuals >1 year of age) sex ratios were also calculated.

Survival and recruitment
Annual adult survival rates of collared individuals were calculated following the methods of Heisey and Fuller (1985) with the aid of the MICRO-MORT (ver. 1.3) computet program. As the exact date of death fot individuals was unknown, the midpoint between last live telocation and first relocation on mortality mode was used for survival analysis (range=4.5-26.5 days). Whenever possible mortality sites were examined for evidence indicating the cause of death. In cases where the mortality sites were not investigated, caribou were assumed dead and included in the analysis. The only estimates of calf tecruitment (calf:cow ratios and calf composition of all observed caribou) were obtained from the 1995 autumn relocation flights.

The annual finite tate of change (λ) was calculated from adult survival rates and calf recruitment following the methods outlined by Hatter and Bergerud (1991). Assumptions for this calculation wete that the calf sex ratio at this period was 1:1, and immigration and emigration was either balanced or negligible. One thousand estimates of survival and recruitment (based on observed values and their associated error) were produced utilizing Monte Carlo simulations. These values were then used to calculated the mean and 95 % confidence interval for the population rate of change. The exponential rate of increase ($r = \ln\lambda$) was calculated to allow compatison with other studies.

Individual and population ranges
Individual, multi-year home ranges were calculated using the 100% minimum convex polygon (MCP) method (Mohr 1947) and the TRACKER (v. 1.1, Radio Location Systems AS, Hudding, Sweden) computer program. Individual home ranges were then plotted to identify any specific areas of overlap. Population and seasonal ranges were also calculated using the 100% MCP method. To determine if caribou exhibited fidelity to specific calving-summering areas, yearly summer ranges were calculated and plotted. If fidelity occurred multi-year ranges were then calculated and plotted to identify the extent of overlap with other collared females. This could not be done for winter ranges as yearly individual relocations were less than that needed to calculate a seasonal range. Instead, yearly individual locations were examined to determine if caribou were wintering in the same general area.

Movements
All locations were mapped by season, using the computer program TRACKER, to assess movements and to identify possible sites of aggregation. Movement rates could not be calculated due to the discontinuous nature of relocations during certain seasons. Locations were displayed upon Manitoba Forest Resource Inventory maps (1983 issue updated with recent forestry and fire information) using ARC-VIEW® (ver 2.1b, ESERI, Redlands, California) in order to provide an estimate of habitat use and distances to geographical features.

All values are reported as mean ± standatd error unless otherwise stated.

Results

Population range and size
The overall population range determined from all relocations (n=456) was 4600 km^2 (Fig. 1). The majority of locations were within a large peatland complex and appeared to be bounded somewhat to the northwest by highway 39. A minimum population size of 50 individuals was determined from the 4 November 1995 relocation flight, while a flight in November 1996 suggested a minimum population of 43 caribou.

Group size
Collared females were essentially solitary (alone or with calf) during the calving/summer period. As the summer progressed, we observed caribou associating with other individual females or a cow/calf pair. During the autumn, winter and spring, caribou were relatively gregarious forming small, loosely associated mixed-sex groups with the latgest groups (maximum of 29 individuals) being noted in early November and April (Table 1). Only summer

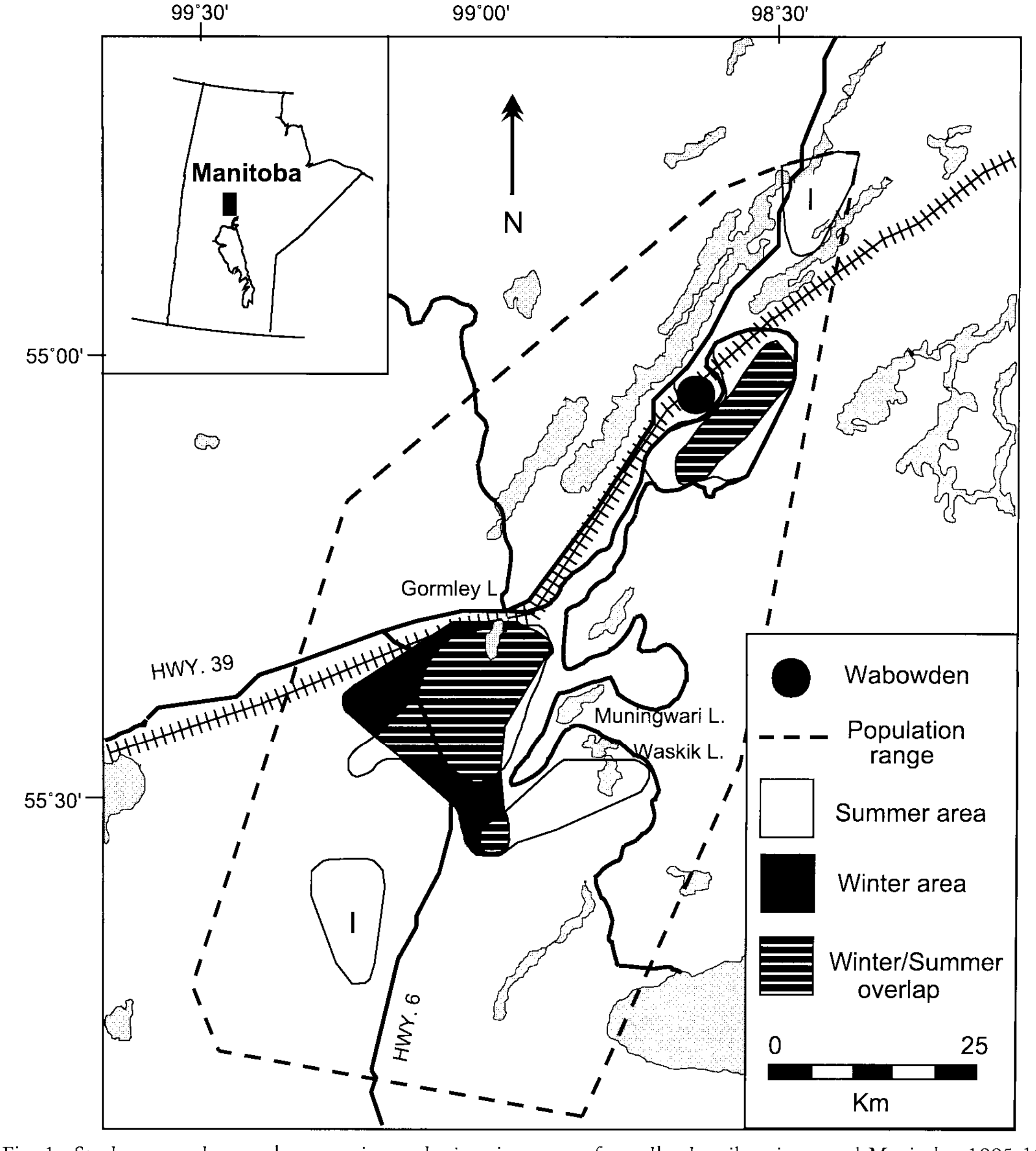

Fig. 1. Study area and general summering and wintering areas of woodland caribou in central Manitoba, 1995-1997. Ranges matked "I" denote solitary individuals. The dotted line tepresents the northern edge of a large contiguous peatland complex.

group sizes were significantly smaller than all other seasons (Dunn's Multiple Comparison Test, $P<0.05$). In 1995, the sex ratio of adults was 0.54 males:1 female during the rut and 0.50 males:1 female in early November (Table 2). Data for subsequent years were insufficient to calculate adult sex ratios.

Survival and recruitment

During the 10 738 caribou days recorded over the study period, thtee of the fifteen radiocollared caribou died. One animal was killed by wolves on her summer range while the deaths of the 2 other caribou could not be investigated. We assumed that neither of these animals wete killed by huntets, as both locations wete relatively remote and inaccessible. The mean annual survival of radiocollared adults based on pooled data was estimated to be 90% with a 95% confidence interval of 80-100%. The extent of direct human-caused mortality on

Table 1. Seasonal group size of woodland caribou in central Manitoba, 1995–1997.

Season	Mean group size	*n*
Summer	1.8 ± 0.2 (1-5)	31
Autumn	7.3 ± 1.0 (2-24)	25
Winter	4.5 ± 0.6 (2-10)	15
Spring	8.8 ± 3.6 (1-29)	7

Data are given as mean±standard error of the mean with range in parentheses. *n* represents number of groups observed.

caribou in the Wabowden area is unknown. During the coutse of this study (January 1995 to June 1997), one uncollared female was killed by a vehicle and a minimum estimate of subsistence harvest of 9 caribou was reported to the authors. The sex and age of these animals wete not ascertained.

Calf recruitment and survival information could only be calculated fot 1995 due to low sightability of females (and calves) in subsequent years. Collared females were first noted with calves on 2 June, and by 9 June, 5 out of 8 observed animals were accompanied by a calf. Relocation flights in early November indicated that at least 5 of the 6 females previously located with calves were still accompanied by them. Calf:cow ratios, based on all observed females, were calculated fot the autumn only and estimated at 0.62:1 in mid September and 0.65:1 in early November (Table 2). The percentage of calves in the observed groups was estimated to be 30 ± 7% in early November. The annual finite rate of change (λ) calculated for November 1995 was 1.19 (95% C.I., 1.02-1.36). The exponential rate of increase (r) determined for autumn 1995 was 0.17 (95% C.I., 0.02-0.31). These results suggested that at least in 1995 the population was stable to inceasing.

Table 2. Adult sex ratios and calf cow ratio of woodland caribou in central Manitoba, as observed during relocation flights in aurumn 1995.

	Male:female ratio	Calf:cow ratio	Total no. of cariibou
Sep.17	0.54 ± 0.14	0.62 ± 0.13	21
Nov. 4	0.50 ± 0.11	0.65 ± 0.11	43

Values are mean±standard error of the mean as calculated from the binomial distribution (Zar, 1984, p. 376).

Seasonal ranges and movements

Seasonal ranges for the population were overlapping and variable in size, with winter and autumn ranges of 3200 km², a summet tange of approximately 2500 km² and a spring range of 1770 km². Individual caribou home ranges averaged 581±74 km² (range=98-1196). All collared females but one had overlapping home ranges that radiated outward from the Gotmley Lake area to the north-east, south-west, or south, extending from 23 to 72 km. Individual females exhibited fidelity to specific calving/summering areas. Multi-year summer ranges were calculated and averaged 83±11 km² (range=29-180 km²). Eighty-seven percent (13/15) of collared females possessed a summer range that overlapped with at least one other collared animal. Individual winter ranges could not be calculated but it appeared that caribou were not always faithful to a specific genetal wintering area.

There were two majot peatland areas used by caribou for both summer and winter (Fig. 1). One area was located within a large open and treed peatland complex of approximately 580 km², 3.6 km east of the town of Wabowden. This complex was surrounded on all sides by upland forest communities and smallet peatlands. The second atea ("Gormley area") utilized by caribou for both the summet and winter was 40 km to the south-west of Wabowden, at the edge of a large contiguos peatland complex.

The six collared females using the Wabowden area during the summer shared approximately half (55±4%) of their summer ranges with each other. One collared female summered apart from this group, 10 km north of the peatland complex, utilizing small peatlands, treed rock, open black spruce stands and lakeshores. All collared caribou that wintered in the Wabowden area testricted their locations within a portion of the summering area (Fig. 1). Most of the summer locations of individuals in the Gormley area were bounded to the north by the railway line, to the west by highway 6, and to the east by Gormley lake, with the exception of one animal whose summer range extended west across the highway. The extent of summer range overlap (37±7%, n=5) of collared females within this area was slightly lowet than that observed for females to the notth. Two females shared parts of their summer ranges, 5 km to the south-east of this group, while one collared female summered to the south-west across the highway (Fig. 1). During the winter, caribou locations tended to extend slightly westward and southwatd. The lone individual to the south-west wintered close to its summer range with uncollared caribou.

For the duration of this study the majority of caribou summered and wintered in the same genetal peatland areas. However, individual caribou did not always exhibit the same pattern each year. Of the seven collared females summering in the northern patt of the study area, thtee utilized the Wabowden area during both the summer and winter, three switched from wintering in the north to the south in subsequent years, and one wintered exclusively in the south. Of the eight collared females summering on the southern portion of the study area, six utilized the Gormley area for both the summer and wintet while two, originally captured in the north during the winter of 1995, winteted in the south the following years. No caribou were observed shifting winter locations from the Gormley to the Wabowden area.

Due to intetmittent flight schedules during the autumn, no evidence of specific rutting areas could be determined. We suspect however, that no common rutting area existed as most individuals were still located in or near (<10 km) their summer ranges by mid October. Post-rut aggregations were observed in early November of 1995 and 1996, when the majority (78-80%) of collared females converged on the wintering grounds of the Gormley area. These females were located in groups ranging from 6 to 23 individuals composed of other collared females, uncollared cows and calves, and mature and immature bulls. All females from the notth exhibited a synchronous south-westerly movement between mid October and early November, with most individuals travelling approximately 30 to 65 km to access the aggregation areas. A small percentage (two to thtee individuals each year) exhibited only short movements (<10 km) during this period, with some of these individuals travelling to the south later in the season. Collared females from the south moved very little (0-14 km), as areas of aggregation were either within or near their summer ranges. On 4 November 1995, 32 caribou were observed in 4 groups ranging from 6-11 individuals, in the Gormley area. Three of these groups were within 3-9 km apart while the other group was observed approximately 15 km to the south and appeared to be travelling in a southerly direction. The subsequent relocation flight in mid December indicated that three of the four females originally from the northern complex had returned to the Wabowden area to winter. In 1996 this general pattern of movement and aggregation was tepeated with the exception that all but one caribou originating from the northern complex remained in the Gormley area to overwinter. The greater frequency of flights between 4 November and 18 November, allowed us to observe caribou movements at a finer scale. Groups appeared to be dynamic during this period, with individuals breaking away to form new associations or join other groups in the area. These groups exhibited an "out and back" movement from the Gormley area, travelling to the west, south-west, or south up to 45 km, with the majority of individuals returning near their point of origin within a two week period.

Mixed-sex aggregations also occutted in early April 1995 when all collared females converged on the Gormley area in one of thtee observed groups. Two groups of 5 and 28 individuals, located <8 km apart, were observed feeding and resting in treed peatlands. A small assembly of three individuals was observed 12 km to the north-east, travelling through open peatlands in the direction of the other two groups. The females wintering in the north had travelled to the area between mid Match and early April following the same travel route used by caribou in the autumn. Five of these caribou returned north to by mid May to calve, having spent less than a month congregating in the southern portion of the study area. Caribou that summered in the southern portion of the study area were located on their summer ranges as early as 20 April.

Only one spring relocation flight was conducted for 1996 and 1997. Results suggested that if a pre-calving aggregation had occurred it would have been before mid April, as locations aftet this date indicated that females were dispersing towatds their summer ranges.

The movement of females from the north to these aggregations appeared to be guided by surrounding landscape features as caribou utilized a common travel corridor through peatlands, which extended across a secondary highway and forestry access road. Knowledge of this route by local hunters and frequent sightings of caribou during late autumn and early spring where this route intetsects roadways suggests traditional use of this travel corridor.

Discussion

Woodland caribou in the Wabowden area form a relatively small herd that exists primarily within a large open and treed peatland complex. Our adult survival rate obtained for the study period is within the 78-93% range observed for caribou throughout North America (Bergerud, 1980; Edmonds, 1988), and at the high end of the 84-90% survival estimated for woodland caribou populations inhabiting the boreal forests of western Canada (Darby, 1979; Fuller & Keith, 1981; Stuart-Smith *et al.,* 1997; Rettie & Messier, 1998). The calf:cow ratio observed for 1995 (0.65) is considerably higher than the 0.27-0.43 range reported during autumn for other woodland catibou studies (Bergerud, 1980; Edmonds & Smith, 1991; Seip, 1992; Chubbs *et al.,* 1993). However, in Newfoundland and Ontario calf:cow ratios have been reported as high as 0.53 and 0.50 in some years (Bergerud, 1985; Chubbs *et al.,* 1993). In addition to the latge calf:cow ratio, the high survival of the calves observed in early June, and the 30% autumn calf composition also suggests that calf survival until early November was high for 1995. Though most studies indicated considerable mortality within the first year (Mahoney, 1990; Stuart-Smith *et al.,* 1997; Rettie & Messier, 1998), high calf survival in some years is not uncommon. Autumn calf compositions have been documented as high as 20 and 25% for some forest and mountain dwelling herds (Bergerud & Elliot, 1986; Bergerud & Page, 1987; Edmonds & Smith, 1991). The high calf recruitment and low adult mortality leading to an exponential rate of inctease of 0.17±0.15, suggests that the population in 1995 was incteasing. Caution is needed however in using these results in the formulation of any management decisions as our data are limited and calf recruitment and adult mortality can vaty considetably from year to year (Bergerud & Elliot, 1986; Bergerud & Page, 1987).

Causes of mortality of both adults and calves were largely unknown. In other studies where woodland caribou inhabited peatland dominated systems, wolves were considered as the main source of adult mortality (Stuart-Smith *et al.,* 1997; Rettie & Messier, 1998). Black bears may also kill calves during a short period in the spring when woodland caribou and bears may be using similar food resources and consequently exhibit an overlap of theit ranges (Rettie & Messier, 1998).

The sex ratio fot adults of 0.5 males per female (approximately 33% males), is similar to the 36% males reported for North American caribou populations (Bergerud, 1980; Edmonds, 1988), but notably less than the 46.5% males reported in peatland systems in north-eastern Alberta by Stuart-Smith *et al.* (1997) and Fuller & Keith (1981).

Home and summer range sizes of the Wabowden herd are consistent with those described for woodland caribou inhabiting peatland systems (Fuller & Keith, 1981; Bradshaw *et al.,* 1995; Stuart-Smith *et al.,* 1997; J. Rettie, pers. comm.). Though these home ranges may be comparable to caribou across Canada, it appears that the summet ranges are on average larger than those reported for caribou utilizing alpine, forest, or island and shoreline systems (Shoesmith & Storey, 1977; Darby & Pruitt, 1984; Cumming & Beange, 1987; Edmonds, 1988).

Fidelity to calving and summering areas by individual cows (as found in this study) has also been observed by caribou to the west of this area (Shoesmith & Storey, 1977), as well as in Labrador (Brown & Theberge, 1985) and Alberta (Edmonds, 1988). Trends in wintering locations, however, showed much variability between and within individuals and this variability was consistent with the behaviour of other woodland caribou populations across Canada (Shoesmith & Storey, 1977; Darby & Pruitt, 1984; Edmonds, 1988; Stuatt-Smith *et al.,* 1997). Regardless of individual variability, it appeats that woodland catibou hetds may possess general wintering areas (this study; Paré & Huot, 1985; Cumming & Beange, 1987; Edmonds, 1988), and as observed here, some populations may exhibit little or no differentiation between winter and summer areas (Paré & Huot, 1985; Ouellet *et al.,* 1996; Stuart-Smith *et al.,* 1997).

The pattern of group formation, with females relatively solitary during the calving and summer periods, and forming larger, loosely cohesive groups during the test of the yeat, generally occurs for most woodland caribou populations across North America (Bergerud *et al.,* 1990; Stuart-Smith *et al.,* 1997; Rettie & Messier, 1998). Our study population appears unusual, however, by exhibiting post-tut and pre-calving aggregation periods, where the majority of caribou congregated in mixed-sex groups on a specific portion of their range. Though studies have indicated that woodland caribou may form aggregations duting the autumn (Darby & Pruitt, 1984), winter (Cumming & Beange, 1987) or late winter (Brown *et al.,* 1986), the pattern of these aggtegations did not serve to concentrate the population to a specific area. Only certain herds of mountain caribou in British Columbia and Alberta have been observed congregating on ttaditional rutting areas (Bergerud & Elliot, 1986; Edmonds, 1988). The purpose of these observed aggregations is unknown. It may be that this group formation serves a social function, or is related to certain dietary or mineral needs. Regardless of the function of these aggregations, increased travel by caribou from the northern peatland complex resulted in higher energetic costs and potentially greater predation risks (Bergerud & Page, 1987). The timing of these movements associated with these aggregations (and seasonal range shifts) coincided with periods of increased activity observed for other caribou populations (Brown *et al.,* 1986; Bergerud *et al.,* 1990; Ferguson *et al.,* 1998). Unlike the findings of a number of studies that stated woodland catibou movements were "apparently random" (Darby & Pruitt, 1984; Cumming & Beange, 1987; Stuart-Smith *et al.,* 1997), the seasonal movements of the collared females appeared to be well defined, predictable, and directional.

Predation has been implicated as the primary factor determining woodland caribou population distribution and range. Within this constraint caribou select sites that provide optimal forage resources, escape from biting insects and allow ease of travel in deep snow (Bergerud *et al.,* 1990; Ouellet *et al.,* 1996; Rettie, 1998). The selection of sites to reduce predation risk is especially important during the calving and wintering periods (Bergerud *et al.,* 1984; Gautier & Theberge, 1986). The type of habitat used to space away from predators varies depending on the landscape structure, and caribou have been observed using islands and shorelines (Shoesmith & Storey, 1977; Cumming & Beange, 1987), alpine and subalpine areas (Bergerud et al., 1984; Edmonds & Smith, 1991), fotested areas (Edmonds, 1988) and peatland systems (this study; Stuart-Smith *et al.,* 1997; Rettie, 1998) during the calving and summering period. The selection of such sites, howevet, can sometimes be at the expense of limited food supplies (Betgerud *et al.,* 1984; Ferguson *et al.,* 1988; Edmonds & Smith, 1991).

We suggest that caribou in central Manitoba may be behaving similarly to those described by Stuart-Smith *et al.* (1997). These caribou are likely restricting themselves within a peatland system to space away from predators and alternative prey, and dispersing (spacing out from each other) during the calving period, to increase predator search time (Bergerud & Elliot, 1986; Seip, 1991). The overlap of the summer and winter concentration areas at the population level suggests that these habitats are able to simultaneously provide avoidance to predators as well adequate food supplies throughout the year. Vegetation sampling within these ateas tevealed that they contained good quantities of foodstuffs such as bog shrubs, graminoids, and horsetails, as well as locally abundant patches of terrestrial and arboreal lichens (K. Brown & F. Messier, unpubl.).

Management implications

To ensure the long-term persistence of caribou in the Wabowden area, the main objective should be to maintain the integrity and connectivity of the peatland system which these animals inhabit. Fragmentation of the area by logging and associated road building should be limited as this may displace animals from such areas, or jeopardize their spacing away strategy, possibly resulting in an increase in caribou mortality. The two areas of concentrated activities should be reserved from cutting if possible. This is especially important considering the southern portion of the study area serves as a focal point for the population. Disturbances in this area that increase mortality, especially during aggregation periods, have the potential to affect the future of the entire population. Buffers should be retained around the peatland system, especially in areas of high use, as cutting stands adjacent to the peatlands may increase local moose densities and facilitate an influx of predators into the system.

The maintenance of the ttavel cotridor between the areas of activity should be considered with a special concern. Additional roads and cutting along this corridor should be minimized. Though this and other populations have been shown to tolerate roads and railways across such traditional routes (Johnson & Todd, 1977), additional distutbances may inhibit caribou movement, resulting in the fragmentation of the herd and possibly overgrazing on parts of the range (Klein, 1980).

If cutting is to occur within the peatland system, access into the caribou range should be minimized. As the amount of legal and illegal harvest of caribou can be a locally important cause of mortality in areas with road access (Johnson, 1985; Benoit, 1996), logging roads within the system should be closed as soon as possible after forestry operations. The use of winter roads (ice roads), whenever possible, would limit the time when huntets and predators could gain easy access into caribou-sensitive areas. In order to discourage moose in the areas that are harvested within the peatland systems (and subsequently associated predators), forestty practices in these areas should promote the rapid recovery of coniferous species such as jack pine and/or black and white spruce.

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Conservation of wild reindeer in Kamchatka

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Abstract: The wild reindeer of Kamchatka were never numerous and probably did not exceed 15 000 in number because of the restricted amount of winter and summer range, and the characteristically deep snow of the peninsula. Before 1960, biologists believed there was 1 population with 3 major wintering areas. The inaccessibility of the interior of the peninsula provided natural protection for wild reindeer and orher wildlife. After 1960, the road system was expanded for rhe benefit of the logging and mining industries, and poorly regulated commercial hunting of wild reindeer expanded. The wild reindeer population declined rapidly, and became fragmented into 3 herds by the early 1970s. The herds in southern and northeastern Kamchatka were reduced to a few hundred animals, but the herd in eastern Kamchatka that was largely protected by the federal Kronotskii Biosphere Reserve recovered. Poorly regulated hunting and competition with domestic reindeer continue to be the major conservation issues facing wild reindeer in Kamchatka.

Key words: herd fragmentation, industrial development, logging, mining, *Rangifer tarandus phylarchus.*

Rangifer, Special Issue No. 12, 95–98

Introduction

Wild reindeer (originally classified as *Rangifer tarandus phylarchus* by Hollister, 1912, but latet lumped with *R. t. fennicus* by Banfield, 1961) are indigenous to the Kamchatka Peninsula. These wild reindeer were never numerous, and probably did not exceed 15 000 in number (Baskin, 1968). Before 1960, biologists believed there was a single population (referred to as the "gteat herd of the Patapol'sky Dol", but in winters with particularly deep snow the wild reindeer concentrated in 3 separate areas (Baskin, 1968) (Fig. 1). The total population was probably limited by the amount of suitable winter range, the characteristically deep snow of Kamchatcka, and a lack of alpine-tundta summer range.

During the 1960s and early 1970s, the domestic reindeer industry was expanded and logging roads were built in the valley of the Kamchatka River. These developments resulted in increased hunting that was poorly regulated, and the wild reindeer population declined (Vershinin, 1972; Vershinin *et al.,* 1975). By the early 1970s the population was fragmented into 3 separate herds totaling about 8500 wild reindeer. In this paper, I review the history of these 3 hetds and discuss factors that influence their population size and conservation. Information for this review came from records of the Game Department of Kamchatka, the Institute of Ecology and Environment of the Kronotskii Biosphere Reserve, and occasional aerial surveys by reserve personnel.

Southern herd.

The Southern herd numbered about 3000 animals in the mid-1970s, and it occupied the best wild teindeer range on the peninsula (Fil, 1973). The population was highly productive with a potential increase of about 350 animals per year, the wolf population was low, and there was little mortality to wild reindeer. However, from 1975 to 1980, the development of roads for gold mining and overhunting by commercial hunting companies resulted in a population decline. About 600 wild reindeer were being killed by huntets annually. By 1985 hunting was restricted, but the herd continued to decline from legal and illegal hunting (Mosolov, 1990a) (Table 1). At that time both wintet and summer pastutes were affected by industrial development (road construction), and the caribou no longer formed large herds, even in winter. In 1995 caribou hunting was completely stopped, and a new territorial reserve (nature park) was established to

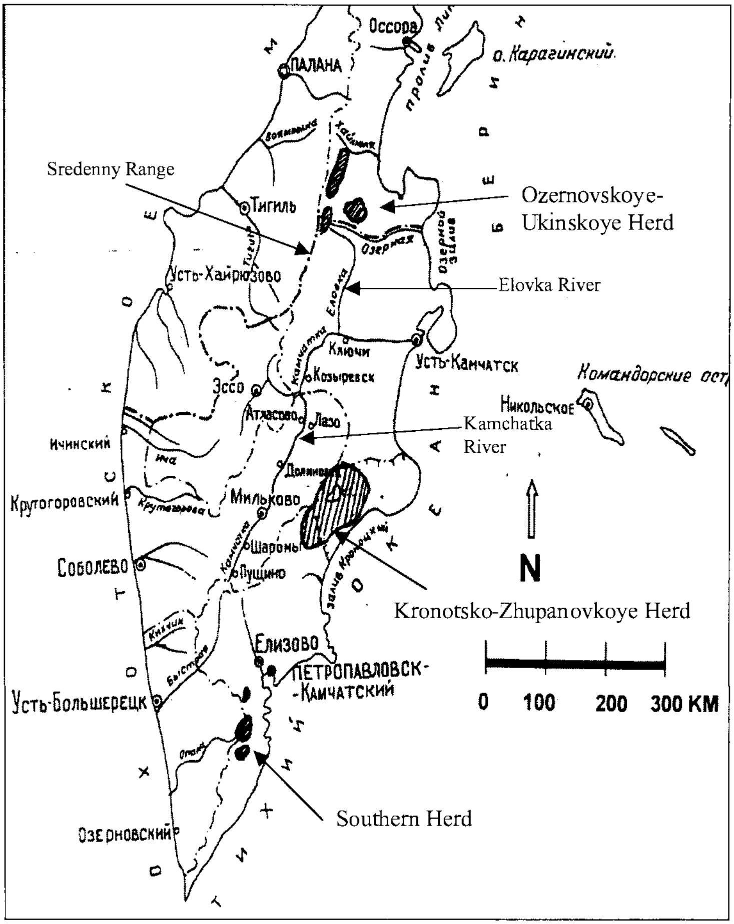

Fig. 1. Present distribution of caribou in Kamchatka.

protect the herd. At the ptesent time the number of caribou in the Southern herd is stable at 300-350 animals.

Ukinskoye-Ozernovsko herd

The northernmost of the 3 herds, this population was initially less influenced by human activity (Vershinin, 1972; Mosolov, 1990a). This area was largely roadless and inaccessible, especially the mountain tundra along the Sredynny Range, which runs from north to south in the central part of the peninsula. However, areas used by this herd to the west of the Sredynny Range had been used for domestic reindeer herding for a long time in summer, and hunting on the winter range was gradually causing a reduction in caribou numbers. The population decline was much slower than in the south until the sawmill industry was developed in the valley of the Elovka River (a northern tributary of the Kamchatka River). The increased access resulted in more, uncontrolled, hunting pressure, and the herd's rate of decline increased (Table 1).

Kronotsko-Zhupanovskoye herd

Wild reindeer in eastern Kamchatka had also been gradually reduced by hunting, from a high of 4500-5000 in the 1940s to about 800 in 1968 (Averin, 1948). Beginning in the early 1900s, a large part of the area had been protected as a national reserve (Zapovednik), where all hunting was prohibited. However, in 1945 the size of the reserve was reduced, and wild reindeer numbers in the area declined. Fortunately, in 1968, the reserve (Kronotskii) was reestablished within the area it had previously occupied, and the reestablished reserve included about 40% of the range used by the reduced population of 800 wild teindeet. Up to 60% of the wild reindeer pastured outside the reserve, but the protection provided by the reestablished reserve allowed the Kronotsko-Zhupanovkoye herd to recover.

Unfortunately, domestic teindeet husbandry was encouraged in eastern Kamchatka in the 1970s, and the Kronotsko-Zhupanovkoye herd faced a new threat. Reindeer husbandry was relatively new in eastern Kamchatka and reindeer had never been herded east of the Valaginsky Range until 1976. The mountain areas of eastern Kamchatka were traditionally winter pastures for wild reindeer that had been preserved and carefully hunted by the aboriginal tribes. In winter, most of the Kronotsko-Zhupanovskoye herd moved to the mountain tundra of the Zhupanovsky Dols, which was reportedly the best wintet pastute for caribou on the Kamchatka Peninsula. By the end of winter, animals from all over eastern Kamchatka, including animals from the reserve, used the area. However, in low-snow winters up to 15% of the caribou from the Kronotsko-Zhupanovskoye herd stayed in the central part of the Kronotskii Reserve on coastal plain tundra (Averin, 1948; Baskin, 1968).

Table 1. Population dynamics of wild teindeer in Kamchatka, 1980-1997.

Herd	Year							
	1980	1983	1985	1987	1990	1992	1995	1997
Southern	1450	800	550	300	220	150	170	200
Kronotsko-Zhupanovskoye	880	1000	1360	1700	1910	2520	2700	2800
Ozernovsko-Ukinskoye	2100	1700	1150	900	650	450	300	350
Total on the peninsula	4430	3500	3060	2900	2560	3120	3170	3350

Reindeer husbandry began to displace wild reindeer and forced a change in the winter and summer distribution and migration patterns of the Kronotsko-Zhupanovskoye herd within 2 to 3 years after it began. Five years later the winter distribution of the Kronotsko-Zhupanovskoye herd changed significantly, and by 1985, 80% of the herd was pasturing in the Kronotskii Reserve (Mosolov, 1990a; b; Table 2). Part of the problem was that reindeer herders shot at wild reindeer to deliberately disturb them and keep them away from domestic herds.

Discussion

Wild reindeer in Kamchatka have been advetsely affected by 2 major factots; unregulated hunting, and competition and displacement by domestic reindeer. Before 1960, when much of Kamchatka was inaccessible to people, wild reindeer were protected by natural refugia. As roads were built for logging, mining and the expansion of teindeet herding, hunting of wild teindeer reached unsustainable levels. Hunting was not easily tegulated by authorities because of the profit-motive, the large area involved, and because of politics. As the peninsula was developed and natural refugia were eliminated, the necessity for formal reserves increased, and the protection provided by the federally protected Kronotskii Reserve became more critical. Territorially protected reserves (Nature Parks) are still subject to the influence of local politicians, and may not always provide protection if othet valuable resources are found within their boundaries.

Reindeer herding has also been a major conservation problem for wild herds in Kamchatka and othet areas of the Far East, and in Siberia as well (Baskin, 1968). Two problems have arisen in connection with reindeer husbandry. Reindeer herders often shoot wild reindeer for food, to sell the meat, or to chase wild herds away from domestic stock, and domestic reindeer compete with wild reindeer for food. Stock protection has been viewed as a legitimate reason for shooting wild reindeer in the past, and domestic reindeer herding has explicitly or implicitly been given priority over the protection of wild reindeer.

From our studies on the Kronotsko-Zhupanovskoye herd, we arrived at the following conclusions about the influence of domestic reindeer on wild reindeer (Mosolov, 1990a; b):

- After 3 to 5 years' competition, caribou can be expected to leave their traditional winter pastures and may be forced to feed on less accessible parts of the mountain pastures, including the steeper slopes of volcanoes. This leads to highet mortality in young animals.
- The telatively poor mountain pastures that comprise most caribou range in Kamchatka can be completely destroyed by large herds of domestic teindeer within about 2 to 3 seasons, and it takes 12 to 15 years to restore some parts of the lichen tundra.
  The high level of distutbance (i.e., shooting and chasing) on winter ranges resulted in decreased group size and in structural changes in the population (percentage of male, female, etc.).
- The presence of domestic reindeer herds on spring and summer ranges results in destruction of the spatial structure of the caribou population (calving and breeding areas, and seasonal migration passages are shifted).

In the Kronotsko-Zhupanovskoye hetd, access to winter range is critical because of the typically deep snow in the area. Mortality is highest during winter, and up to 45% of calves and 30% of yearlings can die. The main winter ranges of the herd are within the Kronotskii Reserve in the mountain tundra zone, and up to 80% of the herd winrers there (Fig. 2). In winter, it is important for wild reindeer to be able to feed undisturbed by hunting and domestic reindeer.

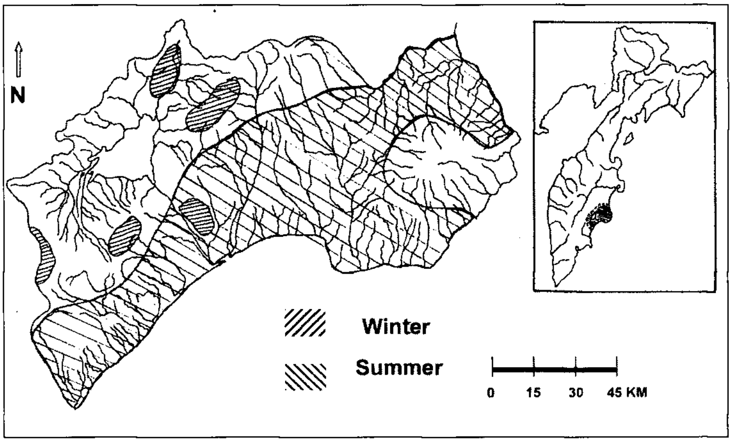

Fig. 2. Seasonal caribou range in Kronotskii Reserve.

Table 2. Proportion of wild reindeer in Kronotskii Biosphere Reserve compared to the total number in eastern Kamchatka (Kronotsko-Zhupanovkoye Herd), 1980-1997.

Year	Caribou in eastern Kamchatka	Caribou in Kronotskii Reserve (% of total)	
1980	880	620	(70)
1983	1000	740	(74)
1985	1360	1080	(79)
1987	1700	1460	(86)
1990	1910	1650	(86)
1992	2520	2200	(87)
1994	2650	2300	(87)
1997	2800	2650	(95)

Management Recommendations

Preservation of wild reindeer on the Kamchatka Peninsula, to a latge extent, depends on the condition of their largest population-the Kronotsko-Zhupanovskoye herd. The Kronotskii Reserve is key to protecting this hetd, but some winter pastures are located outside the reserve, and caribou are vulnerable in these areas. A complete ban on caribou hunting in eastern Kamchatka should be implemented to protect the herd in winter.

In the near future, protection and restoration of wild reindeer in other areas of Kamchatka will be difficult. A more effective system of tegulated hunting needs to be developed, and a highet priority will have to be given to maintaining wild herds. However, as long as 1 viable population exists in eastern Kamchatka, wild reindeer from this herd could be used for reintroduction to other areas when chances for the survival of other herds improve.

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THERE ARE SOME BEAR HUNTING PROBLEMS IN KAMCHATKA

The Eight North American Caribou Workshop,
Whitehotse, Yukon, Canada,
20–24 April, 1998.

Brief communication

Caribou behaviour near BHP's Ekati Diamond Mine, Northwest Territories, Canada, during the first year of construction

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Introduction

The main objective of this study was to measure impacts that mine construction has on caribou, with reference to group size distribution, seasonal movements, and behaviour of the Bathurst caribou herd which migrate through the area.

Study area

BHP's Ekati Diamond Mine is located in the Northwest Territories, Canada, about 300 km northeast of Yellowknife. At approximately 64°40'N latitude and 110°43'E longitude, the mine site is located about 80 km notth of the treeline in tundra habitat. The mine occurs within the geological region known as the Slave Geological Province. The 1997 wildlife study area was approximately 1600 km^2. The northern boundary was extended to include the Sable Lake area; a main part of the claim block where exploration was still occurring.

Methods

Fortythree helicopter aerial surveys were flown between 16 May and 2 October 1997 in the study area to document location of caribou groups, plus their size and direction of movement.

Focal animal (reaction to potential stressors) and scan sampling (activity budgets; 8 min interval) were used to document caribou behaviour on the mine site and over 2 km from the mine site (control areas). Behaviours recorded were feeding, bedded, standing, walking, trotting and running. Reactions to potential stressors were noted from 0 (none) to 3 (severe, runs away).

Results

Relative abundance and seasonal movements of caribou

Caribou group size was not affected by proximity to Ekati Diamond Mine during either the northern (n=98, P>0.50) or southern (n=174, P>0.30) migration.

As caribou approached the mine during the northern migration, direction changed (χ^2=7.87, df=2, P=0.02), with an increase in NW movement. No caribou were observed crossing the proposed Misery Road route within 5 km of the mine, but sample size was small (n=19). This area did have over 30% boulders and similar habitat farthet from the mine also showed less caribou usage. Further work is required to determine whether observed movement patterns are related to mine construction or to other environmental factors.

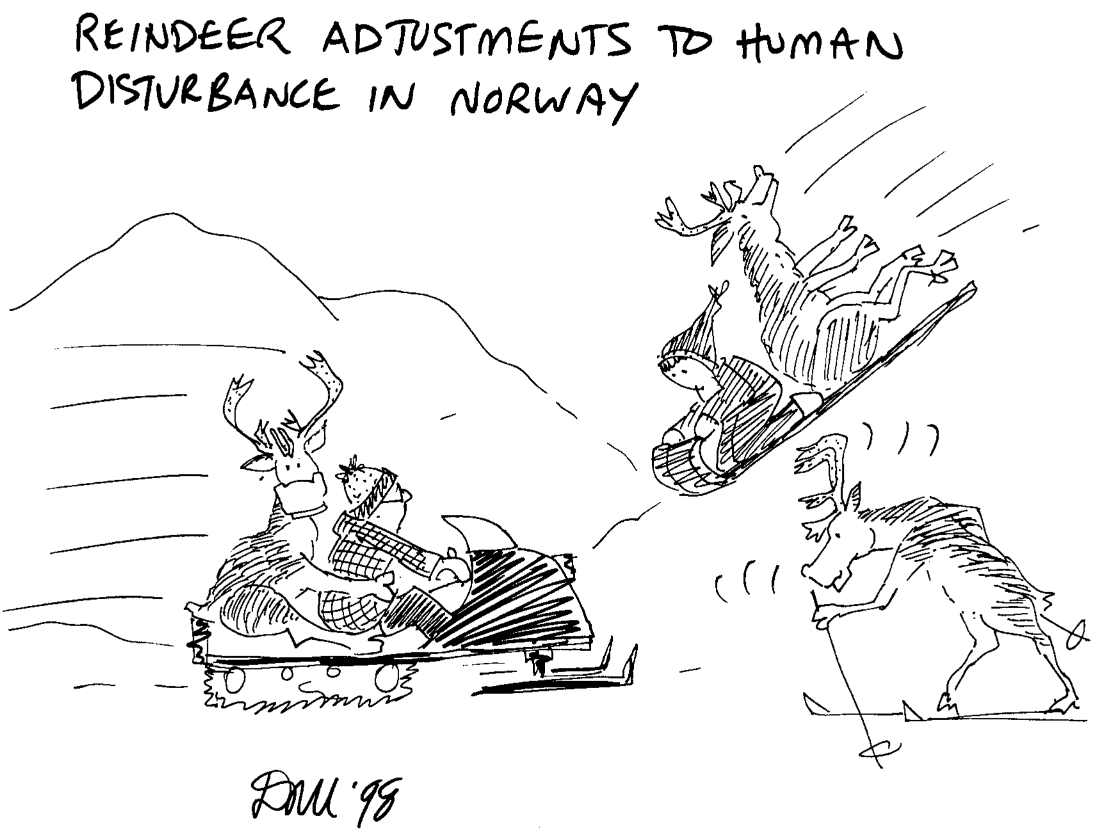
Mine construction and caribou behaviour – Focal animal observations

Caribou did not show any reaction to individual potential stressors, such as truck ttaffic 60-85% of the time. Running response (type 3 reaction) was only elicited by helicopters flying high or low, and low flying planes. Low flying helicopters were the main cause of distutbance at any level. Overall caribou were being disturbed at any level less than 3% of the time.

Mine construction and caribou behaviour – Scan samples
Movement behaviour (walk, trot, run) was more frequent than comfort behaviour (bed, feed, stand) on the mine site as compared to control sites (χ^2=3.24, df=1, P=0.07). Therefore, although not distutbed much by individual stressors, cumulative effect of mine consttuction activities may reduce caribou comfort behaviours.

Future wildlife effects monitoring
A Mine Operational Phase Wildlife Effects Monitoring Plan was developed using a risk-based planning process. It considered all potential stressors, used previous results to characterize likely exposure and involved aboriginal, government and other stakeholders in its development.

Specific alternate hypotheses concerning mine effects on catibou will be tested in 1998. Results will be used to gauge the efficacy of mitigation measures (such as road construction without berms), to modify mitigation measures as necessary, and to refine the monitoring plan.



Fragmentation, overgrazing and anthropogenic disturbance in Norwegian reindeer ranges

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Abstract: Throughout the last centuries, wild reindeer ranges in Southern Norway have been exposed to substantial increases in human use. Historically, wild reindeer ranges srretched uninhibited across most of the mountains of Southern Norway. The number of human transport corridors, hydroelectric development and associated activities, transmission lines, and other forms of human "obstacles" have resulted in a fragmentation of the presumed larger range into 26 smaller and more or less isolated populations. In recent decades, possible impacts of fragmentation have been exacerbated by a marked increase in tourism. The present populations have different hisrorical backgrounds. Mixing of wild with once domesticated reindeer, establishment of feral populations, and different environmental conditions, management practices and intensity of human disturbance over time generates inter-population variation. This results in different responses towards human disrurbance in each independent population. Response may also vary according to within population variation. Over the last 100 yrs, total wild reindeer range in Southern Norway has decreased, while total number of reindeer, and thus, density, has increased, resulting in substantial overgrazing in a few ranges. This is a combined result of fragmentation and poor management. Effects of disturbance or fragmenration on range access have been documented for some populations. These include loss of peripheral ranges crossed by disturbance corridors and inhibition of traditional movements among ranges, with implications for forage intake and herd productivity. It is possible that an cumulative effect of fragmentation, overgrazing and increase in human disturbance could result in decreased population productivity. Howevet, it is difficulr to generalize and ask; how do wild reindeer react to human distutbances, and will they survive an increase in human activities combined with possible additional fragmentation of their ranges? As we have seen, regardless of fragmentation and overgrazing, separate populations of wild/feral reindeer in Southern Norway differ in their reactions towards anthropogenic disturbances because of their inter- and intra-population variation. We need to ask, can a population survive? We are then asking, can that *population* habituate to human activities and simultaneously adapt to fragmenration and specific management practices? In Norway, ongoing and new research programs have been initiated in separate populations ro assess and document interactions between range availability, anthropogenic disturbance, reindeer behavior towards disturbances and herd productivity.

Shifts in the distribution of calving caribou: developing a model for assessing the impacts of development

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Abstract: Fidelity to calving grounds is the accepted standatd for identifying discrete caribou (*Rangifer tarandus*) herds. However, quanrifying variations in calving distribution has been the subject of considerable debare. We used fixed kernel analyses to estimate spatial properties of the calving distribution of the Central Arctic caribou herd (CAH), 1980-95, based on 183 calving locarions from 96 radio-collared females. Size of the total calving area declined from 11 187 km^2 during 1980-1985 to 6585 km^2 during 1990-95. Similarly, size of the concentrated calving area declined from 1209 km^2 during 1980-85 to 483 km^2 during 1990-1995. Calving distribution was bimodal throughout 1980-95, with concentrared calving found both east and west of the Sagavanirktok River. The concentrated calving area east of the Sagavanirktok, without development infrastructures, remained relatively constant in location during 1980-1995. However, the concentrated calving area within the Kuparuk Development Area (KDA) fragmented and shifted south and west. By 1990-95, there was no concentrated calving within the KDA. We conclude that such a shift in calving distribution is the most likely response of the Porcupine caribou herd to future development within its calving ground and should serve as a basis for assessing changes in forage quantify and quality. These changes in forage can then be used to project the effects on calf survival and, hence, population growrh under a hypothetical scenario of oil development.

Survival and reproduction of woodland caribou in the boreal region of northern Alberta

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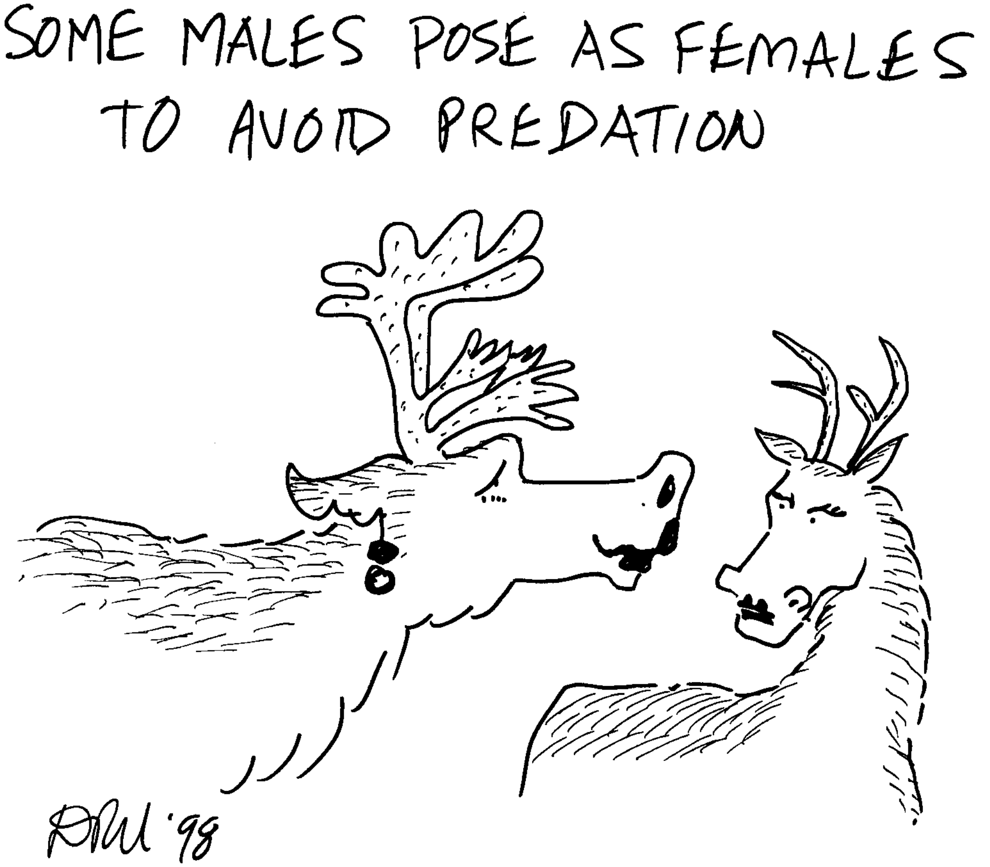
Abstract: A collaborative research program focusing on woodland caribou began in norrhern Alberta in 1991. The partnership involves representatives from government, industry, universiry and Firsr Nation's. Two main goals exist for the research program: (1) to establish a knowledge base of caribou ecology (e.g., popularion dynamics, movements, habitat use, etc.); and (2) to evaluate the effects of human activity on woodland caribou. Knowledge acquired through the research program is to provide support for land-use guidelines that will facilitate industrial activity while at the same time conserving woodland caribou populations. This research is conducted by biologists of the Boreal Caribou Research Program (the amalgamated research subcommittees of the Northeast and Norrhwest Regional Standing Committees on Woodland Caribou). Understanding survival and recruirment are important components of monitoring caribou population dynamics. Since 1991, woodland caribou ecology has been studied in several areas of northern Alberta. A total of 260 caribou have been collared in the areas near Red Earrh (*n*=36), Caribou Mountains (*n*=38), Wabasca (*n*=84), Agnes Lake (*n*=16), Egg Lake (*n*=21), Algar Lake (*n*=18), Crow Lake/other (*n*=7) and in rhe Cold Lake Air Weapons Range (*n*=40). Monitoring of these ateas will continue for at least the next two years. In a recent publication, Stuart-Smith *et al.* (1997; *J. Wildl. Manage.* 61: 622-633) reporred adult survival in a 20 000 km^2 study area of northeastern Alberta averaged 0.88+/-0.03. Calf survival ro March was 18 calves/100 cows. I will presenr an update on caribou survival and causes of adult mortality for the northeastern Alberta study ateas and compare rhese values to those for the Red Earth (northcentral Alberta) and Caribou Mountains (northern Alberta near the Northwest Terrirories border). Implications for population dynamics of woodland caribou will be discussed.



Response distances of Forelhogna reindeer after disturbance by humans on foot or skis

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Abstract: The purpose of rhis study was to measure reindeer fright distances in Forelhogna, Norway, and identify factors involved in Forelhogna reindeer's response towards humans on foot or skis. The study was carried our in March, July and September/October 1996. A comparison among seasons was used in resting whether reindeer in Forelhogna become more shy directly after the hunting season (August 20-September 20) compared to before (July) and winter (March). The reindeer were approached by humans on foot or skis and 5 response distances were measured: sight, fright, flight, running and "curiosity" distance. Seven independent variables (area, season, topography, wind direction, herd size, herd structure and level of insect harassmenr) were recorded to analyze their individual or combined impacts on the responses recorded. Where the reindeer moved after a provocation in relation to wind direction and terrain was also recorded. When possible, the leader of the group when in flight was recorded for mixed groups. The longest average fright and flight distances ±standard error of the mean, respectively, were recorded in winter (193±16 m, 151±19 m), followed by summer (169±15 m, 142±14 m). The longest running and curiosity distances, respectively, were recorded in summer (487±52 m, 71±36 m) followed by winter (215±30 m, 67±11 m). These 4 distances (same order as above) were shortest in autumn, i.e., after the hunting season (107±9 m, 86±8 m, 198±38 m, 42±11 m). In the winter and autumn seasons, smaller groups (<20) had significantly longer running distances than medium(>20 and <75) and larger groups (>75), with clearer results from rhe autumn season (P<0.01). For the summer season, there were no significant difference between group sizes for running distance. There was no significant difference among days with vs days without insect harassment for any distance. When data was combined for all seasons, the independent variables season and group size, respectively, significantly effected the fright (P<0.001, P=0.004), flight (P<0.001, P<0.001) and running (P<0.001, P<0.001) distances. Large groups showed a curiosity response more often than small groups (P<0,05), and when a mixed group showed a curiosity response towards humans, calves <1 yr. were most often the closest animal to the provocer (P<0.001). Curiosity distances for adulr >1 yr. males and females were almost equal. When provoked, reindeer most often moved up slope 73% (level terrain 11% and down slope 16%) and inro the wind 54% (with the wind 21% and sidewind 25%). When a mixed group (males and females) began to move, it was most often an adult female who led the group (P<0.05). Because the fright, flight, running, and curiosity distances were shortest after the hunting season (autumn), we concluded that reindeer in Forelhogna were not more shy (in fact, they were less shy) rowards humans after rhe hunting season compared ro before (July) or winrer (March).

A methodology for predicting effects of displacement on caribou populations: integrating behavior, habitat value, and population dynamics

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Abstract: We used: 1) observed changes in calving distriburion of the Cenrral Arctic caribou herd (CAH) during a period of increasing oil development, 2) documented avoidance of development infrastructure by parturient caribou, 3) observed changes in the phenology and biomass of caribou forage during a period of climate warming, and 4) observed response in early survival of calves of the Porcupine caribou herd (PCH) to climate induced changes in forage to develop a protocol for assessing potential effects of resource developmenr on the population level of the Porcupine caribou herd. During the period of increasing oil developmenr, 1980-1995, concentrated calving by the CAH gradually shifted south and west until concentrated calving no longer occurred in developed areas. During the warming period, 1985-1996, the amount of forage available to PCH caribou of on 21 June was a function of plant biomass available at calving and the rate of increase in forage during the post-calving period. Similarly, early calf survival was a function of plant biomass at calving and the rate of increase in plant biomass. We shifted the calving distribution of the PCH in relation to hypothesized oil development in a manner observed on the CAH, reinventoried forage available at calving and the post-calving rate of increase inforage, and used the relationship between calf survival and plant biomass to estimate resulting calf survival. Porenrial effects of development was assessed by comparing estimated calf survival before and aftet hypothesized redistribution of calving. Potential effects during the period 1985-1990 were minimal, but from 1991 onward potential redistribution of calving caribou subsrantially reduced calf survival. We will conrinue to refine and evaluate this model.

Abstract: The Eight North American Caribou Workshop, Whitehorse, Canada, 20-24 April, 1998.

Caribou calving grounds - dogma and diversity

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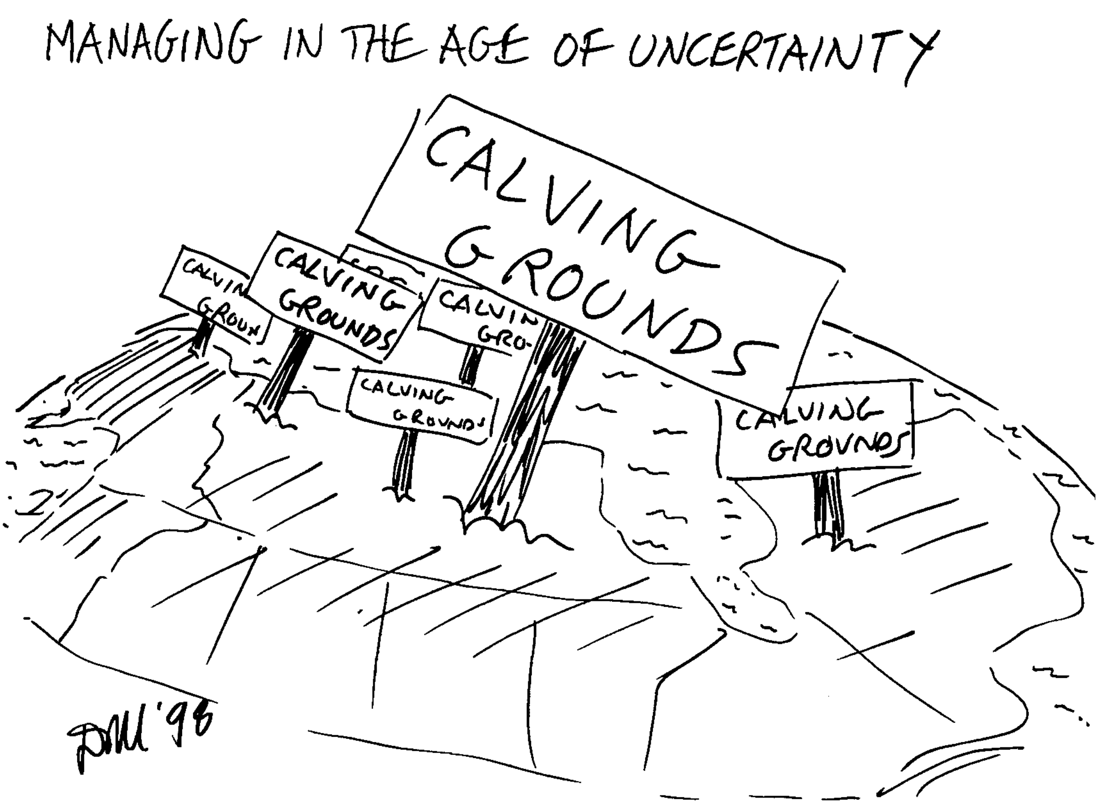
Abstract: Our knowledge for most of the 42 identified caribou calving grounds in the Northwest Territories is fragmentary but is sufficient to reveal the diversity of landscapes and vegetation communities used for calving. We (caribou biologists) frequently state that calving grounds are the most predictable areas seasonally occupied by caribou. But within the diversity of habitats used for calving there may be different models for fidelity depending on the vegetation and terrain. For three major barren-ground caribou herds in the NWT, we now have about three decades of survey information and satellite telemetry for four years. Individual cows calve at similar locations between years and calving grounds largely overlap between years. However over a longer time scale (decades), calving ateas directionally shift and that shift may be rotational with the cows rerurning to areas used decades previously. The fragmentary knowledge that calving ground locations may rotate over decades introduces uncertainty into managing land use activities on calving grounds. And in the face of uncertainty, the precautionary principle should apply to management of caribou calving grounds. (Now published in a report: Gunn & Fournier. 2000. File Rep. No. 123. 177 pp. Available from first author, address above).



The Eight North American Caribou Workshop,
Whitehorse, Yukon, Canada,
20–24 April, 1998.

Brief communication

Modeling energetic and demographic consequences of caribou interactions with oil development in the Arctic

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Introduction

We used empirical data from the oilfields and simulation models to assess the energetic and demographic consequences for caribou (*Rangifer tarandus*) encountering oilfield activity and infrastructure. Activity budgets of female caribou moving through an active oilfield during the insect season were used as input for an ENERGY model, which in turn provided the input for a PARTURITION Model, which was used as input into a POPULATION model (Fig. 1). Activity data were collected for Central Arctic caribou herd during summer in the early 1980s in the newly constructed Kuparuk Oilfield. ENERGY and POPULATION models were developed for the Porcupine caribou herd based on more than two decades of research in Canada and Alaska (Russell *et al.*, in prep.).

Because the models presently are being updated to reflect new findings, the results presented here are preliminary and are intended to demonstrate the conceptual approach, rather than to provide definitive predictions on the impacts of oil development on caribou. Final results will need to be validated by field studies. The potential value of this exercise is to provide a means for quantitatively assessing the impacts of oil development on caribou.

Materials and methods

Activity Budgets

Activity data were collected for Central Arctic caribou herd in the Kupatuk Oilfield during summers 1982-83 (Murphy *et al.,* 1987). Activity budgets were calculated for female caribou under a variety of

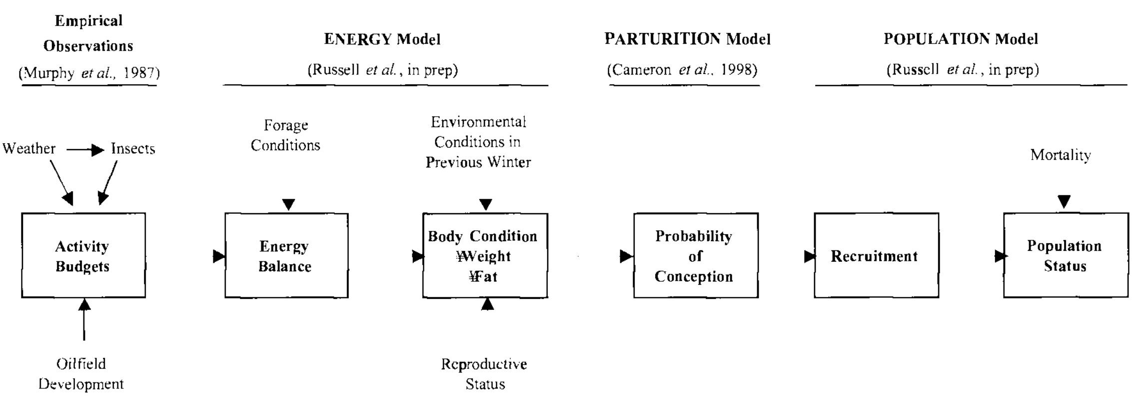

Fig. 1. A conceptual model depicting how empirical data and energy, parturition, and population models will be integrated to predict the effect of oil development on caribou.

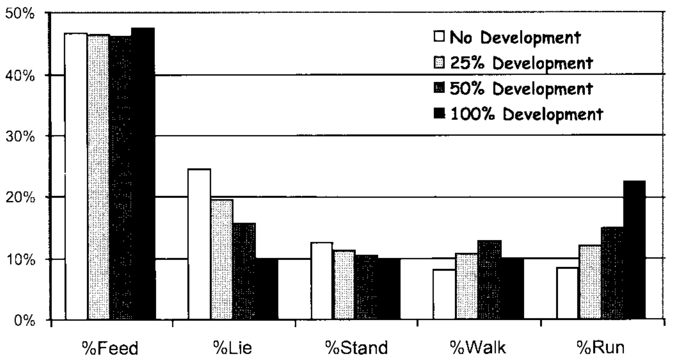

Fig. 2. Activity budgets of female caribou during mid-summer under different development scenarios. Exposure to development ranged from 0 (no development) to 100% development (i.e., animal spent 100% of mid-summer period with 600 m of a pipeline and road with heavy traffic.

insect and disturbance conditions, ranging from mild insect harassment and low disturbance to severe insect harassment and high disturbance (i.e., within 600 m of a pipeline and road with traffic). These budgets then were used to identify distance thresholds where caribou significantly altered their behavior in response to oilfield stimuli. For this modeling exercise, exposure scenarios (time spent in these different conditions) were developed separately for four different summer time periods (post-calving [10-20 Jun], movement [21-30 Jun], early summer [1-15 Jul], and mid-summer [15 Jul-8 Aug]) based on insect conditions recorded during the 1970s - 1990s and on four hypothetical levels of exposure to disturbance, ranging from no exposure to constant exposure (100%). Each exposure scenario (8 scenarios for each season) then was assigned an activity budget derived from empirical data.

Energetics

The ENERGY Model, developed primarily by the Canadian Wildlife Service and the Institute of Arctic Biology (Russell *et al.,* in prep.) simulates the energetic relations of an individual female caribou and predicts metabolizable energy intake (MEI) on a daily basis. Input variables for the model include diet, biomass of fotage, nutrient content of forage, and activity budgets. The model was exercised using settings that simulated both harsh and mild winters; however, only the output from the harsh winter scenarios are presented hete. The model operates on 15 life-cycle periods; activity budgets during four of these periods (noted above) spanning June-August wete modified for this exercise to simulate different insect and disturbance conditions. Output variables used in this exercise include weight of the cow at rut and percent body fat at rut.

Demography

The POPULATION Model, also developed ptimarily by the Canadian Wildlife Service (Russell *et al.,* in prep.) is linked to the output of the ENERGY Model. For this exercise, fall body fat was used to determine the probability of conception. Other than population size, the values used for the input variables are from the Porcupine caribou herd. Output variables used in this exercise include harvestable surplus and population growth rate assuming a fixed annual harvest.

Results and discussion

Activity Budgets

Insects significantly affected caribou behavior by decreasing time spent feeding and lying and by increasing locomotion. Oilfield disturbance affected caribou primarily by decreasing time spent lying and by increasing locomotion. When caribou were harassed by insects and encountered oilfield disturbances, time spent feeding did not change, although lying decteased and running increased with increasing levels of disturbance (Fig. 2).

Energetics

Summer is a time of energetic stress for female caribou because of harassment by insects and the high costs of reproduction and lactation. The model predicts that very high exposure to disturbance can adversely affect energy balance and cause females to lose fat and body mass (Fig. 3). If caribou were to spend 100% of their time within a zone of high disturbance during a year with severe insect harassment, for example, the model predicts they would lose up to 13% of their body mass (Fig. 3). Under a realistic development exposure scenario, however, an individual animal probably does not spend >25% of their time in a high disturbance zone; at 25% the model predicts <2% loss of body mass (Fig. 3).

Disturbance effects are more pronounced in years of severe insect harassment (Fig. 3), although the effects of disturbance and insects do not appear to be additive. The probability of conception can be

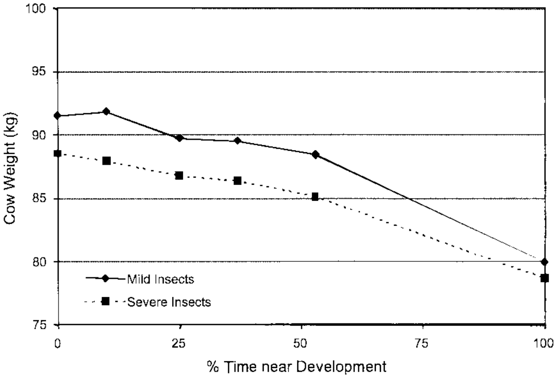

Fig. 3. Effects of insects and disturbance on cow caribou weighr in fall as predicted by an ENERGY Model and varied by exposure to oilfield disturbance.

predicted as a function of body fat or body mass in fall (Cameron *et al.,* 1998), therefore, the effects of disturbance on conception rate can be calculated and used as input for the POPULATION Model.

Demography

After a bad winter, a positive rate of growth can be achieved only under mild insect conditions and limited exposure to development (Fig. 4). If caribou were to spend 100% of their time within a zone of high disturbance during a year with sevete insect harassment, the population growth rate would decrease by 7% (Fig. 4). Under a realistic development exposure scenario (<25%), the model predicts ≤1% decline in the population growth rate.

Wintet conditions appeat to have a greater influence on energetics and demography than do insects and disturbance; indeed, the Central Arctic herd experienced a growth phase from 1978 to 1992 when winter conditions generally were mild (Fig. 5).

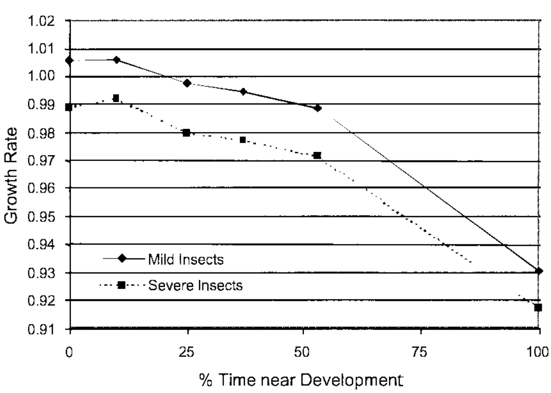

Fig. 4. Effects of insects and disturbance on the population growth rate of an arctic caribou herd as predicted by a POPULATION Model and varied by exposure to disturbance.

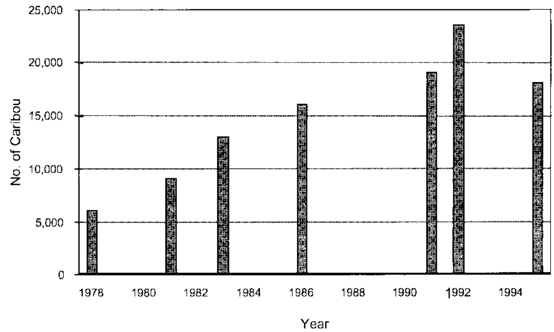

Fig. 5. Popularion esrimates for the Central Arctic caribou herd 1978-1995. Data are from Alaska Department of Fish and Game.

Conclusions

Identifying thresholds of disturbance that cause population-level impacts will provide useful information to assess the costs and benefits of new developments and will help oilfield planners to design infrastructure that accommodates caribou with minimal disruption. Before these models can be applied in this way, however, it will be important to fine-tune all steps in the procedure and to ensure that all empirical input data are as accurate and appropriate as possible. For example, the efficacy of using data from two different hetds for model parameters needs to be evaluated. It also is evident from this initial effort that the condition of animals entering the calving season greatly influences model outcomes. Thus, developing clearly defined and defensible rules for exercising the model is essential. We are focusing our current efforts accordingly.

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CONCLUSION: INCREASED LOGGING CAN OCCUR WITH INCREASED AIR TRAFFIC.

Woodland caribou distribution on winter range in relation to clear-cut logging in west central Alberta - preliminary analysis

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Abstract: This study examined the response of a herd of migratory woodland caribou (*Rangifer tarandus caribou*) in west central Albetta to timber harvesring that fragmented about 2% of their winter range. From 1981 to 1996, 45 caribou were radio-collared and monitored during 3 study periods: 1. the initiation of timber harvesting activity, 2. the completion of first pass timber harvest (50% removal), and 3. 1-2 years following the completion of first pass timber harvest on a portion of the wintet range. Variables examined were overall winter range size, mean individual winter range size, daily movement rates, distance to closest cutblock, percent of locations in cutblocks on winter range, annual adult survival and calf productivity. Based on preliminary analysis, no population response relative to increased timber harvesting was derected. In the post harvest study period only 7 of 852 caribou telemetry locations were within a cutblock. Distribution on the winter range varied by study period with movement away from the harvested area during harvest completion and a pattial teturn after harvesting ceased. Distance of radio-collared caribou from rhe cutblocks was grearest and daily movement rates most restricted during harvesr complerion. Mean individual winter range size decreased after harvesting was completed but overall herd range size remained the same. Caribou avoided using the area fragmented by logging and concentrated in the undisturbed portion of the winter range. Further analysis will examine in more detail this finding. If fragmentation of the winter range continues through timber harvesting and other industrial activities, the 'spacing out' antipredator strategy used by caribou will be compromised. Based on this initial analysis recommended timber harvesting strategies must ensure 1) sufficient area of usable habirat to support current population, 2) maximization of the volume temoved over the smallest area, 3) that forest succession is maintained at the current age and species composition, and 4) avoidance, in the shorr term of presently defined core use areas.

Industrial development and access: effects on movement and distribution of woodland caribou in Northern Alberta

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Abstract: Industrial development and associated road construction have been implicated as factors leading to displacement and declines of ungulates throughout North America. Foresry and petroleum development have a significant influence on the ground accessibility of many areas throughout Alberta. Woodland catibou are listed as a threatened species in Alberta and, because of this special status, have been the focus of landuse guidelines directed at industry. These guidelines evolved with the intent of minimizing exposure of caribou to human activity through: mapping of caribou zones, application of timing restrictions within some of these zones, and access management. In the absence of conclusive data, the caribou guidelines have applied a conservative approach to industry activity within these zones. A recent, intensive industrial development occurring within caribou zone provided a unique research opportunity to evaluate potential habituation or displacement of caribou. A research project was initiated in 1998 to simultaneously quantify the spatial and temporal use of this development area by humans and caribou. Linear developments (i.e. roads, pipelines) and point sources (i.e. well sites, cutblocks) are documented using a geographic information system. Traffic classifiers have also been deployed to document vehicle volume and type. Caribou movements are being intensively monitored using animal borne GPS collars (n=23). Methods of documenting caribou response and preliminary resulrs are presented.

Fright response of reindeer in four geographical areas in Southern Norway after disturbance by humans on foot or skis

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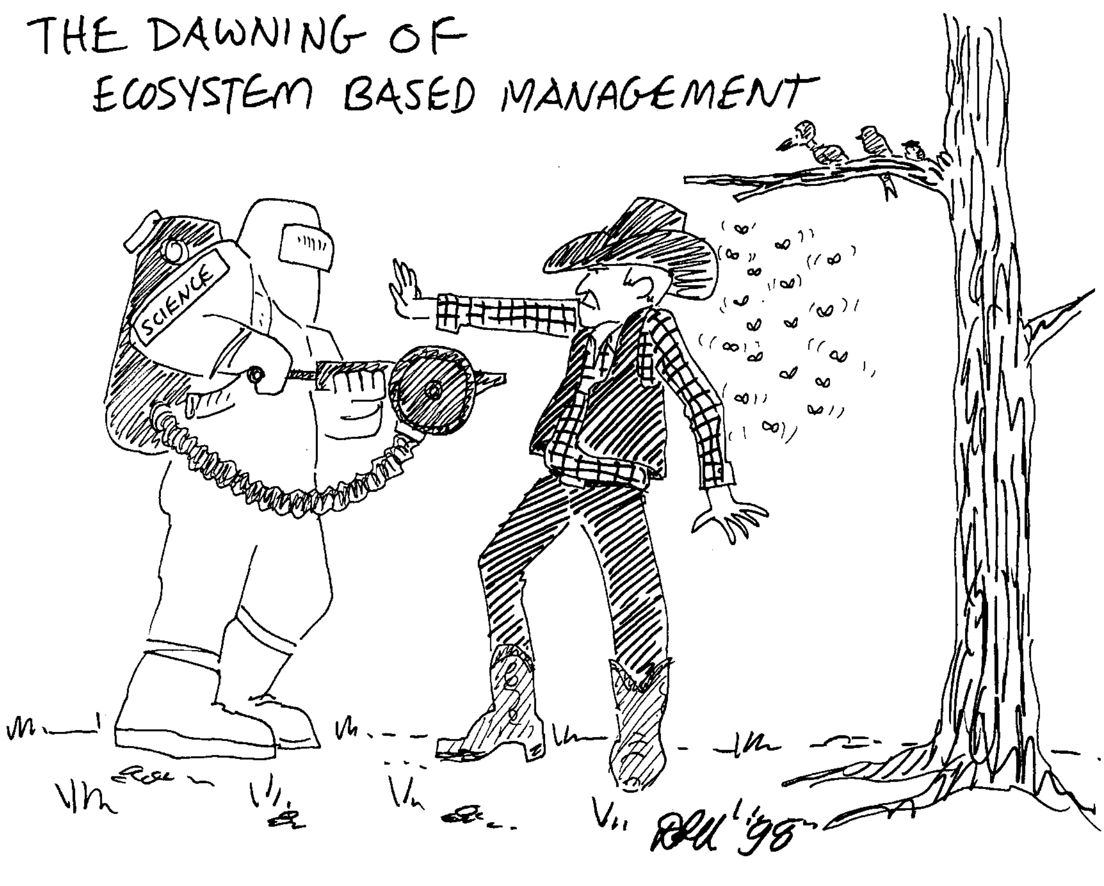
Abstract: The purpose of this study was to identify factots influencing wild reindeer's fright behavior towards human on foot or skis, and compare this behavior among 4 geographical areas chosen according to their degree of human acrivity and hunting. We tested 2 hypotheses; 1.) reindeer that are hunted by humans show stronger fright behavior towards humans after the hunting season than before and 2.) reindeer fright response towards humans on foor or skis is negatively related to the total level of human activity, including, but not limited to, hunting. Reindeer fright distances were recorded during summer, aurumn, and winter in 1 wild, Rondane north/Snøhetta (RN/SH), and 3 feral reindeer populations in Southern Norway; Norefjell (NoF), Ottadalen North (Od), Forelhogna (FoH). The presenr populations in NoF, Od, and FoH originared from domestic reindeer released or escaped in the 1950s and 1960s. For reindeer in NoF, rhe total level of human activity has continuously been high, and there was no hunting since the time of their release prior to this study. Reindeer in Od and FoH have been hunted since 1964 and 1956, respectively, and have simultaneously been exposed to a lower rotal level of human activity compared to NoF. Comparing Od with FoH, human activity in Od is lowest. RN/SH has the lowest level of human activity among the 4 areas, and hunting has occurred since pre-historic time. Fieldwotk was conducted during 3 seasons; winter (March), summer (July; before hunting season), and autumn(September/October; after hunting season) in 1992 (NoF and Od), 1993 (RN/SH) and 1996 (FoH). The reindeer were approached by humans on foor or skis and 4 response disrances were measured: sight, fright, flight and running. Six independent variables (area, season, topography, wind direction, herd size, and herd structure) were recorded to analyze their individual or combined impacts on the responses recorded. In Forelhogna, the 4 tesponse distances ± standard error of rhe mean were significantly longer before the hunting season (222±16 m, 169±15 m, 142±14 m and 487±30 m) than after the hunting season (189±11 m, 107+9 m, 86±8 m, 198±38 m). In NoF, Od, RN/SH fright distances befote and after rhe hunting season were almosr equal. When data was combined for seasons in each area, the 4 distances varied significantly among the 4 areas (P<0.001) and were longest in RN/SH (448±24m, 385±24 m, 324±22 m, 2634±350 m), followed by Od (194±8 m, 143±5 m, 91±4 m, 439±72 m) for running distance and FoH (220±19 m, 149±17 m, 122±16 m, 307±59 m) for sight, fright and flight distance. The 4 distances were shorrest in NoF (173±14 m, 90±9 m, 38±6 m, 221±36 m). Because all the response distances were not longer after the hunting season than before, we rejected hypothesis 1. At this point, there is not enough evidence to support or reject (test) hypothesis 2. When data were pooled for the 4 ateas, geographical area and season had the greatest overall effect on the 4 distances (P<0.001 for all distances).

Session four

Panel Discussion on Lessons in Disturbance Research & Monitoring



The Eight North American Caribou Workshop,
Whitehorse, Yukon, Canada,
20–24 April, 1998.

Panel Discussion: Human developments and their effects on caribou

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Rangifer, Special Issue No. 12, 115–122

Introduction

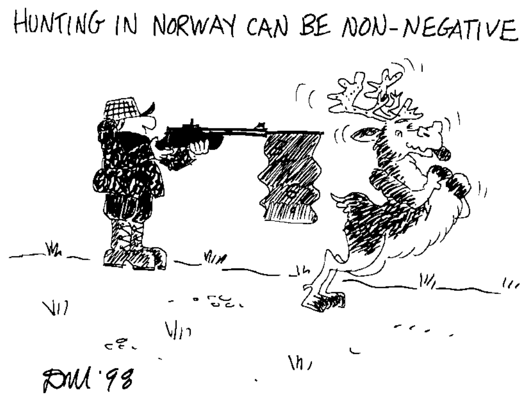
The First Notth American Caribou Workshop held in Whitehorse in September 1983 selected the theme "Caribou and Human Activity" to focus attention on this important and sometimes controversial subject. The purpose of the panel discussion during the 8th North American Caribou Workshop was to update our experience on human developments and their impacts on caribou and examine how we have progressed over the last 15 years. We organized these discussions to contrast the longer term exposure to human activity experienced in Norway to the more modest impacts experienced in North America.

Panel members, representing a variety of areas of background and perspectives, were asked to open discussions on particular issues within their experience. They were advised that an open discussion session would follow their presentations and involve all the participants at the Workshop as well as interested persons from the general public. Panel members were Jonathan Colman (Biology Institute, Department of General Physiology, University of Oslo, Norway), Colin Edey (Nova Gas Transmission Ltd. Calgary, Alberta, Canada), Stephen Murphy (ABR Environmental Research & Services, Fairbanks, Alaska, USA), Robert Florkiewicz (Yukon Department of Renewable Resources, Whitehorse, Yukon, Canada), Joe Tetlichi (Porcupine Caribou Management Board, Whitehorse, Yukon, Canada), and Robbie Keith (Canadian Arctic Resource Committee, Elora, Ontario, Canada).

This paper summarizes the presentations and subsequent discussion, and attempts to identify the issues and explore some of the problems associated with how humans are affecting caribou. A copy of the transcript from this session is available from the author.

Panel Session

Jonathan Colman



Mr. Colman provided an overview of how wild reindeer distributions in Norway historically appeared before recent technology began to fragment them and cause habitat loss due to transportation corridors, hydroelectric developments, and other human made obstacles. This provided an opportunity to contrast the mote acute European experience with that of North America.

Another topic presented by Mr. Colman was the belief that wild reindeer are very adaptable and hunting can be non-negative. Because of the absence of natural predators in Norway, population regulation is more dependent on hunting and when managed properly does not necessarily have to have a negative effect on how wild reindeer will react to other forms of human activity. Stimuli do not have to be positive to promote habituation towards human activities. It can just be non-negative.

Mr. Colman presented background information on a novel research initiative in Norway that incorporates an advisory committee composed of scientists, users and other people interested in determining the effects of high voltage transmission lines on the behavioral ecology of wild reindeer. From this experience it was found that current knowledge in this area was inadequate. It was decided that information was needed on the sensoty perceptions of wild teindeer. A study using domestic reindeer in experimental and control conditions has been designed to determine the hearing range and sensitivity to threshold levels of noise exposure from power lines, snowmobiles, aircraft, vehicular traffic and othet human made noises. This information could be used in determining the effect of transmission line construction and maintenance on wild reindeer behavior, and to what extent its presence could create a physical barrier to movement.

In conclusion Mr. Colman thought that very little has been learned ovet the last 30 years in Norway, and that accessibility has to be contained to reduce disturbance activities like tourism, which may have a stronger negative affect on wild reindeer than visual, stationary obstacles.

Colin Edey

In 1991, the resource development sector in the province of Albetta was moving at a fairly rapid pace. There was concern for the general lack of knowledge about woodland caribou in the province and this resulted in a very conservative position by Government toward resource development and its

possible effects on caribou. Mr. Edey informed us how collaborative agreement with industry and government has integrated resource development with caribou conservation through the establishment of the Boreal Caribou Research Program (the amalgamated research subcommittees of the Nottheast and Northwest Regional Standing Committees on Woodland Caribou).

The establishment of this program has fostered a cooperation among industry in conducting research that otherwise could not be funded by one company or government. Information is shared by all partners and communication between industry and government has improved. This process has furthermore reduced duplication of research efforts across Alberta. The information base on woodland caribou will be used to establish appropriate guidelines for landscape management strategies that will be reviewed annually as knowledge advances.

Research is being carried out to address a number of issues. Studies are presently under way to address sensory disturbance to caribou during late winter when the energy sector is most active. They are examining the changing impacts of predation on moose and caribou caused by the creation of predator pathways through incteased linear access in the forest. The use of gated security to limit the effects of legal and illegal hunting is being experimented with to mitigate the impact of improved access. Ways to prevent habitat fragmentation presents a challenge and is identified as one of the most serious issues to be addressed.

Clearly, Alberta's collaborative research program offers a new approach and is providing a much more enhanced view of caribou biology in the boreal forest.

Stephen Murphy

Mr. Murphy has considerable technical experience studying the effects of anthropogenic disturbance on caribou from oil field developments and military training missions. Major industrial development has been taking place in Alaska's arctic environment fot the last 25 yeats. We learned that potential adverse impacts on catibou can occut directly from habitat loss or degradation, displacement to suboptimal habitats, increased exposure to predators, disturbance, and exposure to contaminants. Indirect effects are numerous but typically stem from increase access and human activity, particularly hunting.

Research that has attempted to quantitatively evaluate these effects has found that caribou respond to disturbance by spending less time lying, more time moving, and by faster rates than did undisturbed caribou. Time spent feeding, however, did not change significantly under different disturbance conditions. It was found that females with newborn calves are most sensitive to disturbance, and these responses generally lessen, as the calves become more independent. It has also been learned that caribou are more reactive to moving stimuli, such as vehicles, than they are to stationary objects, such as pipelines. Apparently the more a stimulus resembles a terrestrial predator (caribou do not appear to perceive low-flying aircraft as predators) the more difficult it is for them to habituate to the disturbance.

Knowing that there are statistically significant changes in behavior does not necessarily imply that they are biologically significant. For population level effects to occur adult natural mortality would have to increase and/or calf recruitment would have to decrease. A possible scenario for this effect would be increased predation, particulatly on newborn calves, due to displacement of animals from preferred habitats such as calving areas. Another possibility is energetic stress do to disturbance to suboptimal habitats or increased energy expenditure because of lack of full mobility. Lower fecundity would affect the population level rather than direct mortality.

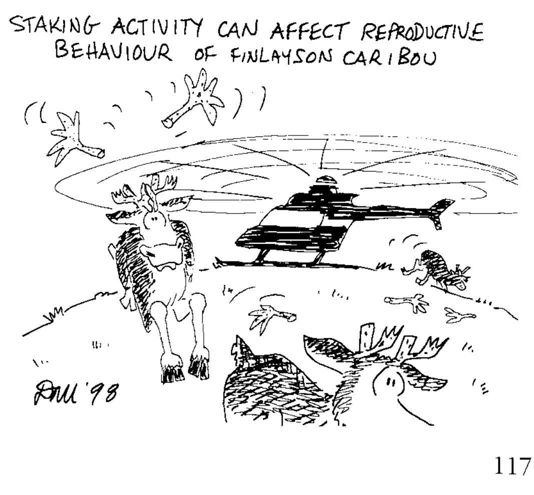
In recent years Mr. Murphy has been working with colleagues to model the energetic costs that caribou incur when disturbed. While these efforts need tefinement and field verification they have been useful in approximating exposure thtesholds that can be tolerated by caribou before they become energetically stressed to the point where population level effects result.

In conclusion, the Alaska experience indicate that caribou are capable of habituating to many types of disturbance, 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.

Robert Florkiewicz

Mr. Florkiewicz presented a case history experience in Yukon for the Finlayson caribou herd in relation to recent mining exploration activity. The Finlayson herd remains the most studied woodland caribou population in Yukon with a 16 year detailed record of its population dynamics. The range of the herd occurs in a heavily mineralized area that has been exposed to repeated rounds of claim staking over the last 30 years. Over a 2-year period from January 1994 to Decembet 1996 there were 14 700 claims staked in the herd's range mostly during the spring through fall season. Claims covered about 3000 square kilometers in the southern portion of the herds 4500 square kilometer summer range. It is important to note that the distance between corner posts of adjacent claims is 1500 feet or about half a kilometer. Field crews have to visit each claim twice, once to set out corner post, and a second time to attach claim tags once the claim has been registered. It is furthermore necessary to access these sites by helicopter to avoid the impact of consttuction of new roads, which is a significant concern for residents in the area. It is quite likely that caribou were exposed to frequent and intense levels of disturbance from helicopter and ground level human activity traffic throughout this period.

Partnerships were developed between Yukon government, the Ross River Dena First Nation, and mining companies to effectively address concern for disturbance to caribou. With this assistance biologists were able to increase survey monitoring of the herd during calving and post-calving periods. Findings from these surveys indicate that calf/female ratios in the southern portion of the herds range, where intensive mining exploration activity took place, was lower than ratios in the northern portion of the herds range, where little or no activity took place during the 95-96 'staking rush'. When compared to the long-term record of calf survival for the herd the pattern is reversed because the southern portion of the hetd's range used to generally have higher calf/female ratios than the



north. After the 'staking rush' mining activity went into a developmental stage in areas of interest and the impact area was reduced to 6 squate kilometers relative to the 3000 square kilometer potential area.

Several lessons were learned ftom this experience;
1) that a 'staking rush' could have a significant single short-term impact on caribou calf survival,
2) that access roads should continue to be kept at a minimum,
3) that by employing map notation as an alternative to physically registering claims disturbance associated with claim staking could be avoided,
4) that shott-tetm monitoring has problems and it is important to establish long-term monitoring to provide an adequate information base for impact assessment.
5) that it is critical to look at the population level responses as opposed to individual mine development footprints, which tends to be the industry standard,
6) that partnerships between government, industry and stakeholders are effective means ofi assessing true and relative costs of this kind of activity.

Joe Tetlichi

Mr. Tetlichi is a Gwitchin First Nation person who opened his remarks by reminding everyone that his people reside in 15 user-communities and are the ones at risk if caribou are greatly affected by industrial development. As chair of the Porcupine Caribou Management Board he emphasized the Board's responsibility to protect the health, habitat and viability of the herd for future generations. The Board is aware of concerns expressed by people for the welfare of this hetd because it is a primary source of food. The herd is threatened by oil and gas development. The Board believes it is essential to provide permanent protection of the herd's calving and is working to achieve this end. The calving grounds are a sacred place to the Gwitchin people and they respect it such that they do not even travel there themselves.

How the Dempster Highway, which bisects the herd's migration route in Canada, is managed is another potential threat to the herd's well being. The Board has made a number of recommendations on how activity is managed on the Highway including compliance by Fitst Nation subsistence hunters as well as how industry is to use the toad to access resources in the herds range.

Other First Nation concerns related to us by Mr. Tetlichi include the fear that the herd may get too large and eventually collapse if they exceed the cattying capacity of their range. As many Gwitchin youth become more urban there is concern in maintaining ttaditional cultural values respecting the caribou. Many of the elders who stood for the conservation of the herd have passed on and their message to keep on fighting has to be remembered.

Mr. Tetlichi closed his presentation with a very interesting story about his late brother-in-law:

He was a very subsistent person. He kept his family well. He came over the mountain one day, and this mountain there was very dangerous, and if you got on one side, you had to make sure and read the clouds and see if there was no wind. If there was wind, you could never go over the mountain. So he got on the other side... to hunt. But when he got on the other side, the wind came. He shot about five caribou, and when he was cutting up the caribou, he found out that he forgot his teapot. But he wasn't worried, because he was a very subsistent person. He knew he had an overnight on the other side of the mountain. He had no blanket, nothing. He knew he was going to make an open camp, but he had no teapot. So after he skinned all his caribou, there was a little part of the stomach there that he took all of the stuff that the caribou eat out of it. He soaked it out, washed it with snow, and he filled it up with snow. Then he threw it on the fire, and he made tea out of that little bag, and he was okay. But after he drank all of his tea, he turned around, and he ate his teapot.

That's why our people are so strong, because you can never beat them, even if they don't have a teapot.

Robbie Keith

Mr. Keith's presentation centered on public policy and whether it is helping or hindering the future of caribou. His organization, the Canadian Arctic Resources Committee, has dealt with many issues concerning caribou over the last 27 years. Recent progress with the successful settlement and implementation of land claims and a growing focus on retaining benefits from development in the north ate seen as positive steps. Agreements between communities and the mining industry, and the devolution of authority from the Government of Canada to the Territories are likewise progress towatd co-management.

Mr. Keith identified a number of issues when he expressed concern for the erosion of government responsibilities, particularly the weaknesses that ate endemic in the environmental assessment process, which has no framework in which the widespread movements of caribou are considered. There is also a sense of a disconnection between the information base and what sorts of decisions are eventually made, and this is further confounded by the general lack of long-term monitoring of the effects of development. The fact that scientific research and the documentation of traditional knowledge are driven by industrial development opposed to starting with the principal of people and sustainable communities as a basis for collecting information is another source of concern.

He also expressed concern with the rapid implementation of land claims and the establishment of boards having to deal with very significant issues while being challenged with agendas that are too full and financial resources too scarce. Traditional knowledge has to be blended with science and supported in such a way that it affects decision-making. For the present the people who hold this information are not those who make the decisions.

There is a demographic urgency that needs to be recognized as the north grows rapidly, and we have to find ways in which people are brought together into a national and international framework. In this regard the development of north-to-north relationships across Canada and with Greenland, Scandinavia, Russia, and Alaska is providing useful connections as we share the lessons we have learned together. There also needs to be some coherence to managing species like caribou that ttavel over great distances, use a variety of habitats, and range across many jurisdictions. The North American Waterfowl Management Plan provides an example that is flawed in many ways, but is a genuine effort to do this.

Open Discussion Session

This discussion covered a range of topics related to human developments and their effects on caribou. It began by examining the experience in Norway. Here it seemed a paradox that populations have become fragmented and are isolated yet the total number of wild reindeer has increased. It was stated that the forces that cause fragmentation are also going to affect large predators more than caribou. Once a lot of ptedators are removed caribou populations will increase and have to be regulated with intensive hunting. Consequently, this often leads to extremely high densities of animals in moderately poor condition occurring within alienated ecosystems.

It was pointed out that the Norwegian experience illustrates the long-tetm insidious affect of "cumulative impacts" and points to the real danger in North America of focusing on one development at a time and forgetting the big picture. Participants attempted to come to terms with this concept because it is not well defined. The time-frames associated with projecting future developments are not clear and there is not a consistent framework for quantifying cumulative impacts. It was generally agreed however that for the present we have a piecemeal approach and an effective framework does not exist. One participant suggested that for jurisdictions like Yukon there is opportunity to learn from mistakes in other areas because development has not proceeded as far and landscape planning could be effective. Meanwhile the other jurisdictions, which have gone down the path of project by project planning, need to step back and reassess whether they want to keep making the same mistakes. It was generally agreed that land use planning be given a strong priority to deal with cumulative impacts.

Discussion quickly centred on the type of processes that will work to look mote collectively at the landscape and hold the long view rather than a short view. Recognition was given to the non-government/public interest sector because they bring a different perspective, keep people accountable and add a lot of good infotmation into the process. For the present, wildlife management planning has been reactive because of development pressures but has to become proactive. Alternatively the impacts will be there before we even have time to react to them. There furthermore has to be political will to protect lands by removing them from economic development. To do these things will require forming alliances among people with shared goals. These people need to be skilled at lobbying and advocacy and be prepared to stay in for the long-term with a sustained effort. It was stated that piling up reports will not effect change, but good lobbyists will.

Several participants made comments regarding the role of co-management in decision making. It was stated that in Norway the communities that have the most hydroelectric developments are the richest communities in the countty. At the time the benefits they got from development probably outweighed the aesthetic values of undisturbed wild reindeer populations. But today some question if it may not be the right thing to do and it might not be worth it. In Norway isolated populations are managed separately and each community is allowed to have their own rules. The question was raised whether local decision-making will work for North America.

Participants pointed out some of the advantages of co-management systems. Many of these comments centred on experiences in Northwest Territories and Yukon where management regimes are approved in a co-management process and communities are directly involved in the development of regulations, plans and policies. It was believed that community based decisions have the advantage because communities are always knowledgeable about wildlife in their region and locals will natutally abide by regulations that ate developed from within. Moreover, local people and First Nations have strong animal and land ethics that will effect change to the benefit of caribou if they are involved. One participant reminded us that co-management was not an issue in 1983 when the Fitst North American Caribou Workshop was held and now we find whole sections of these kind of symposia devoted to the topic. It was further pointed out that for a researcher, co-management bodies are a vessel that one can actually apply their research and be heard.

Along similar lines, the work of the Porcupine Caribou Management Board to integrate ideas from traditional knowledge into decision-making was discussed at length. The Board takes direction from user-communities and shares responsibility with them for management of the herd. A novel approach to harvest management taken by the Board illustrates how they have incorporated ttaditional knowledge into decision-making. To mitigate the impact of the Dempster Highway, which bisects the herds winter range and migration routes, the Board will close the highway to hunting until the leaders pass to ensure that caribou will continue to make use of all the winter range available to them. The decision to do this was not based on scientific information but tather it was based on traditional knowledge. It was suggested that this represented a whole new way of making decisions. It was generally claimed that acceptance of traditional knowledge enables a variety of interests to be recognised.

Several participants expressed concern for caribou management in Quebec where the combined largest population of caribou in the world, the Geotge River and Leaf River herd's, lack a comprehensive management plan. For 15 user-communities there is no co-management system for having an effective voice on how the herd is to be managed and there is a general concern that the population may decline in the near future. It was suggested that they learn from the Yukon/NWT management experience and form an inter-jurisdictional board much on the same lines as the Porcupine Caribou Management Boatd. We were reminded that developing an effective co-management system takes a long time and can be very frustrating, but is well worth the effort. In later discussions it was hoped that by holding the 9th North American Caribou Workshop in Quebec it may help to bring communities, academics, and decision-makers together for herd management.

Another area of discussion examined the role of science in determining the consequences of disturbance. It was stated that information is not readily accessible unless one goes through a plethora of scientific papers and there is a need to pull this information together into a useable form that can be used in current environmental assessment processes. Apart from this problem another participant cautioned that science can be as a destructive force in ttying to affect policy change, because it can be a tremendous smokescreen. For example massive amounts of science have been applied into the possible effects of oil and gas development in the Arctic Refuge issue, and yet we are always on the cusp of losing the Arctic Refuge. Not because there isn't enough science but because it can be made look like its never good enough. Anothet participant cautioned that as scientists we not only have to be ever-vigilant of not adding to the scientific smokescreen, but additionally we have to be very cautious about applying the same standards to ourselves as we do to industry. This comment served as reminder to participants that the caribou research and management studies we carry out is in itself a human activity that can greatly effect caribou. An additional concern was raised by a participant who used controlling mosquitoes negative effect on bird life as an example of how scientists should not "just look at one thing" when providing advise to decision-makers. Consequently it was acknowledged that our science system needs to become more entrenched in ecosystem management as a way of thinking.

Participants attempted to come to terms with what type of human activities can negatively affect caribou. It was generally agreed from a review of both Norwegian and North American research that caribou ate not as reactive to stationary objects such as pipelines, as they are to moving stimuli associated with ground based activity. The example of population response of the Finlayson herd to explotation crews making repeated visits to sites for staking mining claims illusttated this impact and contrasted with findings from aircraft over flight tesearch, which may require hundreds of overpasses to get a detectable response. It was further stated that the consequences of these distutbances are greater when they resemble predation risk as is the case with North American caribou. Improving access into catibou tange was repeatedly identified as the single most detrimental human activity and the cause of fragmentation of wild reindeer in Norway.

The discussion also broached the question of the usefulness of model building to approximate tolerance thtesholds for caribou to disturbance and whether this should be looked at by othet jurisdictions or is it an academic exercise. Some of the problems associated with the Porcupine herd energetic model were identified and included the need for field verification, determination of realistic exposure thtesholds, and the general difficulty of trying to abstract the real world. There seemed to be consensus however that models can be very useful. Using the model helps to think about possible scenarios and helps to find out what factors are important. It helps people to think more clearly about the situation and make decisions by examining biological processes and possible outcomes.

One thread of discussion pursued the usefulness of a source book on the ecology of caribou. It was suggested that this could be a compendium of knowledge about caribou in North America and would serve as an effective way of presenting information to the broader public. There was general agreement that a project of this kind be undertaken.

Concluding Remarks

To the extent the group reached a conclusion it was generally agreed that management processes that include co-operative agreements between industry, governments, and stakeholders generate meaningful dialogue and could provide the right kind of research needed to identify and effectively mitigate potential impacts. As we interactively shared our experiences it became apparent that the establishment of co-management systems and the acceptance of traditional ecological knowledge enable a variety of interests to be recognized and contribute significantly to appropriate decisions about where and how developments should occur. Recent progress in these areas in Alberta, NWT, and Yukon represent substantial improvement over the last 15 years since the First North American Caribou Workshop was held.

The experiences shared with us by our Norwegian colleagues illustrate unequivocally that 'cumulative impacts' are a reality that can lead to alienation of whole large mammal ecosystems. It was furthermore made clear that there are weaknesses endemic in the current environmental review processes that cause a piecemeal approach to quantifying these effects. Fot an effective framework to exist will tequire proactive land use planning that for caribou in particular is not obstructed by inter-jurisdictional barriers. Designating protected areas for caribou that are withdrawn from development may be required to offset the long-term insidious effect of cumulative impacts.

With respect to our state of knowledge about caribou responses to human activity it was concluded that the types of activity that most disturb caribou are those that resemble predation risk such as stimuli from ground based activity. North American caribou are furthetmore less likely to habituate to this type of activity because they usually co-exist with a full complement of predators. It was further stated that the most detrimental result of human activity that can cause caribou population level responses is the development of improved human access and should be discouraged as a mattet of policy. There was consensus that models provide a useful tool for shaping our thinking about human effects on caribou and work should continue to determine realistic exposure thresholds and establish field verification.

The question of how best to incorporate scientific knowledge into environmental assessment infrastructure was repeatedly raised. We were warned that research could be used as a smoke screen to effecting policy change and that it should be used in a constructive way recognizing its limitations. It was repeatedly stated that no matter how much information is brought forward it will require formation of alliances and sustained lobbying on the political front to effect change. Concern was raised that scientific information is not readily accessible and should be put together into a useable form not only for current environmental assessment processes but also for the general public. It was recommended that a composite publication incorporating the great deal of information on caribou that has been generated over the last 2 decades be synthesized as a single and definitive source book.

It seemed disttessing to participants that the combined latgest caribou populations in the world located in eastern Canada lacked comprehensive management planning. It was suggested that the contribution of these proceedings help to bring continuity to management of the George River and Leaf River herds. In that interest the transfer of the 9th North American Caribou Workshop to Québec may provide an instrument to that end.

Session five

Nutrition & Physiology

SOME CARIBOU WERE NOT AS POLITE IN PROVIDING GOOD URINE SAMPLES

The Eight North American Caribou Workshop,
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Overwinter changes in urea nitrogen:creatinine and cortisol:creatinine ratios in urine from Banks Island Peary caribou

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Abstract: Over 200 snow urine samples were collected from Banks Island Peary caribou between March 1993 and May 1998. Most (n=146) samples were collected during 3 time periods in 5 successive years: early winter (3 November-3 December), mid-winter (9 February-1 March), and late-winter (23 April-2 May). We determined the ratios of urea nitrogen:creatinine (U:C) and cortisol:crearinine (C:C) for each sample. U:C ratios had significant year, rime, and year x time intetaction effecrs. Mid-winrer ratios were higher than early or late-winter ratios. U:C ratios ranged from 0.53 to 19.05 mg/mg, and were lowest in 1997-98. Five calf caribou sacrificed in February 1994 had significantly (P<0.02) higher U:C ratios than other caribou in mid-winrer. Three adult male and 2 calf caribou sacrificed in November 1993 had U:C ratios similar to other caribou in early wintet. Sacrificed caribou were in similar condition to animals that have been harvested for subsistent use in other years, not overly fat nor in an advanced state of starvarion. U:C ratios for Peary caribou range from 10 to *ca.* 100-fold higher than those reported for barren-ground caribou; ratios >60-fold higher than those indicative of prolonged undernutrition in barren-ground caribou were common. This difference is likely because the winter diet of Peary caribou has a higher crude protein content than that of barren-ground caribou. C:C ratios had significant year and year x time interaction effects, and were highesr in 1996-97 and 1997-98. C:C ratios of sacrificed caribou were similar to those of other animals during early and mid-winter. C:C ratios for Peary caribou ranged from 0.0120 µg/mg to 0.2678 µg/mg; ratios indicative of morbidity in mule deer were common. C:C and U:C ratios from the same individuals were not correlated (R=-0.073). Monitoring U:C tatios of Banks Island Peary caribou may provide useful management information.

Key words: *Rangifer tarandus pearyi,* snow urine analysis.

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Introduction

The use of the ratios of metabolites from urine voided into snow has become popular for assessing winter nutritional deprivation in ungulates (White *et al.,* 1995; DelGiudice & Seal, 1988). Snow urine samples are obtained and assayed for metabolites such as urea nitrogen and cortisol (DelGiudice *et al.,* 1989; Saltz *et al.,* 1992; Parker *et al.,* 1993), and their levels are reported as ratios with urinary creatinine (Coles, 1980; DelGiudice *et al.,* 1988). A progressive increase in the ratio of urea nitrogen:creatinine (U:C) over winter should occur only when endogenous protein is being catabolized at an accelerated rate (DelGiudice *et al.,* 1987). An increase in the ratio of cottisol:creatinine (C:C) over wintet should occur as a result of increased glucocorticoid secretion caused by chronic nutritional deprivation (Saltz & White, 1991).

The collection of snow urine to assess the nutritional status of wild ungulates is of particular utility fot low density or endangered populations. DelGiudice & Seal (1988) demonstrated the management value of U:C ratios for white-tailed deer (*Odocoileus virginianus*). They classified deer into three categories of malnutrition: early (U:C <4 mg/mg), prolonged-reversible (U:C 4-<23 mg/mg), and prolonged-irreversible (U:C >23 mg/mg). Subsequently, Case (1996), proposed that U:C >0.25 mg/mg could be used to distinguish barren-ground caribou (*Rangifer tarandus groenlandicus*) which had experienced prolonged undernutrition and remain undernourished.

The Banks Island Peary caribou (*Rangifer tarandus pearyi*) population was estimated at 709±128 (standard error of the mean) ≥1 year-old animals in 1994 (Larter & Nagy, 1997) and has been designated as an endangered population by the Committee on the Status of Endangered Species in Canada (COSEWIC). As part of a comprehensive range study program we wanted to document the levels of snow urine ratios (U:C and C:C) from Peary caribou during the course of the winter to determine if snow urine ratios could have some practical management applicability. We were unwilling to assume that baseline U:C levels determined for barren-ground caribou would necessarily apply to Banks Island Peary caribou because of substantial differences in the basic winter diet. Mould & Robbins (1981) documented that as protein intake increases in elk (*Cervus elaphus*), less urea nitrogen is recycled and urinary urea nitrogen increases. Barren-ground caribou typically have a winter diet dominated by lichen (Klein, 1991) which has a vety low protein content (Person, 1975). The winter diet of Banks Island Peary caribou contains substantial proportions of legumes (*Astragalus* spp. and *Oxytropis* spp.) and *Dryas integrifolia,* but virtually no lichen (Larter & Nagy, 1997). Forages in the winter diet of Banks Island caribou have a much higher protein content than lichens, which typically have ≤3% (Soppela *et al.,* 1992; N. Larter & J. Nagy, unpubl.). Legumes on the winter range of Banks Island caribou have 11-15% crude protein content (N. Larter & J. Nagy, unpubl.).

In this paper we: 1) document ovetwinter and annual variation in urea nitrogen:creatinine (U:C) and cortisol:creatinine (C:C) ratios from Banks Island Peary caribou, 2) assess whether the ratios increase over winter as would be expected if increasing nutritional deprivation was occurring, 3) assess whether the ratios are affected by differences in winter snow conditions, and 4) document ratio levels found in different sex and age classes from a small sample of animals from which we had measures of fat reserves and physical condition (Larter & Nagy, 1996).

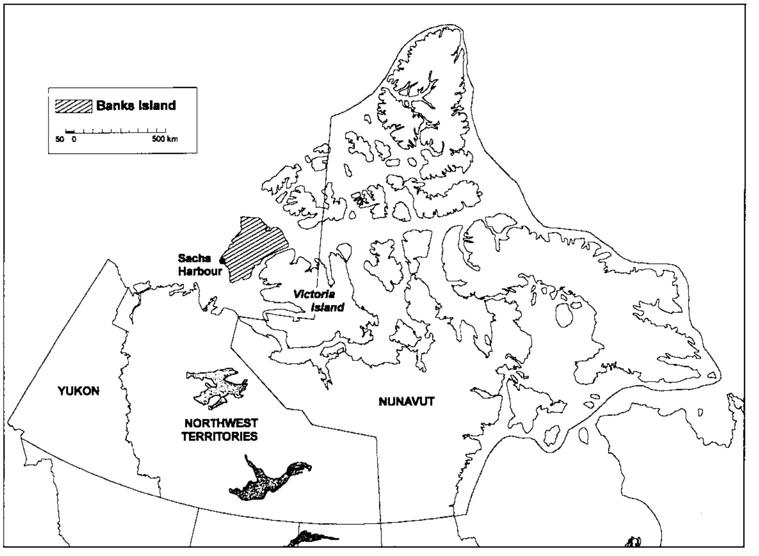

Fig. 1. Northern Canada with Sachs Harbour on Banks Island, Northwest Territories indicated.

Study Area

Banks Island is the most western island in the Canadian Arctic Archipelago and covers approximately 70 000 km² (Fig. 1). The climate is Arctic Maritime along coastal areas where weather stations are located, tending toward Arctic Desert inland (Zoltai *et al.,* 1980). Winters are long, mean monthly temperatutes ate below 0 °C from September through May, and cold, mean minimum daily temperatures range from -30 to -40 °C from December to March. Summers are short and cool, mean maximum daily tempetatutes range from 5 to 10 °C from June through August. Thete is little precipitation, an annual mean of 9 cm (Zoltai *et al.,* 1980). Sachs Harbour (population 125) is the only permanent settlement on the island. Zoltai *et al.* (1980) provided a general overview of the geology and glacial history of Banks Island.

Habitat descriptions wete adapted from Kevan (1974), Wilkinson *et al.* (1976), and Ferguson (1991). There are 4 major terrestrial habitats: 1) wet sedge meadow, 2) upland barren, 3) hummock tundra, and 4) stony barren. Wet sedge meadows (WSM) are generally level hydric and hygric lowlands characterized by *Carex aquatilis, Eriophorum scheuchzeri,* and *Dupontia fisheri.* Upland barrens (UB) are well drained sites found on the upper and middle parts of slopes. Vegetation is dominated by *Dryas integrifolia* and *Salix arctica.* Hummock tundra (HT) is found on moderately steep slopes and is characterized by individual hummocks which are vegetated primarily by dwarf shrubs (*D. integrifolia, S. arctica,* and *Cassiope tetragona*). Stony barrens (SB) have a coarse gravelly substrate and are sparsely vegetated. This habitat is 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 (*Ovibos moschatus*) and Peary caribou (*Rangifer tarandus pearyi*) are the dominant resident herbivores; population estimates from 1994 were 64 608±2009 and 709±128 ≥1 year-old animals of each species respectively (Larter & Nagy, 1997). Other resident herbivores include Arctic hares, ptarmigan and lemmings. During summer there is a substantial population of nesting snow geese (*Chen caerulescens*), which was estimated at 431 000± 48 000 (95% CI) in 1995 (R. Kerbes, pers. comm.). The major resident predators are arctic wolves (*Canis lupus arctos*), polar bears (*Ursus maritimus*), and arctic foxes (*Alopex lagopus*).

Materials and methods

Seven to 14 day field trips were made by snowmobile to research camps located on south central Banks Island during early (3 November-3 December), mid- (9 February-1 March), and late-winter (23 April-2 May). We conducted field trips during wintets 1993-94, 1994-95, 1995-96, 1996-97 and 1997-98. During each field trip we collected fresh snow urine samples (≥25 g) left by Peary caribou that were observed during travel. Not all observed caribou provided a sample. An average of 10 samples were collected per trip (range 3 to 20). Samples were kept frozen in individually labelled ziplock bags and transferred frozen to the laboratory in Inuvik at the end of each field trip. We recorded the location of each sample using a global positioning system, and the sex-age class of the caribou that had left the urine sample whenever possible.

In the lab we thawed each frozen urine sample at room temperature and transferred the liquid into 50 ml plastic centrifuge tubes. The liquid in the tube was gently shaken and a subsample of *ca.* 5 ml was pipetted into a 12 x 75 mm tube. This tube was capped and placed in a freezer to tefreeze the contents. The remaining liquid in the 50 ml centrifuge tube was stored frozen for backup. Frozen subsamples were shipped to the Veterinary Pathology laboratory at the Western College of Vetetinaty Medicine, University of Saskatchewan. Urine samples were analyzed for their concentrations of urea nitrogen (mmol/l), creatinine (µmol/l), and cortisol (nmol/l). We converted the values to mg/dL by multiplying urea nitrogen mmol/l by 2.797, creatinine µmol/l by 0.01167, and cortisol, nmol/l by 0.03636 respectively. We present the ratio of utea nitrogen:creatinine (U:C) in mg/mg and the ratio of cottisol:creatinine (C:C) in µg/mg.

Fifty-eight urine samples were collected opportunistically during other field research trips in 1993 and 1998. Samples were collected 21-30 March, 18-20 May, 26-30 October, 4-12 December in 1993, and 22-23 May, 1998. These samples were analyzed as above. Some of the samples collected during November and December 1993 and February 1994 were collected from animals that were sacrificed as part of a caribou collection. Adult male and calf caribou were selected for the collection because it was anticipated that these sex-age classes would be the first to show signs of severe undernutrition (Larter & Nagy, 1996). For each of these animals we collected a urine sample and the following information: sex, age, depth of back fat, kidney fat index (KFI) (following Riney, 1955), visual femur marrow analysis (Riney, 1955) and femur marrow fat content (Neiland, 1970). For a more detailed accounting of the methods see Larter & Nagy (1996).

Starting in winter 1994-95, for each early, mid-, and late-winter field trip we measured snow conditions in the 4 major terrestrial habitats: wet sedge meadow, upland barren, hummock tundra, and stony barren. We measured snow conditions by collecting snow cores to determine snow depth and density, and/or by using a Rammsonde penetrometer (Raillard, 1992; Larter & Nagy, 1994). Ten stations were located along fixed transects in each habitat. At each station we took 2 snow cores, 5 penetrometer measures, and recorded ambient temperature (°C). In winter 1993-94, snow depths and hardness were measured during early and late winter. In March 1993, measurements were limited to depths and densities in wet sedge meadow and upland barren habitats. We used snow measures from upland barrens as indices of relative winter severity for caribou between years, and report mean measures for each time period.

All ratio data were natural-log transformed because snow-urine metabolite ratios are log-normally distributed (White *et al.,* 1995). We used an unbalanced ANOVA for two-way design with intetaction (ptoc GLM SAS 6.11 for Windows, SAS

Institute Inc., 1995) to see if there were significant (P<0.05) time (early, mid-, late-winter) or year effects on the transformed ratios of U:C or of C:C. If rhere were significant time or year effects we used the Scheffé multiple comparisons test (proc GLM SAS 6.11 for Windows, SAS Institute Inc., 1995) to see where those differences were. We present the results as median ratios. We used correlation analysis to assess the individual relatedness of the transformed ratios. We used the Mann-Whitney U test to compare U:C and C:C ratios from animals in early, mid-, and late-wintet with sacrificed animals, and opportunistic collections during other months.

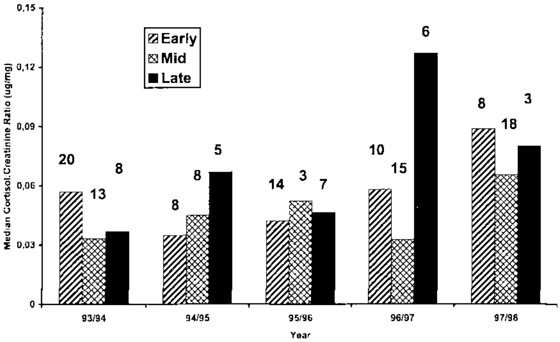

Fig. 3. Median cortisol:creatinine ratios (µg/mg) for all early, mid-, and late-winrer periods from winters 1993-94 to 1997-98. Sample size is indicated above each histobat.

Results

The ratios of urea nittogen:creatinine (U:C) had significant time, year, and time x year interaction effects. Ratios increased or remained fairly constant from early to mid-winter. From mid- to late winter the ratios increased during 3 years, decreased during 1 year, and remained relatively constant duting 1 year. Mid-winter values were significantly (P<0.05) higher than early and late-winter values, which were similar (Fig. 2). U:C ratios wete significantly (P<0.05) lower in 1997-98 than in 1996-97, but 1997-98 ratios were similar to 1993-1996 ratios. U:C ratios from the 5 calves sacrificed in February 1994 were significantly (P<0.02) higher than ratios determined from other animals during mid-winter (median 14.49, range 7.21-16.86 mg/mg versus median 7.08, range 2.64-17.62 mg/mg). U:C ratios from the 3 males and 2 calves sacrificed in November 1993 were similar (P>0.05) to those detetmined from other animals during early winter (median 8.17, range 3.94-15.76 mg/mg

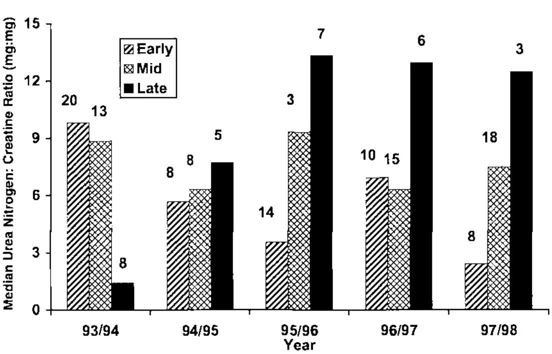

Fig. 2. Median urea nitrogen:crearinine ratios (mg/mg) for all early, mid-, and late-winter periods from winters 1993-94 to 1997-98. Sample size is indicated above each histobar.

versus 5.54 median, range 1.04-15.83 mg/mg). Although none of the sacrificed animals were fat there were no signs of an advanced state of starvation and they were in similar condition to animals that have been harvested for subsistence use in othet years. The nutritional state of calves during winter 1993-1994 must have been adequate because over-winter growth of leg bones was documented in these animals (Larter & Nagy, 1995). U:C ratios ranged from 1.04-15.83 mg/mg during early-winter, 2.64-17.62 mg/mg during mid-winter, and 0.53-19.05 mg/mg during late-winter.

The ratios of cortisol:creatinine (C:C) had significant year and time x yeat interaction effects. Ratios in 1997-98 wete significantly (P<0.05) higher than those from 1993-1996, but wete similar to those in 1996-97 (Fig. 3.). C:C ratios from animals sacrificed in November 1993 and February 1994 were similar (P>0.05) to tatios determined from othet animals during early and mid-winter (median 0.0873, range 0.0170-0.1532 µg/mg versus median 0.0514, range 0.0120-0.1464 µg/mg and median 0.0356, range 0.0166-0.0892 µg/mg versus median 0.0426, range 0.0157-0.2082 µg/mg, respectively). C:C ratios ranged from 0.0120-0.1532 µg/mg during early-winter, 0.0157-0.2082 µg/mg during mid-winter, and 0.0145-0.2678 µg/mg during late-winter. There was no correlation (R=-0.073) between C:C and U:C ratios from the same individuals. The highest recorded C:C ratio was 1.2206 µg/mg from an adult caribou of unknown sex in May, 1998.

U:C ratios recorded in mid-May 1993 were significantly (P<0.05) lower (median 1.43, range 0.34-5.73 mg/mg) than those recorded in late-winter or March 1993 (median 13.07, range 8.48-20.93 mg/mg). The lowest ratio recorded was 0.11

mg/mg in mid-May 1998. Ratios in May 1998 (median 0.47, tange 0.11-1.34 mg/mg) were similar to those in May 1993 and were significantly lower than ratios in either late winter or March 1993. The highest U:C tatio recorded was 20.93 mg/mg in March 1993. Ratios in Match 1993 were all high but were not significantly higher than those recorded for sacrificed animals in February, 1994 (median 14.49, tange 7.31-16.86 mg/mg). U:C ratios increased significantly ($P<0.05$) from October 1993 (median 4.77, range 2.28-8.66 mg/mg) to December 1993 (median 9.26, range 6.24-12.43 mg/mg). Ratios in December 1993 were greater than those in eatly wintet and similat to those of sacrificed animals in February 1994 (Fig. 4).

Mean snow depth, snow density, and snow hardness in upland barrens generally increased from early to mid-winter and remained similar from mid- to late-winter (Table 1). The greatest mean snow depth (30.0 cm), and mean snow density (0.401 g/cm³) in upland barrens were all recorded in March 1993; mean snow hardness was not measured. During winter 1997-98, snow depth, density, and hardness were generally the lowest recorded for each winter period.

Discussion

U:C ratios of Banks Island Peary caribou were low in early winter and increased significantly from early to mid-winter. They were also highest in March, 1993 when snow conditions wete the most exttreme measured (Table 1). These findings would be expected if endogenous protein was being catabo-

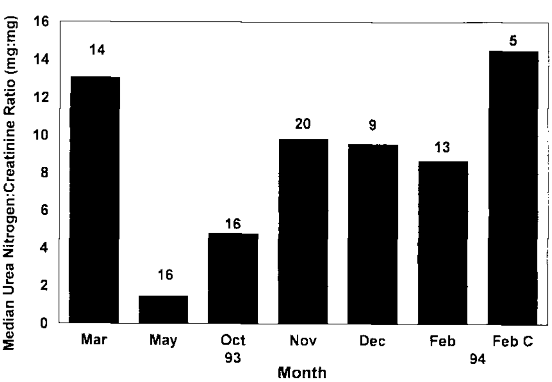

Fig. 4. Median urea nitrogen:creatinine ratios (mg/mg) from samples collected between March 1993 and February 1994. The February 1994 histobar includes all samples while the Feb. C histobar documenrs the median level of only the sacrificed animals. Sample size is indicated above each histobar.

Table 1. Mean (± standard error of the mean) snow depth (cm), snow density (g/cm³), and snow hardness (number of penetrometer hits) found covering upland barren habitat for all early, mid-, and late-winter periods from winters 1993-94 to 1997-98 and for March 1993. Mean depth (n=70), mean density (n=20) and mean hardness (n=50) unless otherwise noted in parentheses.

	March 1993	1993-94	1994-95	1995-96	1996-97	1997-98
Depth (cm)	30.0±4.5 (5)					
early winter		16.1±0.6 (50)	17.7±1.0	10.1±0.6	11.3±0.7 (68)	6.7±0.6 (62)
mid-winter			21.5±1.4	16.4±0.6	13.2±0.9	8.4±0.6 (65)
late winter		28.2±1.3 (50)	20.3±0.8	13.4±0.7	16.5±1.2	6.2±0.7 (64)
Density (g/cm³)	0.401±0.016 (5)					
early winter			0.248±0.010	0.257±0.019	0.287±0.017 (18)	0.236±0.015 (12)
mid-winter			0.327±0.016	0.157±0.010	0.245±0.010	0.273±0.016 (15)
late winter			0.306±0.009	0.258±0.010	0.267±0.011	0.199±0.028 (14)
Hardness (# hits)						
early winter		5.6±0.4 (50)	5.4±0.6	1.1±0.2	1.4±0.2	0.8±0.1
mid-winter			17.5±1.6	9.0±2.3	4.8±1.4	4.7±0.6
late winter		20.0±1.8 (50)	10.8±1.1	5.1±0.9	8.5±1.6	3.4±1.0

lized at an accelerated rate as winter progressed (DelGiudice *et al*, 1987) or winter severity increased, and indicate that information on U:C ratios may provide useful management information. Some of the highest U:C ratios measured were from sacrificed animals that did not show signs of irreversible nutritional deprivation (based upon fat depots), and were generally regarded as being of similar fatness to animals harvested previously by the local residents. Therefore, the range of ratios documented is likely within the normal range experienced by Banks Island Peary caribou. It is unlikely that we reported levels indicative of prolonged-irreversible as reported for barren-ground caribou (Case, 1996) and white-tailed deer (*Odocoileus virginianus*) (DelGiudice & Seal, 1988).

Cortisol is a glucocorticoid that controls the metabolism of enetgy reserves in animals experiencing chronic stress (Stephens, 1980). One would expect elevated levels when animals have teached the prolonged-irreversible stage of malnutrition. For mule deer C:C ratios of 3 ng/mg reflect normal winter values; values >10 ng/mg suggest high sttess and muscle catabolism likely leading to death (Parker *et al*, 1993). No C:C ratio we measured for Banks Island Peary caribou was <12 ng/mg (high 1220.6 ng/mg). C:C ratios showed little effect of time, yeat, or winter severity, and showed no correlation with their associated U:C ratios. Levels up to 30-fold greater than mule deer were not fatal, but common in Peary caribou. Unlike the late 1980s and early 1990s, there were no recorded overwinter die-offs of caribou on Banks Island during this 5 year study (Nagy *et al.*, 1996). The animals taken during winter 1993-1994 were taken because of concern that Octobet freezing rains would cause an overwinter die-off of caribou (Larter & Nagy, 1994), but that was not the case. It is likely that the nutritional balance of the animals we have measured over the past 5 years has been adequate and we were unable to measute C:C ratios for animals undergoing any physiological stress because of a low nutritional plane.

Snow conditions were the most extreme measured in March 1993 (Table 1). U:C ratios were highest in Match 1993, C:C ratios were not. There was no positive relationship between increasing U:C ratios and increasing winter severity for the other winters although U:C ratios were lowest during the mild winter of 1997-98. There was no relationship between winter severity and C:C ratios whatsoever. C:C ratios were highest in winters 1996-97 and 1997-98 which is puzzling; winter 1997-98 was the mildest winter of the 5 when considering snow conditions (depth, density, and hardness) and forage was more readily accessible. Possibly the lack of any relationship between U:C and C:C ratios indicates that snow conditions over the past 5 years were being well within the norm.

The apparent decrease in U:C ratios from mid- to late-winter could have resulted from, differences in snow dilution, differences in sex-age class composition of the samples, small sample size for late-winter, or from extraordinary late-winter conditions. Snow density tends to be greatest in April. Urine tends to either cut straight through the snow to gtound level or to spread out across the top of the snowpack. Snow urine samples in April tend to appear more dilute than at other times of the year. Differences in snow dilution have shown little or no effect in U:C or C:C ratios elsewhere (Saltz & Cook, 1993; White *et al.*, 1995), and we assume that to be the case with our study.

White *et al.* (1995) showed sex-class differences of U:C ratios in elk (*Cervus elaphus*). They warned that the unknown proportions of each sex-age class may influence the mean ratio which is assumed to tepresent a population measure. We acknowledge that lack complete information on the sex-age class of each sample, but if our analysis had been further partitioned by sex-age classes it would have been of limited utility due to small sample sizes. Different sex-age class composition of the caribou from which samples were collected during each field trip may add additional variability to our estimates. However, we are dealing with a small population, and believe that the samples collected during any time period are a random sample of the population. During each sampling period samples were collected from animals from ≥2 sex-age classes. In retrospect, because the ratios we reported appear to be from the normal range in the winter nutritional plane of Banks Island Peary caribou, variability based upon animal sex-age is less likely to affect the results.

Small sample size and, what appear to be extraordinary values for late-winter 1993-94, have likely played a major role in creating an apparent decrease in U:C ratios from mid- to late-winter. In 1993-94, U:C ratios were significantly (P<0.01) lower in late- than mid-winter. Late-winter 1993-94 ratios were similar to levels found in May 1993 and May 1998, the lowest ratios recorded. In 1995-96, 1996-97, and 1997-98 U:C ratios were higher in late- than mid-winter. In 1994-95 mid- and late-winter U:C ratios were similar. Therefore, in only 1 of 5 late-winter periods have U:C ratios been lower than the ptevious mid-winter. Late-winter ratios would be expected to remain at or above mid-winter ratios. Samples during late-winter were collected over the shortest time period (10 days). A short term rare event, possibly a recent nutritional event, could have had more effect on the samples than if they were collected ovet a longer time frame. We have no explanation for such a reduction in ratios. Samples were collected from 3 different sex-age classes from 3 different groups. Snow depth and hardness were relatively greater in late-winter 1993-94 than other years. An increase in the number of late-winter samples will hopefully elucidate this problem and give us a better idea of the overall relationship.

U:C levels for Banks Island Peary caribou ranged from 10 to *ca.* 100 fold higher than those reported for barren-ground caribou from the Bathurst population collected in March (Case, 1996). U:C levels for barren-ground caribou from the adjacent Bluenose population, also collected in March, showed similar levels to those reported by Case (1996), ranging from 0.06 to 1.61 mg/mg (n=24, median 0.40 mg/mg; N. Larter & J. Nagy, unpubl.). Case (1996) proposed that U:C >0.25 mg/mg could distinguish barren-ground caribou which had experienced prolonged undernutrition and remain undernourished. Only 1 of the 204 samples from Banks Island Peary caribou was <0.25 mg/mg. It is unlikely that all sampled individuals were undernourished. The crude protein content of lichen which Bluenose and Bathurst barren-ground caribou subsist on during winter is <3% (Sopella *et al.*, 1992) whereas legumes which are a major constituent of the winter diet of Banks Island Peary caribou has a ctude protein content of 11-15% (N. Lattet & J. Nagy, unpubl.). Increases in crude protein intake increases urinary urea nitrogen in elk (Mould & Robbins, 1981). One could speculate that the levels proposed by DelGiudice & Seal (1988) to indicate malnutrition in deer: early (U:C <4 mg/mg), prolonged-reversible (U:C 4-<23 mg/mg), and prolonged-irreversible (U:C >23 mg/mg) may be comparable for Banks Island Peary caribou because the crude protein content of the winter browse diet of deer and the winter diet of Banks Island Peary caribou may be similar; only further sampling will tell.

U:C ratios we report for Banks Island Peary were substantially greatet than those tepotted for barren-ground caribou. U:C ratios: 1) increased from early to mid-winter, 2) were highest when winter snow conditions were the most severe, 3) were lowest during the mildest winter, and 4) varied from March 1993 to February 1994 (Fig. 4) as predicted if we assume that forage becomes increasingly difficult to acquire as winter progresses resulting in an accelerated rate of endogenous protein catabolism. C:C ratios we report for Banks Island Peary caribou were substantially gteater than those tepotted for mule deer, but unlike U:C ratios did not vary as predicted if animals were experiencing chronic stress. Some of the highest U:C ratios were recorded from calves sacrificed during mid-winter 1993-94. Based upon fat depots and local knowledge, these animals did not show signs of irreversible nutritional deprivation. Therefore, we lack U:C and C:C ratios detetmined for animals experiencing severe nutritional sttess, and presume that the past 5 winters have not been so severe as to create severe nutritional stress for the population.

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Increases in body weight and nutritional status of transplanted Alaskan caribou

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Abstract: Body weight and natality rate in ungulates can be useful indices to nutrition, but they may also be influenced by genetic and climatic factors. Because caribou (*Rangifer tarandus granti*) are distributed as discrete populations or metapopulations (i.e., herds) that are usually reproductively isolated from each other for unknown periods, it is difficult to separate the influence of genetics and nutrition on body weight, especially where historical data are lacking. To help elucidate the influence of nutrition on potential variation in body weight and natality of caribou in Alaska, we reviewed data for body weight and natality in 5 populations which resulted from transplants to previously ungrazed ranges, or to areas where reindeer and caribou had been absent for many decades. In 2 of 5 populations body weight increased significantly, and likely increased in the other 3 populations, but data were insufficient. Natality rate increased in all 5 populations, proportion of fecund yearlings was high and 3 of the 5 newly established herds increased at about the maximum biological potential for the species ($\lambda \approx 1.35$). In the Adak transplant, a lactating yearling was documented. These 5 transplanted populations provide additional evidence that body weight and natality rate in Alaskan caribou are sensitive to changes in population density and relatively short-term (i.e., 10 years) increases in grazing pressure independent of climate and genetics.

Key words: natality, *Rangifer tarandus granti.*

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Introduction

Changes in body weight and natality can be useful indices of nutrition in ungulates (McEwan & Wood, 1966; Klein & Strandgaard, 1972; White *et al.*. 1981; Clutton-Brock *et al.*, 1982; Peters, 1983; Reimers, 1983; Reimers *et al.*, 1983; Skogland, 1983; 1984; Beninde 1988; Crete & Huot, 1993; Gaillard *et al.*, 1996; Reimers, 1997). However, body weight and natality can also be influenced by genetic and climatic factors that must be controlled when comparing disparate populations (c.f. Klein, 1965; Røed & Whitten, 1986; Beninde, 1988). Experimental transplants can sometimes provide such control and help biologists assess the influence of grazing history and population density on herd nutrition (Klein, 1968). In this paper we review 5 Alaskan caribou transplants and recent data on changes in body weight and natality in transplanted and parent herds, and make inferences about the importance of population density, previous grazing pressure, and climate on body weight and natality in Alaskan caribou. We consider the term "herd" to be synonymous with population or metapopulation because opportunities for interbreeding occur, but are uncommon, and dispersal seems to occur at very low levels (Valkenburg *et al.*, 1996; Valkenburg, 1997).

Adak Island transplant

In response to a request from the military, caribou were transplanted from the Nelchina herd (Fig. 1) to previously ungrazed Adak Island in 1958 and

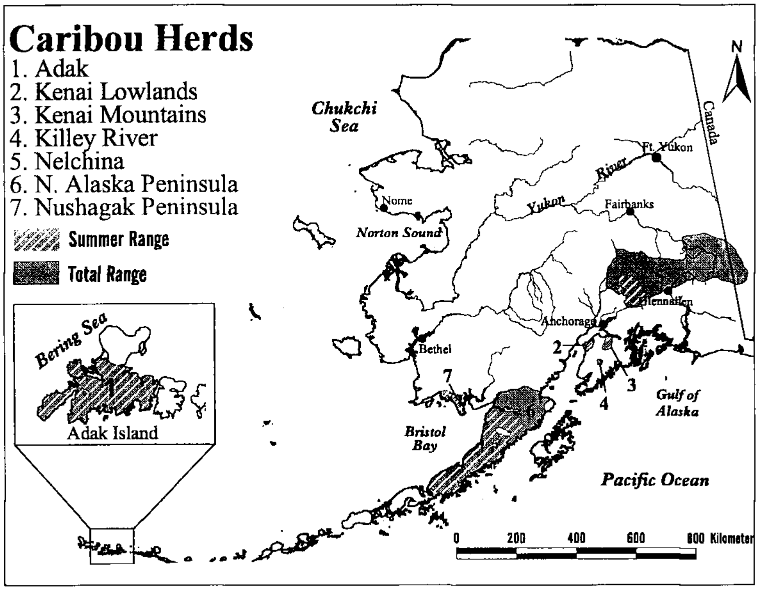

Fig. 1. Location of transplanted and parent herds.

1959 (Jones, 1966; Burris & McKnight, 1973). Catibou were captuted as 1- or 2-day-old calves and held in captivity for 5 to 8 weeks before being released. Following release, calves from both transplants were bottle fed until 6 August and then left to fend for themselves. The Adak transplant was unique because caribou were removed from the parent herd as newborn calves, and thus had no opportunity to acquite parasitic oestrid larvae (*Hypoderma tarandi* and *Cephenemyia trompe*).

Data on body weight and nutrition of transplanted caribou are scant, but it appears that body weight and natality increased (Table 1). On Adak, mean weight of 5 "adult" bulls taken in August 1964-1968 was probably higher than in the parent Nelchina herd, but Skoog (1968) presented no estimate of variance, and a statistical test was not possible (Table 1). Howevet, *most* (compared with 13% in the parent herd) yearling females were pregnant on Adak, and a lactating yearling (indicating the animal conceived as a calf) was killed in autumn 1966 (Glenn, 1967). In addition to increased production in young females, the Adak herd also exhibited maximal population growth (Table 1).

Kenai Peninsula transplants

The first Kenai Peninsula transplants took place in 1965 and 1966, and the caribou were again taken from the Nelchina herd. Release sites on the Kenai Peninsula had teceived no grazing by reindeer or caribou since about 1900 (Davis & Franzmann, 1979). At the time of the transplants the Nelchina hetd was at the beginning of a population decline following a peak of about 70 000 in the early 1960s, and reduced nutrition was probably affecting body weight (Eberhardt & Pitcher, 1992). The Kenai Mountains hetd formed from caribou released in 1965 (Spraker, 1992). Most caribou from the 1966 transplant moved southwest and formed the Kenai Lowlands herd, but some also went northeast and joined the Kenai Mountains herd (Spraker, 1992) (Fig. 1). Although there are no data on body weight or relative nutritional status in the years immediately following the transplant, a bull immobilized and measured in the early 1980s from the Kenai Lowlands herd had antlers unofficially scoring 476 2/8 Boone and Crockett points, more than any other caribou in the Boone and Crockett records (Boone & Crockett Club, 1993). The shed antlers of this animal were retrieved and mounted and ate on display at the Anchotage Department of Fish and Game office. However, the Kenai Lowlands herd increased slowly, apparently because of ptedation (Spraker, 1992).

In contrast to Kenai Lowlands herd, the Kenai Mountains herd initially increased rapidly from 15 in 1965 to 339 by 1975 (λ=1.37) (Sptaker, 1995). The herd then fluctuated in size with lows of about 200 and 300 in 1978 and 1988, respectively, and highs of 450 in 1986 and 500 in 1996. In April 1996, when the herd was at its peak of about 500, the mean weight of a sample of 11 female calves was similar to the heaviest cohorts of calves from the parent Nelchina herd during 1992-1997 (Table 1).

In 1985 and 1986 caribou were again relocated to the Kenai Peninsula from the Nelchina hetd. At that time, the Nelchina herd was growing, from a herd size of about 27 000, and approaching a moderate density of about 0.5 caribou/km^2 (Van Ballenberghe, 1985). The 2 transplants resulted in formation of 3 additional herds, the largest of which became known as the Killey River herd (Fig. 1). This herd increased from about 70 caribou in summer 1987 to about 350 in 1997 (λ=1.18). In 1996,

Table 1. Population and range characteristics of 5 introduced caribou herds and their parent populations.

Herd	Year of introduction	Elevation of summer range (m)	Approximate mean number of days in growing season[a] (dates)	Mean rate of population increase (λ)[b]	Maximum summer density achieved (caribou/km^2)	Mean weight (kg) of 10-month-old female calves, mean, *n* (year of sample)	Mean weight (kg) of adult males, $\bar{x}$ (range, *n*)
Adak	1958, 1959	0-500	165 (15 May-30 Oct)	1.30[c]	1.0		280 (229-318, 5)[d]
Kenai Mountains	1965, 1966	600-1500	135 (15 May-30 Sep)	1.37[e]	0.3	57.6, 11 (1996)	
Kenai Lowlands	1966	20-100	150 (1 May-30 Sep)	<1.05	0.5		
Killey River	1985, 1986	600-1500	135 (15 May-30 Sep)	>1.26[f]	0.8	65.7, 10 (1996)	
Nelchina	n.a.	1000-2000	105 (15 May-1 Sep)	approx 1.15[g], approx 0.9[i], 1.10[j]	4.7	range 47.6-57.0, 9-29 (1992-1997)	255 (200-299, 9)[h]
Northern Peninsula	n.a.	0-1200	135 (1 May-15 Sep)	1.00[k]	1.4	51.4, 19 (1995), 48.4, 14 (1997)	
Nushagak Peninsula	1988	0-100	135 (1 May-15 Sep)	1.38[l]	0.8	57.1, 15 (1995), 50.9, 10 (1997)	

[a] Growing season is defined as the time when new growth (usually *Eriophorum*) is available in spring to the time of the first killing frost in autumn.

[b] Population increase during the first 10 years after transplant in transplanted herds, or at the time of the transplant in parent herds.

[c] Calculated from 1959 to 1967. Ten 3-month-old calves were released in 1958 and 14 were released in 1959, so herd growth was delayed until these animals reached maturity (Burris & McKnight, 1973).

[d] Weights from Hemming (1971), Jones (1966), and unpublished data given to D. Klein from 2 bulls collected by J. Hemming. Standard deviation = 34.5.

[e] The herd increased from 15 in 1965 to 339 in 1975. Initial growth rate inflated by high proportion of females in the transplant.

[f] One year after the transplant there were 70 caribou, and they increased to at least 281 by 1993.

[g] Growth during the Adak transplant in 1958 and 1959 (Skoog, 1968).

[h] Data from Skoog (1968), no estimate of variance given.

[i] Probable growth during the transplants to Kenai Lowlands and Kenai Mountains herds in 1965 and 1966 (Van Ballenberghe, 1985).

[j] Growth rate at the time of the transplant that formed the Killey River herd in 1985 and 1986. Growth rate was reduced by harvest (Tobey, 1993).

[k] Growth rate at the time of the transplant to Nushagak Peninsula (late 1980s).

[l] Growth rate was initially elevated by the high proportion of females in the transplant (Hinkes & Van Daele, 1996). Growth rate was calculated from 1988 to 1996.

the mean weight of a sample of 10-month-old female calves exceeded previously recorded calf weights for all Alaskan herds (Valkenburg, 1997) (Table 1). These calves were significantly heavier ($P<0.001$, $t=4.84$) than calves weighed during the same period in the Kenai Mountains herd, despite similarities in elevation, growing season length, and physiographic characteristics of their ranges (Table 1).

Nushagak Peninsula transplant

In 1988, caribou were transplanted from the Northern Alaska Peninsula herd to a vacant range on the Nushagak Peninsula about 100 km to the west (Fig. 1). The transplanted caribou increased rapidly (Table 1), and all females aged 2 years or older were fecund during 1988-1993 (Hinkes & Van Daele, 1996). At the time of the transplant, the Northetn Peninsula hetd had been stable in size at a relatively high density (about $0.6/km^2$). When body condition in both herds was assessed in April 1995, Nushagak calves were significantly heavier ($P=0.005$, $t=2.98$) than Northern Peninsula calves (Table 1), and 2-year-old females were commonly producing calves in the Nushagak herd. However, despite being transplanted to ptistine range, Nushagak Peninsula caribou calves never became as large as calves in the Killey River herd or other low-density Interior herds (Table 1) (Valkenburg, 1997). In 1997, when population density had increased to $0.8/km^2$ in the transplanted Nushagak herd, body weight of calves was not greater than in the Northern Alaska Peninsula herd ($P=0.28$, $t=1.11$) (Table 1).

Discussion

The 5 transplanted herds reviewed here provide additional evidence that body weight and natality in many established Alaskan herds are significantly limited by density-dependent nutritional factors that are independent of climate and genetics. On Adak, the longer growing season, lack of parasitic insects, and potential availability of green forage in winter could have accounted for increased body weight and productivity compared with parent stock in the Nelchina herd (Jones, 1966; Thomas & Kiliaan, 1990). On the Nushagak Peninsula, however, body weight of calves was greater in the transplanted herd from 1992 to 1995 despite the similat summer climate and physiography (Hinkes & Van Daele, 1996) (Table 1).

The Kenai transplants also demonstrate the potential for increased body weight and fecundity on pristine ranges. Calves from the 1996 cohort in the Killey River herd were significantly larger than any of the Nelchina cohorts. In the Kenai Mountains hetd initially, and in Killey Rivet herd natality in 2-year olds must have been much higher than that reported for the Nelchina, because the Kenai Mountains herd grew at nearly the biological maximum (indicating virtually all yearlings were pregnant), but the highest reported pregnancy rate in Nelchina yeariings was only 13% (Skoog 1968; Bergerud 1980: 568).

Although changes in body weight and natality tate were not obviously related to crude summer density across herds (Table 1), declines in body weight and natality occurred after relatively short periods of grazing pressure as density within herds increased. Decreasing summer nutrition is the factor most likely to cause observed declines in natality and body weight (Skogland, 1984; 1985; Eloranta & Nieminen, 1986; Reimers, 1997). Reduced body weight and natality began to occur in the Kenai Mountains herd after only 10 years of grazing, and summer density increased only to about $0.3/km^2$ before herd growth slowed. In 1995 crude density was still only about $0.5/km^2$ when body weight of female calves was similar to the patent Nelchina herd where summer density was $4.7/km^2$ (Table 1).

Inherent physiogeographic and climatic factors, rate of population growth, and opportunity for dispersal undoubtedly determine the summer density that herds can achieve. For example, on St. Matthew Island very high summer densities were achieved ($18/km^2$) because of the high quality and quantity of summer forage, the long growing season, lack of opportunity for dispersal, and high population growth rates due to the virtual absence of predators (Klein, 1968).

On mainland ranges where large predators are present, predation can have a profound dampening effect on population growth rate and density when functional and numerical responses occur and prey vulnerability increases as nutrition declines (Dale *et al*, 1994; Valkenburg *et al*, 1996). Population growth was apparently restrained immediately aftet introduction due to predation by wolves (*Canis lupus*), coyotes (*C. latrans*) and dogs (*C. familiaris*) in the Kenai Lowlands herd (Spraker, 1995). However, in the Kenai Mountains herd and the Killey River herd, although both wolves and grizzly bears (*Ursus arctos*) were present and lightly hunted, near maximum caribou population growth continued fot 10 years after introduction. This could either be due to a lag in predator hunting behavior, the low vulnerability of caribou on a very high plane of nutrition, or both. In the Nushagak herd large predators are scarce and particularly vulnerable to hunting.

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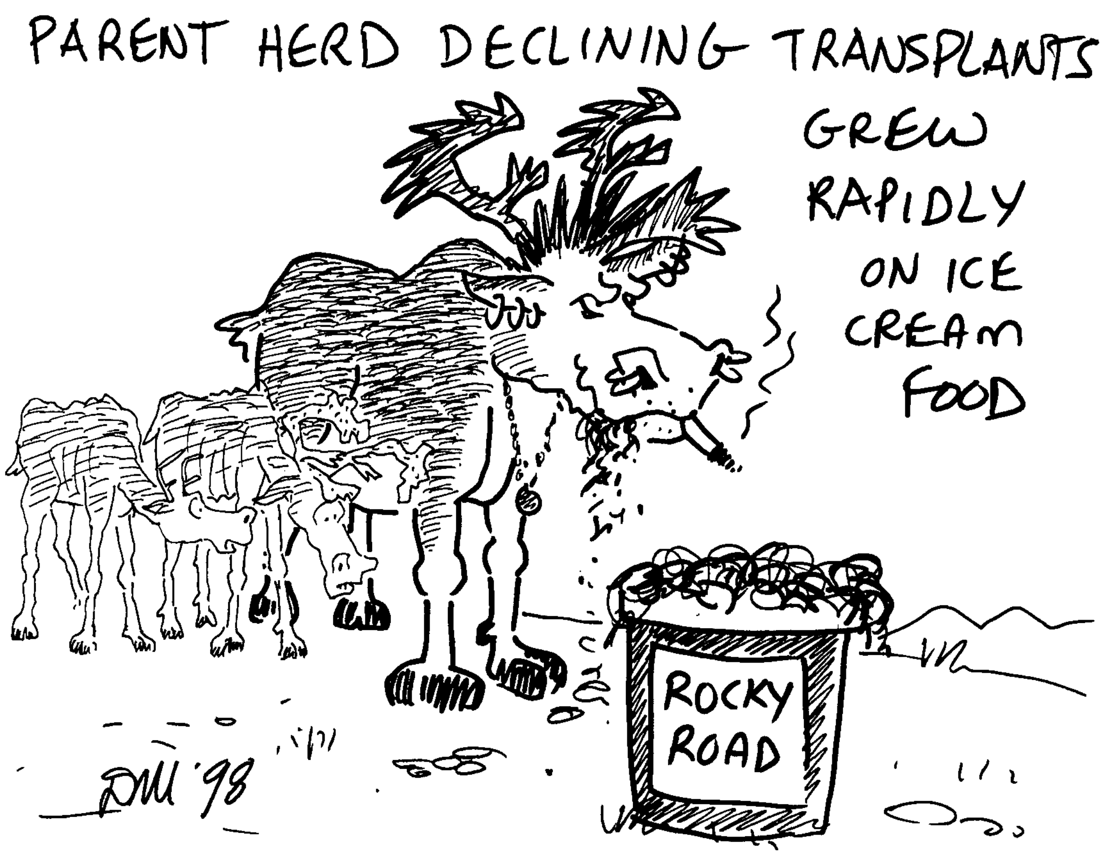

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Brief communication

A model for predicting the parturition status of arctic caribou

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Key words: body weight, fecundity, *Rangifer*, reproduction.

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Introduction

Fecundity of reindeer and caribou (*Rangifer tarandus*) varies directly with body weight ot condition at bteeding (Dauphine', 1976; Reimers, 1983; Eloranta & Nieminen, 1986; Lenvik *et al.,* 1988; Thomas & Kiliaan, 1991; Cameron *et al.,* 1993; Gerhart *et al.,* 1997). Fot barren-ground caribou (*R. t. granti, R. t. groenlandicus*), such relationships have been derived for individual herds, but few attempts have been made to expand models across subpopulations or subspecies. Here, we compare parturition/body weight relationships for the Central Arctic herd (CAH) and Porcupine herd (PCH); generate a combined probability model for individual females; and offer a population-level model from which mean parturition rate can be predicted from a sample of body weights in autumn or early winter.

Materials and methods

In late September/October 1987-91 and mid November 1990-94, respectively, 51 female caribou from the CAH and 125 females from the PCH were darted or netted from a helicopter, weighed, and equipped with radiocollars (Cameron *et al.,* 1993; Gerhart *et al.,* 1997). During the following late May/June, CAH females were relocated once or more, as required, by fixed-wing aircraft and classified as parturient or nonparturient based on calf presence, antler retention, and/or udder distention (Cameron et al., 1993; Whitten, 1995). For PCH females, parturition status was based on serum progesterone levels at capture: those with concentrations >1.5 ng/ml were considered pregnant in mid November (Gerhart *et al.*, 1997) and, thetefore, parturient in late May/June (Russell *et al.,* 1998). PCH females were further classified as lactating or nonlactating based on characteristics of the milk and udder (Gerhart *et al.,* 1997).

To determine if the body weights obtained for the PCH wete reasonable estimates of those ca. 1 month earlier (i.e., consistent with data for the CAH), we compared weights in late September/October with those in mid November 1992-94 for both lactating (n=35 and 39, respectively) and nonlactating females (n=43 and 9, respectively).

Analyses were restricted to sexually-mature females; that is, those either observed with a calf or known to have calved previously. Relationships between parturition status, a binary variable, and body weight were described using univariate logistic regression (Hosmer & Lemeshow, 1989). A model of herd parturition rate was derived by incorporating the normal-distribution parameter of the weight sample into a response surface (Cameron & Ver Hoef, 1994).

Table 1. Body weights[a] ± standard error of the mean, and parturirion models for female caribou[b] of the Central Arctic herd (CAH) and Porcupine herd (PCH).

	CAH[c]	PCH	CAH & PCH
Body weight, kg			
Partutient, $\bar{x}\pm s_{\bar{x}}$ (n)	91.0±1.4 (36)	92.0±0.8 (96)	91.7±0.7 (132)
Range	72-106	77-110	72-110
Nonparturient, $\bar{x}\pm s_{\bar{x}}$ (n)	84.9±2.0 (15)	84.9±1.7 (34)	84.9±1.3 (49)
Range	72-97	64-104	64-104
P-value[d]	0.01	<0.0001	<0.0001
Logistic regressions			
Parameters: β_0	-7.690	-8.029	-7.929
β_1	0.097	0.102	0.101
P-value[e]	0.0251	0.0002	0.00001

[a] Sep/Oct (CAH) or mid Nov (PCH).
[b] All sexually marure.
[c] Cameron & Ver Hoef, 1994.
[d] Comparison of means.
[e] Significance of slope, β_1.

Results and discussion

Body weights of PCH females in late September/ October were not significantly different from those in mid November, either for lactators (93.2 *vs.* 90.0 kg, P=0.21) or nonlactators (100.3 *vs.* 99.4 kg, P=0.77). Hence, pooling weight data across herds was justified, despite temporal differences in sampling.

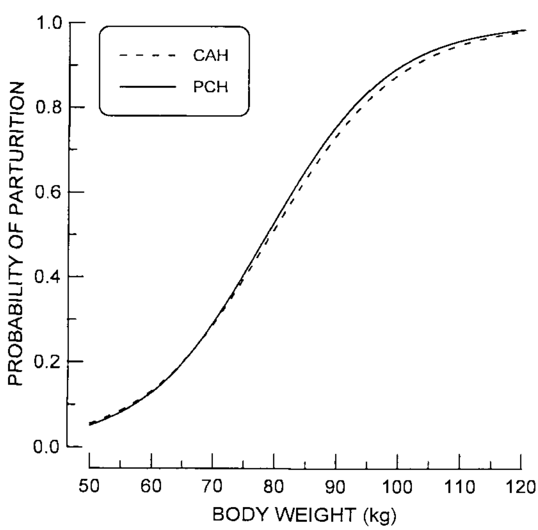

Fig. 1. Logistic regressions (Table 1) relating parturition probability of female caribou ro body weight in autumn or early wintet, Central Arctic herd (CAH) and Porcupine herd (PCH).

Mean autumn or early-winter weights of subsequently parturient females were significantly higher than those of nonpatturient females for the CAH (P=0.01) and PCH (P<0.0001), as well as for the two herds combined (P<0.0001) (Table 1). Univariate logistic regressions for the CAH and PCH (Fig. 1) were significant (P=0.0251 and 0.0002, respectively; Table 1) but not significantly different (P>0.8). Data for the two herds were therefore consolidated, and a single, highly-significant model (not shown) was generated (P=0.00001; Table 1).

A model for predicting hetd parturition rate, incorporating the combined logistic regression, was plotted in relation to various means and standard deviations of body weight (Fig. 2). Note that sensitivity varies with the patameters of weight distribution.

These new logistic-regression and population models may also apply to othet arctic caribou in Alaska and Canada. In the Western Arctic herd, for example, post-rut weights of females ≥3 years of age ($\bar{x}$=89.5 kg, range 74-109; Skoog, 1968:25) are similar to those reported here (Table 1).

Models encompassing subarctic herds, however, will require additional adjustments. Logically, to achieve the same parturition probability, larger-bodied females must maintain or acquire proportionately more nutrient reserves than their smaller countetpatts. Scaling body weight to skeletal size in a multiple logistic regression will therefore be necessary to broaden the application.

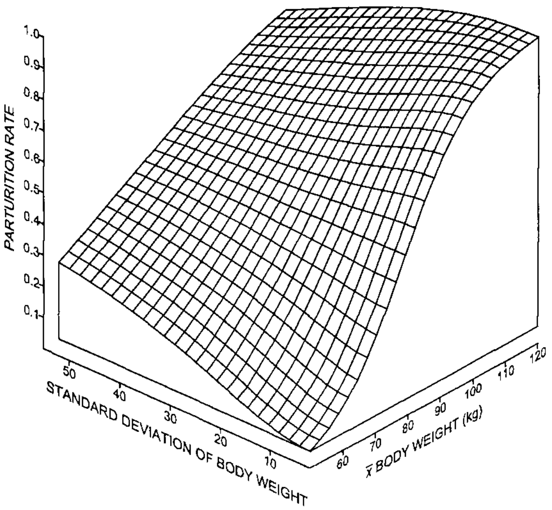

Fig. 2. Response surface of parturition rate of adult female caribou, Central Arctic and Porcupine herds, in relation to the mean and standard deviation of body weight in autumn or early winter.

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Abstract: The Eight North American Caribou Workshop, Whitehorse, Canada, 20-24 April, 1998.

24-h activity pattern of wild reindeer in summer with emphasis on behavior compensation at night due to limited grazing during the day

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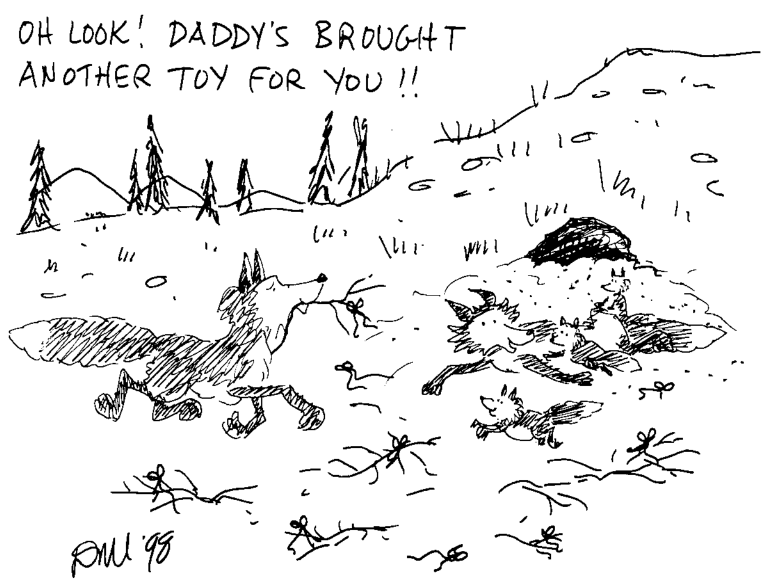
Abstract: It is inaccurate to estimate an animal's enetgy budget and resources availability without a complete 24-h record of the animal's activity and tange use. The purpose of rhis study was to document 24-h activity patterns of wild reindeer (*Rangifer tarandus tarandus*) during summer in a Southern Norwegian mountain range, with special emphasis on feeding behavior and range use. Extreme variation in daily summer activity patterns of reindeer can result from harassment by parasitic insects. This study concentrates on nutrient and energy compensation at night in the form of an optimal activity pattern and forage use as an adaptation to limited grazing and ruminating during the day. We used 3 methods of sampling animal activity; 1) instantaneous scanning of groups at 15 min intervals, 2) timing detailed activity sequences of focal females for ≤30 min, and 3) non-systematic *ad libitum* observations. From approximately June 25-Sept. 1, wild reindeer in Sourhern Norway are harassed by biting and parasitic insects. We hypothesized that on days with severe insect harassment, reindeer will have differenr activity patterns between "day" and "night". This night activity pattern should reflect an energy/nutrient acquiring and energy conserving strategy and supporr rhe predictions below. Two assumptions for this are; 1) that insect harassment only occurs during "day", and furthermore, is dependent on appropriate climatic conditions necessary for insect activity, and 2) during "night", climatic conditions do not allow for insect activity and therefore, reindeer are not harassed. We predicted for a night following a day with high insect harassment, that during the night compared to day; 1) reindeer will compensate for the daily constraint of insect harassment by spending more time feeding and feed more intensely, i.e. search less and feed standing still more, during feeding bouts, 2) the choice for reindeer for where ro feed, and thus what to feed on, is limited by the distances to the closest snow patch, thus, the distance to closest snow patch will be greater, allowing for more freedom of choice and use of optimal forage, 3) when feeding, reindeer will urilize the highest quality forage available, 4) reindeer will spend more rime lying (including ruminaring), and 5) reindeer will use less time walking and running and considerably less time standing. This is the first systematic information gathered on wild reindeer behavior during summer nights using direct observational methods. Averaged over rhe summer season (1997) for scan samples, reindeer used 30%, 28%, 21%, 14%, and 7% feeding, lying, standing, walking, and running, respectively, during the day (06:00-23:59), compared to 47%, 42%, 1%, 9%, and 1% in the same activities, respectively, at night (00:00-05:59). When active during the day, reindeer moved an average of 90 m from the closest snow patch, compared to 126 m at night. These preliminary results from the first season (1997) lend support to predicrions 1, 2, 4, and 5. We could not distinguish among vegetation types occupied while feeding and vegetation actually ingested.



Climatic influence on forage quality, growth and reproduction of reindeer on the Seward Peninsula I: climate and forage quality

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Abstract: Forage quanrity and quality during spring and summer play an important role in rangifer productivity by influencing body condition, rates of growth, breeding success, and winter survivorship. Annual variarions in summer weather influence forage availability and digestibility, which in turn, affect animal productivity. A study investigating the effect of climate on forage plant emergence and qualiry and subsequent reindeer productivity was conducted during 1996 and 1997 on reindeer ranges of the Seward Peninsula, Alaska. Climatological models were developed using Growing Degree Days (GDD) to examine the effect of heat accumulation on forage plant emergence and chemistry. Models using temperature to examine plant chemistry (GDD vs nitrogen, GDD vs. Neutral Detergent Fiber, GDD vs. Acid Detergent Fiber) were found to be better predictors of plant quality than models that used date. Fiber concentrations in graminoids were ar a minimum during midseason, in contrast, to deciduous shrubs that exhibited low fiber concenrrarions in the spring with progressive increases through midseason to senescence. Fiber concentrations in forbs fluctuated less dramatically than either graminoids or shrubs. We developed a dereministic model relating climate variables to reproductive success of yearling reindeer based on observed relationships between temperature and planr chemistry.

Climatic influence on forage quality, growth and reproduction of reindeer on the Seward Peninsula II: reindeer growth and reproduction

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Abstract: Birrh weights and growth rates of caribou and reindeer calves have been shown ro be influenced by summer and winter range conditions. Reproducrive performance has been shown ro be influenced by autumn body weight. Unlike reindeer in many herds, reindeer on the Seward Peninsula frequently give birth at one year of age. This early breeding requires rapid summer weight gain and thus may be dependent on high quality forage. Yearly variation in forage quality is strongly influenced by weather, therefore age of first reproduction should be correlated with climatic variation. We used data collected from reindeer on the Seward Peninsula from 1987-1997 to show that the proporrion of yearlings lactating in June and July is positively related to Growing Degree Days (GDD) the previous May and June, and negatively related to both GDD the previous July and snow depth the winter prior ro birth. Plant nitrogen and fiber data suggest that this may be due to the effects of GDD on forage plant emergence in May and June and plant fiber formation in July. Our model suggests that low snow years improve female condition at the time of birrh, rhereby influencing birrh weight and calf growrh rate during lactation, and that warm spring and cool summer temperatures optimize plant quality and decrease insect harassment. These favorable weather conditions allow calves to reach higher weights prior to the breeding season, thus increasing rhe proportion of pregnanr yearlings the following spring. The model fit is very good, suggesting that these three climatic vatiables, snow depth, spring temperature, and summer temperature, are the primary factors affecting yearly variation in age of first reproduction in this teindeer herd.

Development and verification of a fugacity-based bioaccumulation model for terrestrial ecosystems: an application to a lichen-caribou-wolf food-chain of the Northwest Territories

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Abstract: A fugacity-based bioaccumulation modeling approach is presented to assess the exposure of organic contaminants to terrestrial organisms. The essence of rhe model is to characterize the extent of food absorption and food digestion, which are crucial factors controlling biomagnification. The effect of food digestion on biomagnificarion is determined through static head-space analyses on field collected food and fecal samples. Dietary intake and absorption data ate available from the literature for many terrestrial organisms. These dara, along with head-space analyses results are used to paramaterize the gastro-inrestinal magnification factors in the model. In June of 1997, lichens and caribou fecal samples were collected from the calving grounds of the Bathurst caribou herd (66°55'N, 109°50'W). Environmental concenrrarions of organics in the samples were measured at the Gteat Lakes Institute and are used for model verification. Out semi-empirical modelling approach is applied to an arctic terrestrial ecosystem to predict internal concentrations of organic chemicals in barren ground caribou (*Rangifer tarandus*), and wolf (*Canis lupus*) from observed concentrations in two common lichen species (*Cladina rangiferina* and *Cetraria nivalis*) found throughout the grazing range of the Bathursr caribou herd.

Differences in tissue ^{15}N natural abundance reveal seasonal shifts in diet choice of reindeer and caribou

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Abstract: As part of a comprehensive study of reindeer forage relations on the Seward Peninsula, Alaska, we are investigating ^{15}N natural abundance values for a suire of *Rangifer* forage plants and the resulting isotope chemistty in animal tissue (including antler, hooves, muscle, and blood), ro test the hypothesis that variation in tissue stable isotope chemistry of *Rangifer* is a reflection of variation in diet composition over temporal and/or sparial scales. Here we show examples from reindeer, caribou, and moose how enrichment or depletion of $\delta^{15}N$ in animal tissue can contribute to our understanding of seasonal shifts in their diet composition, and discuss the strengths and caveats of this methodology. For example, reindeer antler exhibit a marked enrichmenr $\delta^{15}N$ values over the season (based on core vs. periosteum antler values) reflecting the importance of deciduous shrub-based dietary nitrogen early in rhe summer, as compared to a graminoid-derived nitrogen larer in the season. By contrast, captive reindeer kept on a uniform dier show consranr antler values that are greatly enriched in $\delta^{15}N$ due to a large portion of their diet consisting of isotopically enriched pasture (($\delta^{15}N = +3.5‰$) and commercial feed ($\delta^{15}N = +2.1‰$). Comparison of reindeer and moose antler support our contention that animal isotope signatures are functionally related to diet, rather than to other ecological variables. Reindeer antlet exhibit a gradual enrichment in isotopic signature over the season reflecting the increasing importance of graminoids in their dier. By comparison, rhe $\delta^{15}N$ of moose antlers from interior Alaska start out depleted, reflecring a diet of isotopically-depleted woody browse, then show an enrichmenr of the heavy isotope later in the season consistent with a diet of green biomass, including aquatic plants, and finally exhibit an isotopic depletion as the animals return to feeding on woody shrubs. In contrast to ttaditional approaches to diet selection (e.g., visual observation and fecal pellet analyses), measurements of stable isotope chemistry represents an assessment of dietary relationships that integtate dietary histoty on a weekly, seasonal or yearly basis, depending on the target tissues analyzed. We contend that stable isotope chemistry used singly or in combination with more traditional approaches to examine forage relationships, represents a potentially powerful merhod to evaluate the foraging ecology of norrhern, free-ranging ungulates.

Comparison of physical characteristics of Yukon woodland caribou herds

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Abstract: Information from radio telemetry studies has found that woodland caribou living in the snow shadow region of southwest Yukon spend parr of the winter in the subalpine and alpine. Other woodland caribou living in areas with high snowfall in central and eastern Yukon have rraditional winter ranges in forested lowlands. We test the hypothesis that those woodland caribou which winrer in the alpine are phenotypically different than woodland caribou wintering in foresred environments. We compared five physical measurements from 382 female woodland caribou in eleven Yukon herds. Results found a significant (14 cm) diffetence in shoulder height for forest-wintering groups over alpine-wintering groups. But there was no significant difference in other body measurements or in body proportions. It is unlikely the difference in shoulder height is due to winter nutririon since body score did not differ between forest and alpine-wintering groups. Our results provide no support for the hypothesis that condition wintering in deep snow results in selection for caribou with longer legs.

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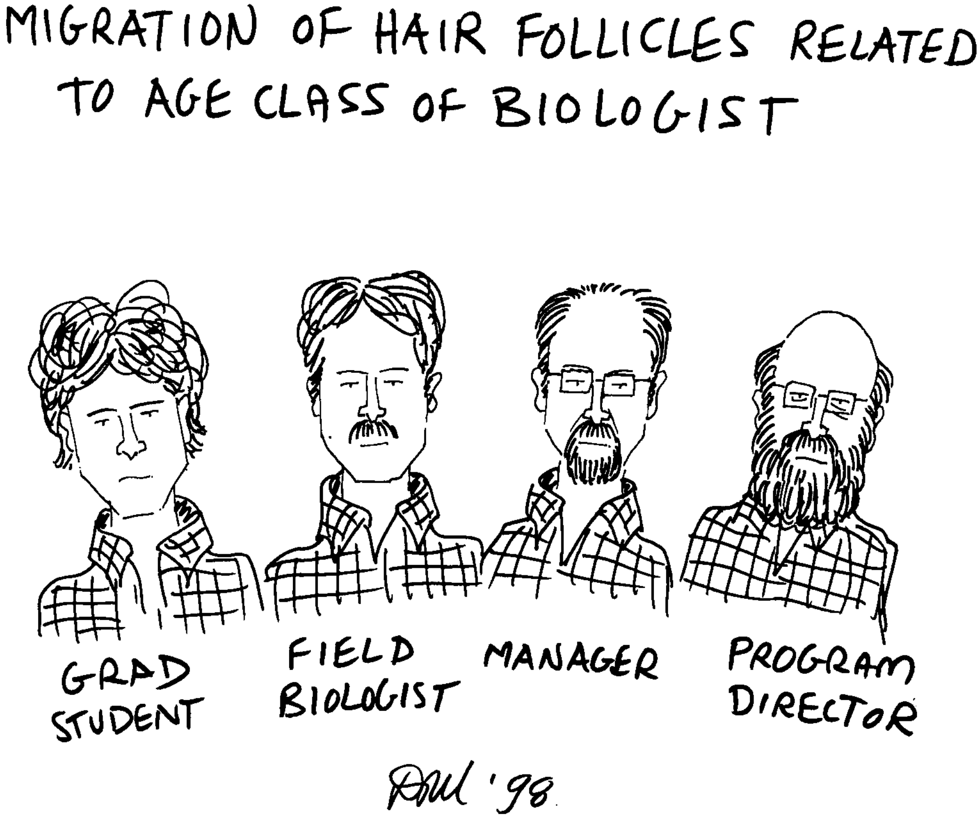

Abstract: The Eight North American Caribou Workshop, Whitehorse, Canada, 20-24 April, 1998.

Antler characteristics of reindeer and caribou

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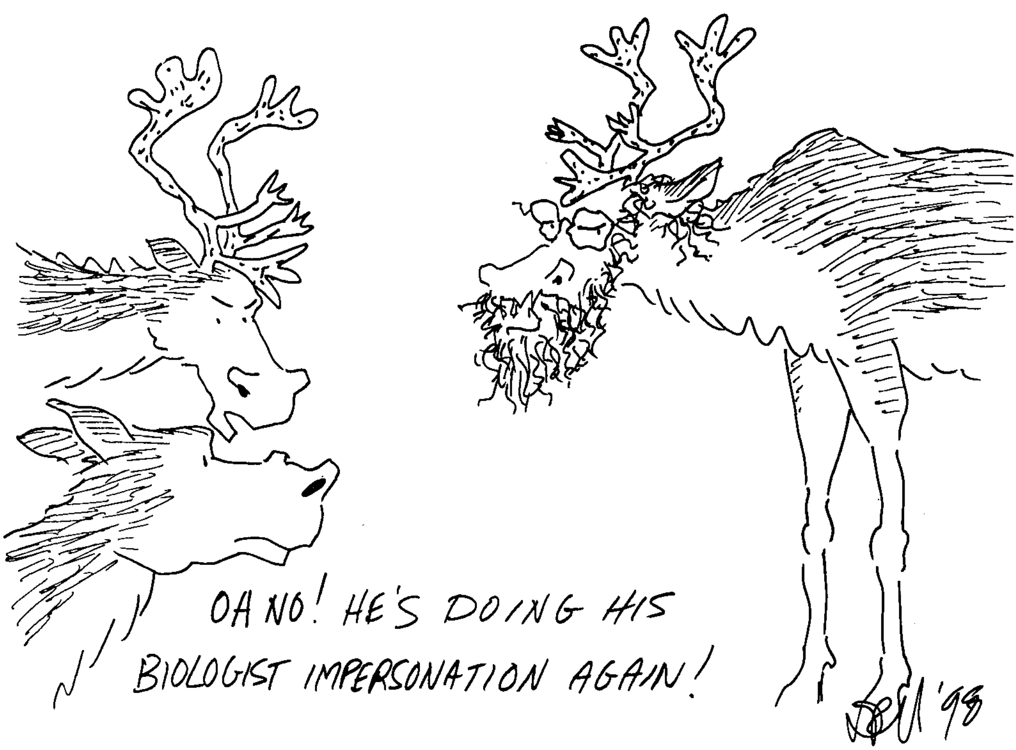
Abstract: Caribou and reindeer are the only species of deer in which females and calves are capable of growing antlers. Both caribou and reindeer are being raised at the Large Animal Research Station (LARS), Institute of Arctic Biology, Universiry of Alaska Fairbanks and provide an opportunity to closely monitor antler growth and compare anrler characteristics between sex/age classes and subspecies. Information on antlet growth, cleaning, casting and regrowth has been collected on an opportunistic basis ovet the past 5 yeats. These data will be used to depict the annual antler cycle in caribou and reindeer. A subsample of cast antlers has been weighed and measured from the coronet, along the inner curve to the tip of the inner (longest) tine. Adult male antlers (≥3 yrs old) were heavier ($P<0.05$) and longer ($P<0.05$) than those of adult females in both subspecies. Among females, reindeer had heavier ($P<0.001$) and longer ($P<0.001$) antlers than caribou in all age classes. There were not enough male antlets available to compare between subspecies and age. Pedicle/firsr antler growth was measured from the day of birth rhrough to ossification of the first antler in female reindeer calves (1994) and female caribou calves (1997). Palpable pedicles were evidenr on the day of birth and measurable pedicle growth began in both subspecies by 2 weeks of age. This was followed immediately by growth of the first antler. Increase in body mass over the first 17 weeks did not differ between female reindeer (n=4) and female caribou (n=5) calves. However, in the same time frame, reindeer anrler growth rate was significantly ($P<0.006$) greatet than that of caribou. Only female reindeer calves produced secondary tines in the first growing season. Castration of male caribou (n=2) and reindeer (n=2) on rhe day of birth did not prevent pedicle/antler growth in these calves. In both our reindeer and caribou, housed under the same conditions and eating the same food, pedicle induction was evident at birth and not dependent on post natal steroids. The rapid growth of reindeer calf antlers is consistent with the heavier and longer female reindeer antlers found in all age classes. This suggests a genetic difference rhat may be related to the earlier sexual maturity of the reindeer.



Mechanisms of summer weight gain in northern caribou herds

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Abstract: Northern caribou (*Rangifer tarandus granti*) encounter dramatic seasonal shifts in nutrient availability. Fat and protein reserves depleted during winter are replenished in summer and early aurumn. To examine rates and patterns of summer weight gain, 46 Central Arctic herd (CAH)(1988-91) and 76 Porcupine caribou herd (PCH)(1992-94) females were captured and weighed in early July and then tecaptured and re-weighed in late September or October. For PCH females, a body condition score was also recorded, allowing estimates of protein and fat composition. In early summer, non-lactating females in the PCH were significanrly heavier rhan those in the CAH (87.8 kg *vs.* 79.6 kg, $P=0.001$), while corresponding weights of lactating females were not significanrly different (81.8 kg *vs.* 79.8 kg, $P>0.3$). By autumn, however, both lactating and non-lactating females in rhe PCH were heavier rhan those in rhe CAH (lactating, 93.3 kg *vs.* 85.4 kg, $P=0.01$; non-lactating, 100.9 kg *vs.* 94.1 kg, $P=0.0006$). Rates of gain for lactating females were significantly higher in the PCH than in the CAH (120 g/d *vs.* 61 g/d, $P=0.0001$), while rates for non-lacraring females were similar (168 g/d vs. 159 g/d, P>0.4). For non-lactating females of the CAH, summer weighr gain was inversely related to July body weight (gain=0.51*July weight + 55.05, $r=0.75$, $P=0.001$), suggesting a "target" autumn weight of 107 kg (i.e., the x-intercept); lactating CAH females exhibired a similar, but not significant, response (gain=-0.13*July weight+15.77, $r=0.41$, $P>0.16$). For both lactating and non-lactating females of the PCH, summer weighr gain and July weight were unrelated ($P>0.7$ and $P>0.9$, respecrively), but there was a significant inverse relationship between the percentage of weight gained as prorein and body protein teserves in July, independenr of lactation status (pgain=-3.23*July protein + 92.7, $r=0.40$, $P=0.0001$). This suggests a "target" protein reserve of 28.7 kg. Conttasting mechanisms for replenishing body reserves are discussed in relation to differences in resource availability of the two herds.

Composition of milk during lactation

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Abstract: We have developed a set of criteria to determine wherher a caribou is in full lactation, in the process of weaning or has just weaned her calf, based on milk composirion. Criteria were derived from the analysis of 276 milk samples obtained from females of rhe porcupine caribou herd (PCH) and the central arctic herd (CAH) in the months of June, September, Ocrober and November. Milk composition changed matkedly with date with a general increase in dry matter (DM), protein (P) and fat (F) and a decline in lactose (L) in November compared with June. These major changes include a linear increase in P with F and non-linear changes of P with L and L with DM. Independent of these relations we noted four different populations of milk chemistries, Types I...IV, following the producrion of colostrom. Through field observations, and those made ar the Large Animal Research Station, we conclude that Type I milk typifies that for females in peak milk production, Type II for early weaning, Type III for weaning and Type IV a clear liquid produced immediately after weaning (see Table). Thus a milk sample taken in October through November can be used to diagnose a female's stage of the weaning process. In terminal lactation the increase in P and F is associated with a decline in L. Finally, fat is removed and the remaining clear liquid is rich in N, presumably in the form of amino acids given its sweat taste. Three ro 4 weeks posrparrum, 90% of 82 caribou with calves were producing Type I milk, and 10% produced Type II. Females that had lost their calves shortly aftet birth produced Type IV milk. By late September, 98% of 41 females with calves were producing Type II milk. Caribou with a calf at foot in November ($n=99$) were classified as recently weaned (Type IV; 15.1%), weaning (Type III; 48.5%) and extending lactation (Type II; 36.4%).

STAGE	TYPE	DM	LACTOSE	PROTEIN
Peak	I	20-40	>3	4-10
Early W	II	30-40	2-4	10-18
Late W	III	10-48	<2	6-20
Weaned	IV	0-10	<0.5	<7

Meal patterns in reindeer : implications for interpretating feeding behavior in caribou

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Abstract: The seasonal cycle in voluntary food intake in free-ranging and ad libitum fed reindeer and caribou is a well-documented phenomena (White *et al*, 1984: *Can. J. Anim. Sci.* 64 (suppl.): 349-350). Very little is known, however about theit daily meal patterns. This information is needed to asses how feeding behavior (i.e. meal size, meal duration, and frequency) is altered to accommodate radical intake changes (1.8 to 2.3 times in magnitude) between summer and winter intake. We analyzed 24-hour feeding behavior using data collected fot sevetal weeks (during early and mid winter) from individuals and groups of reindeer. Four adult non -pregnant female reindeer were used for the study. Animals were housed ourdoors in a group pen at the Large Animal Research Sration, University of Alaska, Fairbanks. Reindeer were fed pellered concentrate (QTX, Alaska Feed Company, Palmer) and snow ad libirum. Individuals were rorated on a daily basis through a single feeding pen equipped with an electronic scale and 24 hour feeding acrivities were recorded. Sampling interval was 5 minutes. Food residues were measured daily (nearest 1 g). To assess the influence of socialization on feeding behavior animals were observed randomly 4 times a day. Three criteria were used to define meals: minimum amount eaten (50 g), maximum time during which the minimum amount must be eaten (5 min), and the minimum interval during which no feed was earen (>15 min<30 min). Earing that occurs berween meals is designated as nibbling. These criteria determine the initiation and termination of meals and intermeal intervals (Baile, 1975: *Digestion & Metabolism in the Ruminant*). Relations between variables were determined with polynomial tegressions. Significance level was set a $P<0.05$. A total of 246 meals were analyzed. There was no evidence of social facilitation of feeding. Average meal frequency (±standard error of the mean) per day were 7.4±0.33 with a range of 3-11 meals/day. There is a strong correlation between meal size and % of total number of meals (r=0.96; $P<0.001$). Reindeer preferably ate small meals (50-250 g). Meal size increased with duration of the pre-meal interval (r= 0.99; $P<0.001$). We found no correlation between meal size and post-meal interval (r=0.70; $P>0.05$). However, the after-meal interval does not exceed on average 200 min, similar to data from concentrate fed sheep. This could suggest some type of undetlying feeding rhythm. A possible candidate could be rumination. Resting bouts in caribou during winter have a similar duration on average 126±55 min during daytime bouts and 127±73 min during nighttime bouts (Maier, 1996: Ecological & *Physiological aspects of Caribou activity & responses to aircraft overflights*). Comparison of analysies of meals for reindeer wirh sheep adapted to a 60% concentrate ground suggest striking similarities of feeding behavior berween both species. Caribou and people, coexistence into the future.

Habitat selection by calving caribou of the Central Arctic herd

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Abstract: This poster presents the hypotheses, objective, and methods for a study of habitat selection by the Central Arctic caribou (*Rangifer tarandus granti*) herd (CAH) at calving. The CAH calves between the Colville and Canning River on the Arctic Coastal Plain, Alaska. Research has suggested a change in caribou distribution of the CAH. The primary objective of this project is to estimate how changes in distriburion have influenced habitat use and selection. We will examine habitat selection of radio-collared caribou at calving. Habitat use at calving will be investigated for possible relationships with vegetation, topography, climate, development, and snow ablation on calving grounds. This study will provide further understanding of dynamic environmental and anthropogenic influences on habitat use of CAH calving caribou.

Antlers in relation to age, condition, and fecundity of caribou

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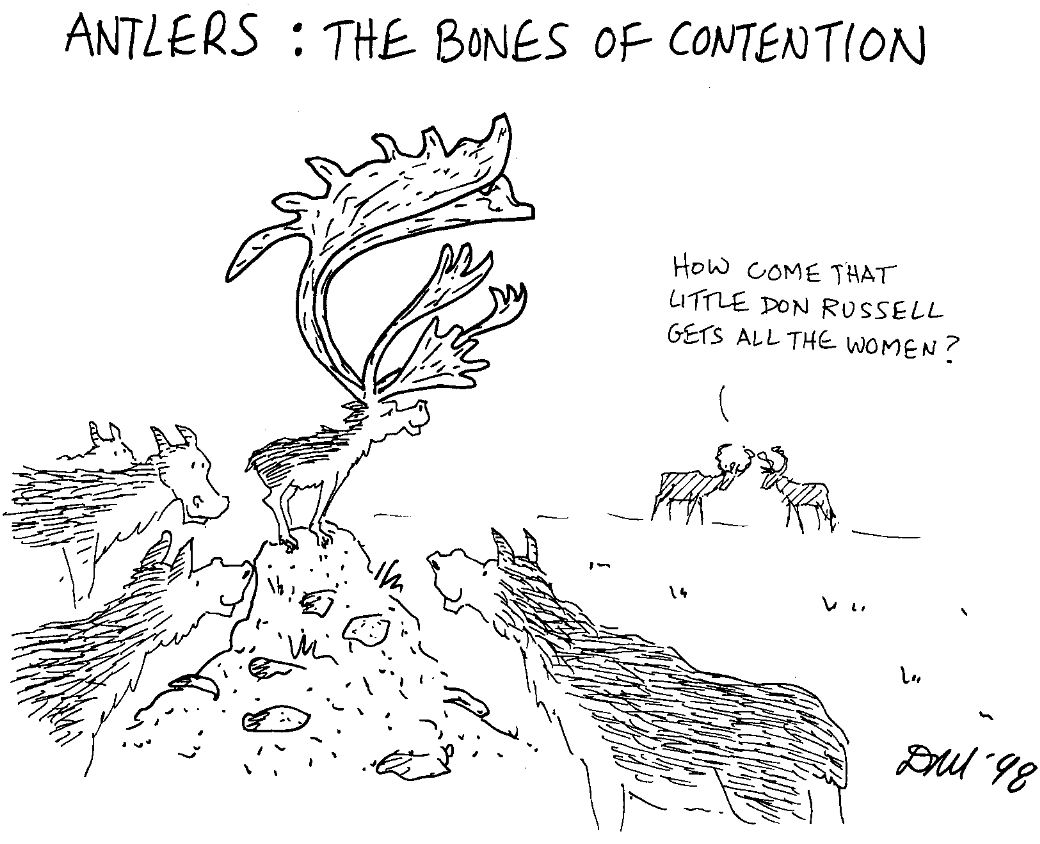
Abstract: Consideting the importtance of antlers in dominance and rank of caribou, few data are available on their size and weight. We examined the relationship between weight of antlers and age, body size, fat reserves, and fecundiry in a sample of 1036 caribou. We also recorded the frequency of two, one, and no antlers at two seasons. Samples were obtained in December and March from 1982 through 1987 from the Beverly herd of barren-ground caribou (*Rangifer tarandus groenlandicus*) in north-central Canada. Weight of antlers increased with age of female caribou even after age 5 years. Antler weight was significantly but weakly related to body size, condition indices, and fecundity. Therefore, antler weights can be used to predict pregnancy rates and physical condition only if large numbers of anrlers are obtained.



Session six

Habitat

FOR REASONS UNKNOWN CARIBOU
SPENT A LOT OF TIME IN BOGS

The Eight North American Caribou Workshop,
Whitehorse, Yukon, Canada,
20–24 April, 1998.

Wetland habitat selection by woodland caribou as characterized using the Alberta Wetland Inventory

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Abstract: We examined habitat selection by woodland caribou (*Rangifer tarandus caribou*) in northwestern Alberta based on a wetland classification system developed for the Alberta Vegetation Inventory. Our rwo objecrives were to describe caribou habitat use, and to assess the utility of the wetland classification system in land-use planning on caribou range. We used a geographical information system to ovetlay the locations of radio-collared caribou on the habitat map. Using a "moving-window" analysis of habitat availability, we examined patterns of habitat selection by 16 individual female caribou during five seasons annually over two years. We did not detect significant differences in habitat selection patterns among seasons. Caribou showed significant preferences for both bogs and fens with low to moderate ttee cover relative to marshes, uplands, heavily forested wetlands, water, and areas of human use. The werland classification system appears to have value for broad-scale planning of industrial activity on caribou range. More-detailed descriprions of vegerarion, especially understory species, are required to refine this system for operational-level forest harvest planning.

Key words: habitat availability, habitat use, peatlands, *Rangifer tarandus caribou.*

Rangifer, Special Issue No. 12, 153–157

Introduction

In boreal woodlands, caribou distribution has been strongly linked to wetlands (Bradshaw *et al.,* 1995; Rettie, 1998). Most vegetation classifications that exist for northern Alberta focus on merchantable forests. Much less attention has been given to wetlands or stands of non-merchantable trees. Recently, a system has been developed which allows rapid classification of wetlands across large areas using airphoto interpretation (Halsey & Vitt, 1996). That system, referred to as the Alberta Wetland Inventory Classification, and similar ones are being used by forestry companies and government agencies for operational-level planning in Alberta, Saskatchewan, and Manitoba (Rettie, unpubl.; Wynes, unpubl.; Halsey *et al.*, 1997). If the classification also differentiates among habitat types as they are used by caribou, it will aid in integrating catibou habitat needs with forest-management planning. We examined caribou habitat use in relation to the classification system to determine its usefulness in predicting caribou distribution.

Study Area

The study area included approximately 2750 km^2 (28.5 Townships) of a >11 000 km^2 caribou range in the Red Earth Creek area of north-central Alberta, located 130 km northeast of the town of Peace Rivet (AFWS, 1993). At the time of our study, about half the estimated total of 300 caribou in the population used the study area.

The study area was within the Mid Boreal Mixedwood ecoregion (Strong & Leggat, 1992). Dominant forest types wete black spruce (*Picea mariana*) on poorly drained sites and vatiable combinations of aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), and white spruce (*Picea glauca*) on moderately well- to well-drained, upland sites. Labrador tea (*Ledum goenlandicum*), bog cranberry (*Vaccinium vitis-idaea*), and mosses were common understory

Table 1. Wetland classification system (from Halsey & Vitt, 1996).

Classification Level Attributes	Code
Wetland Class	
Bog	B
Fen	F
Marsh	M
Swamp	S
Shallow Open Water	W
Vegetation Modifier	
Forested (>70% tree cover)	F
Wooded (>6 - 70% tree covet)	T
Open (≤6% tree cover)	O
Wetland Complex Landform Modifier	
Permafrost presenr	X
Patterning present	P
Petmafrost or patterning not presenr	N
Local Landform Modifier	
Internal lawn/collapse scar	C
Internal lawn with islands of forested peat plateau	R
Iternal lawns	I
No internal lawns present	N
Shrub cover >25%, rree cover ≤6%	S
Graminoid dominated, shrubs ≤25%, trees ≤6%	G
Miscellaneous	
Anthropogenic	A
Upland	Z

plants on poorly drained sites. Wetlands comprised bogs, fens, marshes, swamps, and areas of shallow, open water (Table 1; Appendix). Topographic relief was less than 100 m. Mean annual precipitation in the region is about 380 mm (Strong & Leggat, 1992), with about 150 mm of that falling as snow (Morton & Wynes, 1997). Maximal winter snow depths of 50-70 cm occurred in February and March (Morton & Wynes, 1997). Human activity in the area was related primarily to oil and gas exploration and production (access roads, well sites, pipelines), and two paved roads that transected the study area from north to south and south to east. Commercial logging had occurred only in the extreme southern and eastern portions of the area at the time of our study, and involved a total land area of <2000 ha (<1% of the study area). The total area of disturbed lands, including roads, borrow pits, and clearcuts, was 3325 ha (1.21% of the study area; Table 2).

Materials and methods

Caribou were captured using a net gun and were fitted with VHF radio-transmitter collars. Using fixed-wing aircraft, we located radio-collared caribou between January 1995 and February 1997. We flew surveys about once per week in fall (15 Sep.-14 Nov.), early winter (15 Nov.-15 Jan.), late winter (16 Jan.-1 Mar.), and spring (1 Apr.-15 May), and once per month in summer (16 May-14 Sep.) The number of days between successive surveys varied from 6-36. Locations were classified by season.

Caribou were located visually whenever possible. We estimated the error associated with telemetry locations by placing collars in the study area at points unknown to the survey crew and locating them as if they were placed on animals (Morton, 1997). Location error was calculated as the difference between the location based on telemetry and the actual location. Separate estimates were made for locations where visual contact was made with a target (a tree matked with surveyors' flagging) and where no visual contact was possible (no marked target).

Habitat classification was done at a scale of 1:20 000 by L. Halsey and D. Vitt, University of Alberta, based on Alberta Wetland Inventory

Table 2. Occurrence of habitat types in the Red Earth study area. Codes for habitat types are included in Table 1.

Habitat Type	Area (ha)	Proportion (%)
Anthropogenic (A)	3 325	1.21
BFXC	51	0.02
BTNI	2 395	0.87
BTNN	35 360	12.85
BTNR	12 066	4.38
BTXC	1 220	0.44
BTXN	6	0.01
FONG	690	0.25
FONS	38 414	13.96
FOPN	25	0.01
FTNI	2 081	0.76
FTNN	34 674	12.60
FTNR	6 527	2.37
MONG	2 291	0.83
SFNN	969	0.35
SONS	16 490	5.99
SOWN	231	0.08
STNN	7 516	2.73
WONN	1 382	0.50
Upland (Z)	101 454	36.86
Unclassified (not used in analyses)	8 061	2.93
TOTALS	275 228	100

Classification Standards (Halsey & Vitt, 1996). Wetland types were differentiated by the presence of organic matter, vegetation cover, presence of permafrost, and landform (Appendix 1).

Locations of radio-collared caribou and the wetland classification were digitized and incorporated into a geographical information system (GIS). We determined habitat use by caribou by overlaying caribou locations on the wetland classification within the GIS, and comparing habitat used with habitat available.

We defined "habitat used" as that within a circle (buffer) centred on the telemetry location. We assessed three different measures as potential buffer radii: 1) the estimated telemetry error (from field tests, as described above); 2) the 50th percentile of daily movement rates; and 3) the mean daily movement rate. We tested the effect of varying buffer size on habitat selection indices (described below) with a multivariate analysis of variance (MANOVA), and used the most-conservative measure (largest radius) for further analyses.

We calculated available habitat separately for each caribou location using the procedure developed by Arthur *et al.* (1996). "Available habitat" was that surrounding an individual caribou location within a circle with a radius equal to the distance that the animal was likely to move between successive locations. We considered that distance to be the 95th percentile of all distances moved by all caribou between surveys, and calculated a separate radius for each of three survey intervals: 6-9 days, 10-20 days, and 21-36 days.

For both use and availability, we calculated the proportion of the total classified habitat within each circle (used and available). Multiple locations for each animal were grouped by season to produce a single set of selection indices for each caribou per season (animal season). Locations were deleted if the interval between successive locations was >36 days, if >50% of either habitat used or available was unclassified, or if <4 locations were available for an individual animal during a single season. We chose those limits to reduce potential biases due to low sample frequency or small sample sizes.

We coded the habitat data for individual animal, season, and buffer radius. The data were processed with a program written in C++ to determine the resource probability function (RSPF) for each animal season (Arthur *et al.*, 1996). The RSPFs were the set of resource selection indices (b_i) where $I=1$ to H, where H is the number of habitat types.

Because the selection indices for each animal season formed a composition (i.e., always totaled 1.0), we used them to create 10 synthetic variables based on the differences in sequential pairs of b_i values (Arthur *et al.*, 1996). Using the synthetic variables, we examined the effects of two factors on habitat used: 1) the radius of the buffer; and 2) season.

We made post-hoc multiple comparisons using paired t-tests on ranks of each habitat type (experimentwise alpha value=0.05) using Holm's modification of the Bonferroni approach, as recommended by Arthur *et al.* (1996). We tested seasonal variation in wetland selection patterns by comparing data from each season.

Results and discussion

We obtained 897 locations from 16 radio-collared female caribou during the surveys. The mean daily movement rate was 660 m. The 50th percentile of daily movement rates was 430 m.

Locational errors based on radio-telemetry were estimated to be 107 m ($s=199$ m, $n=47$ locations tested), and 126 m ($s=257$ m, $n=44$ locations tested) for visually confirmed and non-visually confirmed locations, respectively. The maximum locational error was 204 m, calculated for locations that were not visually confirmed (Morton, 1997).

Of the 897 locations, we deleted 293 (33%): 52 because relocation intervals exceeded 36 d; 1 because >50% of habitat used was unclassified; 156 because >50% of habitat available was unclassified; and 84 because there were fewer than 4 locations in the season in question. The remaining data (604 locations) comprised 94 animal seasons, with a median of 6 locations per animal season (range= 4-10).

To define the radii of circles of available habitat, we used the following 95th percentiles of distances moved by caribou between surveys:

6-9 days = 15.7 km;
10-20 days = 21.8 km;
21-36 days = 23.9 km.

Twenty habitat types were identified in the study area based on wetland class and appropriate modifiers (Tables 1 and 2). Eleven of the 20 categories each comprised less than 1% of the study area. To reduce the number of habitat categories, we grouped habitat types together according to wetland class and vegetation modifier. The classification system is hierarchical, and those two attributes are the coarsest levels. This grouping exercise produced

	b_i	BF	MO	SF	Z	WO	A	ST	SO	FO	FT	BT
BF	0.02		–	–	–	–	–	–	–	–	–	–
MO	0.02	+		–	–	–	–	–	–	–	–	–
SF	0.02	+			–	–	–	–	–	–	–	–
Z	0.04	+	+	+					–	–	–	–
WO	0.05	+	+	+				–	–	–	–	–
A	0.05	+	+	+				–	–	–	–	–
ST	0.07	+	+	+					–	–	–	–
SO	0.08	+	+	+	+	+		–		–		
FO	0.16	+	+	+	+	+	+	+	+		–	–
FT	0.20	+	+	+	+	+	+	+	+	+		
BT	0.29	+	+	+	+	+	+	+	+	+		

Fig. 1. Mean selection indices (b_i) and significant differences between ranks of pairs of the 11 habitat types for woodland caribou in the Red Earth area from January 1995 to February 1997. Each row presents the mean selection index value for the habitat type and whether that type was selected significantly more (+) or less (-) than each other habitat type (as listed in the columns). A blank cell indicates no significant relationship. The resulrs represent selection patterns from 94 animal-seasons of data. Codes for habitat types are included in Table 1. Rows are sorted from least to most selected habitats.

11 habitat types for analyses: 9 wetland types (BF, BT, FT, FO, SF, ST, SO, MO, WO), plus anthropogenic (A) and upland (Z) categories. Unclassified habitat was excluded from all analyses.

We did not detect any significant differences in the pattern of habitat selected among buffer radii that represented habitat use (MANOVA, approximate F (Wilks' lambda)=0.99, df=20 540, P=1.00). Therefore, we chose the largest of the three values (660 m) to define habitat used because we assumed that this value would better capture uncommon habitat types.

Based on data from the 660-m-radius buffers, we did not detect significant differences in habitat selection among seasons (MANOVA, approximate F (Wilks' lambda)=0.58, df=40, 305, P=0.22). Therefore, data were pooled from all 94 animal seasons for multiple comparison tests of selection among the 11 habitat types.

Based on a multiple comparison of tanks, we found that caribou selected among wetland types (Fig. 1). Forty-five of 55 pair-wise comparisons showed significantly different selection between the two habitat types being compared. Caribou strongly preferred bogs and fens with low to moderate tree cover (BT, FT, and FO) relative to othet wetlands with substantial standing water during at least part of the year (swamps, marshes and open water), forested uplands, and areas modified by human activity.

We did not collect data that would explain the apparent low preference of caribou for uplands. Factors may have included differences in predator activity, human activity, or forage availability.

Upland habitat is a diverse category that comprised about 37% of the study area. Had we tested for habitat selection among upland habitat categories, we likely would have detected preferences for specific types. For example, in Saskatchewan caribou selected upland black spruce communities in addition to peatlands (Rettie, 1998).

A "moving window" approach to habitat use/availability studies is appropriate if habitat types are not evenly distributed (equally available) across the landscape and availability is likely to change with animal location (Arthur *et al.*, 1996). We believe that this approach allowed us to more-accurately reflect the choices of habitat available to individual caribou because areas progressively furthet from an animal's location became increasingly less accessible.

The Alberta Wetland Inventory allowed us to identify habitat preferred by caribou at a large scale that would be appropriate for forest-management planning. Rettie (1998) concluded that coarse-scale habitat selection is fundamental to caribou distriburion, and that caribou should select habitat to avoid predation at coarser scales. By delineating broad areas that have a mosaic of suitable habitat, timber harvest could be planned to reduce fragmentation of those areas. In our analyses, the three wetland types with the highest selection indices (BT, FT, and FO), comprised nearly half (49%) of the available habitat. The classification system also may aid in identification of suitable range beyond that known to be occupied.

However, Rettie (1998) and Bradshaw *et al.* (1995) found that at the finest level of selection, caribou habitat use was related to food availability. As in the Red Earth area, caribou made extensive use of peatlands year-round in their study areas (west-central Saskatchewan and east-central Alberta, tespectively). Diets in Saskatchewan were primarily horsetails (*Equisetum* spp.), graminoids, and buckbean (*Menyanthes trifoliata*) in spring, lichens, shrubs, and horsetails in summer, and lichens, sedges, and horsetails in winter (Thomas & Armbruster, 1996).

Interpretation in the wetland inventory we used is based latgely on visual inspection of airphotos, and does not allow identification of the availability of food (primarily lichens) or other resources (e.g., relief from deep snow cover). Because of the influence of those factors on caribou habitat use, more-detailed vegetation descriptions of each wetland type, including composition of the shrub, forb, and moss layers, are necessary if the Alberta Wetland Inventoty classification system is to be used for caribou habitat management purposes at the operational level of planning fot forestry (e.g., annual operating plans).

Acknowledgments

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Appendix

Definitions of wetland types (from Halsey & Vitt, 1996).

Peatlands - wetlands that develop an accumulation of dead plant material (peat) of >40 cm due to decreased decomposition and to stable seasonal water levels. Two types of peatlands are recognized, including:

Fens - mineral-rich wetlands influenced by surface-running water. Fens may be open[1], shrubby, wooded[2], or forested[3].

Bogs - acidic wetlands that receive water only from precipitation. Bogs may be open, wooded, ot forested.

Marshes - open, non-peat forming wetlands with fluctuating seasonal watet levels. Vascular plant production is high.

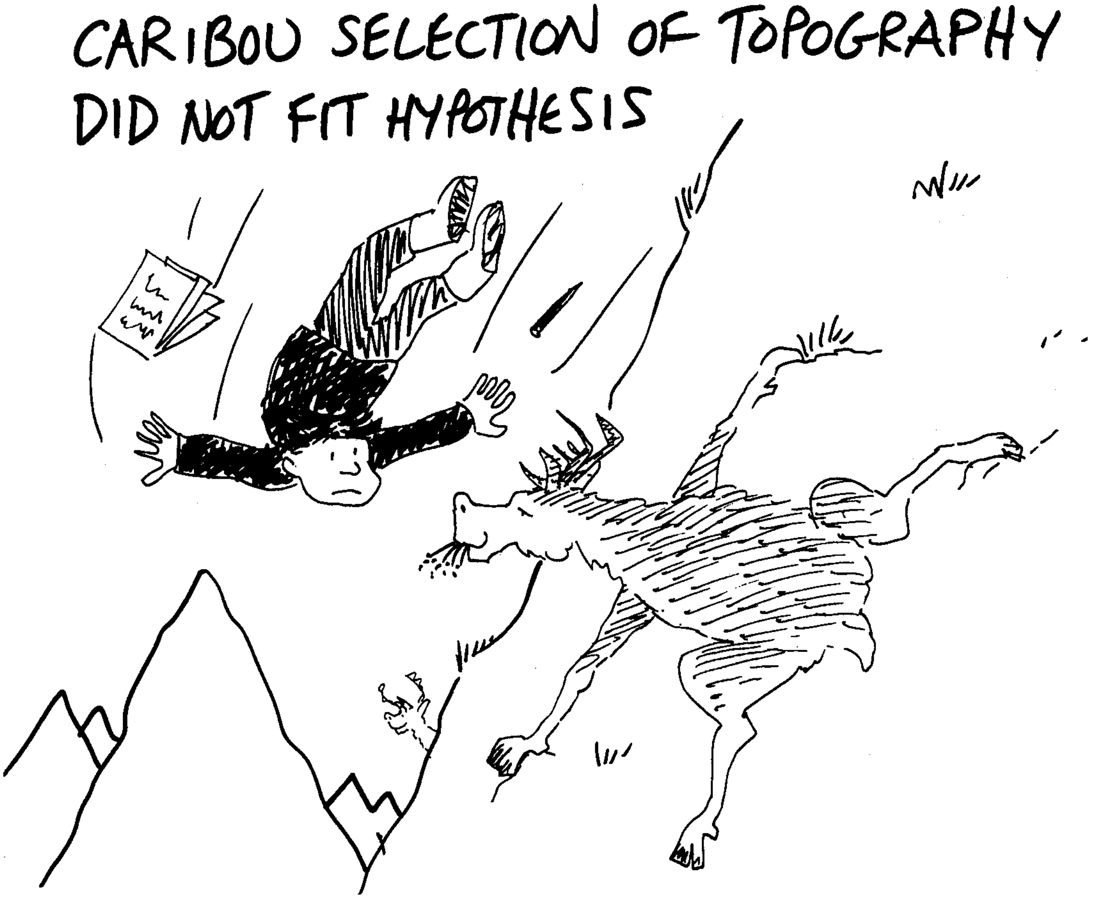
Swamps - forested, wooded, or shrubby non-pear forming wetlands with fluctuating seasonal water levels. Vascular plant production is high.

Shallow open water - non-peat forming wetlands with water <2 m in depth at midsummer.

[1] "Open" refers to sites with ≤6% canopy closure.

[2] "Wooded" refers to sites with >6-70% canopy closure by tree species.

[3] "Forested" refers to sites with >70% canopy closure by tree species.


CARIBOU SELECTION OF TOPOGRAPHY DID NOT FIT HYPOTHESIS

The Eight North American Caribou Workshop,
Whitehorse, Yukon, Canada,
20–24 April, 1998.

Feeding site selection by woodland caribou in north-central British Columbia

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Abstract: We examined rhe foraging habirs of the norrhern woodland caribou ecotype (*Rangifer tarandus caribou*) at the scale of the individual feeding site. Field data were collected in north-central British Columbia over two winters (Dec 1996-Apr 1998). We trailed caribou and measured vegetation characteristics (species composition and percent cover), snow conditions (depth, density, and hardness), and canopy closure at terrestrial and arboreal feeding sites, and at random sites where feeding had not occurred. Logisric regression was used to determine the attributes of feeding sites that were important to predicting fine scale habitat selection in forested and alpine areas. In the fotest, caribou selected feeding sites that had a greater percent cover of *Cladina mitis* and *Cladonia* spp, lower snow depths, and a lower percentage of debris and moss. Biomass of *Bryoria* spp. ar the 1-2 m stratum above the snow significantly contributed to predicring whar trees caribou chose as arboreal feeding sites. In the alpine, caribou selected feeding sites with a greater percent cover of *Cladina mitis, Cladina rangiferina, Cetraria cucullata, Cetraria nivalis, Thamnolia* spp., and *Stereocaulon alpinum* as well as lower snow depths.

Key words: arboreal, cratet, foraging, lichen, *Rangifer*, snow.

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Introduction

The habitat requirements of the northern woodland caribou ecotype of British Columbia are largely unknown (Harrison & Surgenor, 1996). This ecotype has been the subject of few studies, but is known to inhabit areas of low to moderate snow depths in low elevation forests, and to forage primarily on terrestrial lichens during winter (Hatler, 1986; Cichowski, 1993; Lance & Mills, 1996; Wood, 1996). Most caribou research in British Columbia has focused on the mountain caribou ecotype which spends little time in low elevation areas during the winter, but fotages instead on arboreal lichens at high elevations (Servheen & Lyon, 1989; Terry, 1994).

Further understanding of the life history strategies of the northern woodland caribou ecotype is important in view of increasing demands for timber in the province. Wintering populations of this ecotype use low elevation forests that are valued for commercial wood products (Cichowski, 1993; Wood, 1996). Consequently, they are likely to be negatively affected by habitat alteration, fragmentation, and increased road access.

As part of a larger research project to define the processes that affect the movements and distribution of northern woodland caribou across the landscape, we investigated the influence of forage species, abundance, and accessibility on the selection of individual feeding sites during winter. Specifically, we examined:

1. the influence of snow depth, density, and hardness as well as vegetation composition and abundance on the selection of terrestrial feeding sites at small spatial scales in forested and alpine habitats; and
2. the influence of lichen biomass on the selection of arboreal feeding sites.

Study Area

The group of caribou chosen for this study is known as the Wolverine herd (Heard & Vagt, 1998), and ranges throughout a 5100-km² area, approximately 250 km northwest of Prince George, British Columbia (Fig. 1). Terrain varies, from valley bottoms at approximately 900 m to alpine summits at 2050 m, and is characterised by numerous vegetation associations resulting from diverse topography,

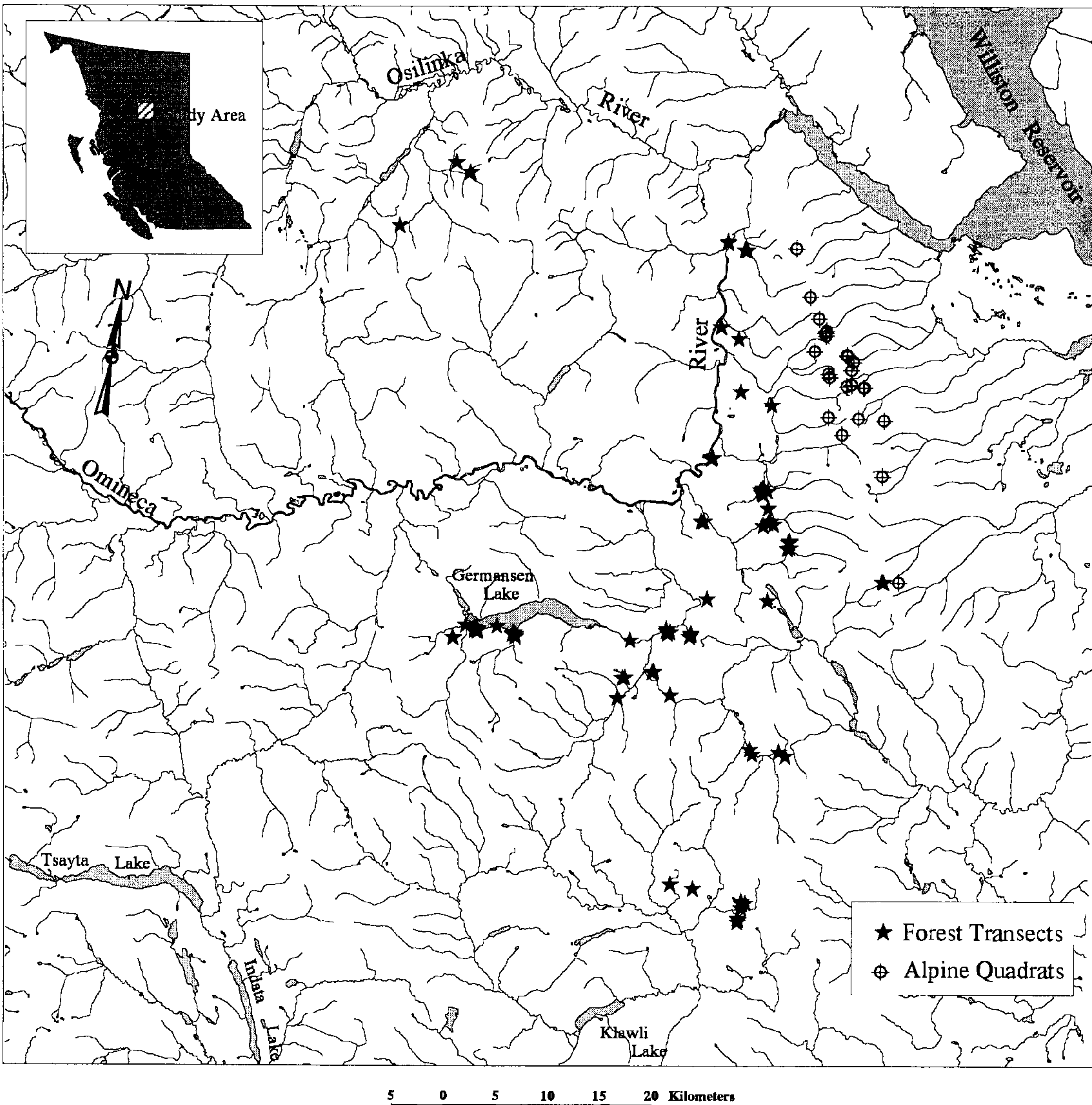

Fig. 1. Foresr rransecrs and alpine quadrats located across the winter range of the Wolverine herd (Dec 1996-Apr 1998).

soils, and succession. Forest types below 1100 m have been influenced extensively by wildfires and are dominated by lodgepole pine (*Pinus contorta*), white spruce (*Picea glauca*), hybrid white spruce (*P. glauca* x *P. engelmannii*) and subalpine fir (*Abies lasiocarpa*). Between 1100 and 1600 m, a moist cold climate prevails with forest types consisting primarily of Engelmann spruce (*P. engelmannii*) and subalpine fir (*A. lasiocarpa*). Elevations greater than 1600 m ate alpine tundra and are distinguished by gentle to steep windswept slopes vegetated by shrubs, herbs, bryophytes, and lichens with occasional ttees in krummholz form (MacKinnon *et al.*, 1990; DeLong *et al.*, 1993).

Materials and methods

Field investigations occurred at two to three week intervals between December and April, 1996-1997 and 1997-1998. After locating recent tracks of GPS-collared caribou or groups of non-collared caribou in the forest by air or ground survey, we assessed the immediate area for signs of foraging behaviour. Terrestrial feeding sites were characterised by meandering tracks, craters, and/or sniffing holes. Arboreal feeding sites were characterised by trampling, broken twigs, and fallen arboreal lichen at the base of trees. If some sign of foraging behaviour was present, we selected a random starting point in the snow along the caribou tracks greater than or equal to 20 paces from any ecotone border. Following this, we placed a measuring tape along a section of track that traversed a relatively homogenous stand or vegetation type, and all terrestrial (cratets) and arboreal feeding sites found on a 100-m segment of track (transect) were counted. Using a tandom number table, a maximum of 12 sites wete randomly selected on the ttansect for measurement: 3 sites where there had not been tetrestrial feeding, 3 trees where there were no signs of arboreal feeding, and, if present, 3 crateting sites and 3 atboreal feeding sites (Fig. 2).

For statistical analyses, measures at feeding and non-feeding sites wete pooled across transects. To minimise the likelihood of recording the behaviour of the same animal more than once (i.e., pseudoreplication; Hutlbert, 1984), we limited the number of samples to not exceed the observed or, where animals were not sighted, the average number of caribou typically occutring within a group during the winter (n=9; Wood, 1996; C. J. Johnson, unpubl.). Furthermore, because we wanted to sample all collared animals and visit as many geographically unique locations as possible, we restricted the maximum number of 100-m transects sampled at one location to 3, regardless of the number of animals observed. To further reduce the effects of spatial autocorrelation and allow an opportunity for changes in behaviour across space, and presumably time, successive transects were separated by a distance of 100 m. Thetefore, at a location, we sampled a maximum of 9 terrestrial and 9 arboreal feeding sites and the 18 associated random sites across 3 transects.

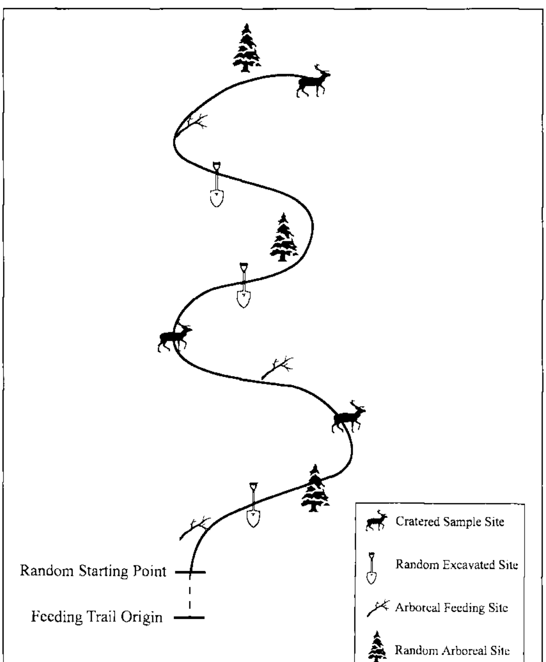

Fig. 2. Schematic representation of the sampling design used along a 100-m segment of recent caribou tracks in the snow.

In the alpine, safety concerns and the aggregated distribution of the feeding sites required us to use a 50 X 50-m quadrat rather than a 100-m segment of track. All cratets in the quadrat were counted, and we randomly selected 3 to 6 craters for measurements, depending on time and weather constraints. The corresponding non-feeding sites were located at a tandom compass bearing and random number of paces (1-20 paces) from the sampled craters, regardless of the quadrat boundaties. For statistical analyses, measures at feeding and non-feeding sites were pooled across quadrats.

At all tetrestrial feeding and random sites, snow depth was measured to the nearest 0.5 cm, and the penetrability (i.e., hardness) of the upper layer was estimated with an instrument of out own design which was similar to the Rammsonde penetrometer. A British Columbia Ministry of Environment, Lands, and Parks (1981) Snow Survey Sampling Kit was used to measure snow density by inserting a cylinder of known volume vertically into the snow, tecording the depth minus the soil plug, and weighing the contents. Because the scale used to measure the mass of the cored snow is insensitive at low snow depths, density could not be reliably calculated for alpine sites. For cratered sites, the least disturbed edges were used for sampling. Following snow measurements, the snow was cleated and the percent cover of ground vegetation was assessed with a 0.5 m X 0.5-m point frame consisting of 16 vertical pins (Bookhout, 1994). Lichen and moss were identified to species, genus or morphological group, depending on ease and reliability of field classification. Species that occurred at fewer than 10 sample sites were pooled with the next most similar species or genus group, or were excluded. Percent covet of evergreen dwarf shrubs, grasses (Poaceae), and sedges were also recorded. However, with the exception of grass at alpine sites, there was no evidence of grazing on those plant types, so they wete excluded from the analysis. At forested terrestrial sites, a moosehorn coverscope (Moosehorn Coverscopes, Medford, Oregon, USA) was used to assess percent canopy closure by taking one measure directly above each sampled site.

At each arboreal feeding and associated random site, a lichen clump (*Bryoria* spp.) with a predetermined oven-dried weight was used as a Standard Lichen Unit to visually estimate arboreal lichen biomass (Antifeau, 1987; Stevenson & Enns, 1993). The number of similar Units that occurred within the reach of a typical caribou (1-2 m above the snow) was counted and multiplied by the mass of the Standard Lichen Unit to obtain total biomass within the 1-2-m stratum. Tree species and diameter at breast height were also recorded.

We used multiple logistic regression analyses to estimate the influence of percent cover of vegetation, snow conditions, and canopy closure on the selection of terrestrial feeding sites by caribou in forested and alpine areas. To assess the selection of atboreal feeding sites, we tested a simple logistic regression model, consisting of foraged versus random ttees as the dependent variable and grams of arboreal lichen in the 1-2 m stratum as the independent variable.

For the multiple logistic regression models (terrestrial forest and alpine), the Wald backward elimination procedure (SPSS Version 8.0) was used to identify the most parsimonious model for describing site selection of cratering locations (Menard, 1995). As recommended by Bendel & Afifi (1977), the α of 0.05 was relaxed to 0.15 during the backward elimination procedures to reduce the likelihood of excluding important variables. We used Pearson correlation values and tolerance scores with a collinearity thteshold of 0.20 (Menard, 1995) to diagnose the presence of multicollineatity amongst the independent variables. Collinearity is the product of two or more highly correlated variables. It is an indication of redundancy within the statistical model and can lead to inflated error terms and in extreme cases render matrix inversion unstable (Tabachnick & Fidell, 1996). Although logistic regression is robust to most multivariate assumptions, data and model screening procedures were employed as recommended by Menard (1995) and Tabachnick & Fidell (1996); procedures were reported only if model validity was threatened.

For both terrestrial and arboreal feeding sites, we used the proportional teduction in the χ^2 statistic (R^2_L) to indicate how much the inclusion of each significant explanatory variable improved model fit; the higher the value, the better the measured variables explain the differences between selected and random sites (i.e., analogous to the linear regression R^2) (Hosmer & Lemeshow, 1989). Odds ratios were used to interpret the effect of each explanatory variable on the response variable and are more intuitive than the regression coefficient when discussing the relative strength of each explanatory variable. Univariate logistic function plots were used to graphically present the relationships between statistically significant vegetation, debris, and snow variables and the predicted probability of a caribou selecting a feeding site (Tabachnick & Fidell, 1996).

To provide a relative measure of the availability of forage species, we used Bonferroni corrected 95% confidence intervals to test differences in mean percent cover of lichen, mosses, grass, and debris between feeding and random sites, and among species (Neter *et al.,* 1990). The relationship between tree diameter at breast height and amount of arboreal lichen was investigated with a simple linear regression equation. An α of 0.05 was used for all tests of statistical significance.

Results

Over the two winters we examined caribou feeding sites along 85 forest transects and 23 alpine quadrats (Fig. 1). We sampled 461 terrestrial (206 feeding, 255 random) and 356 arboreal (102 feed-

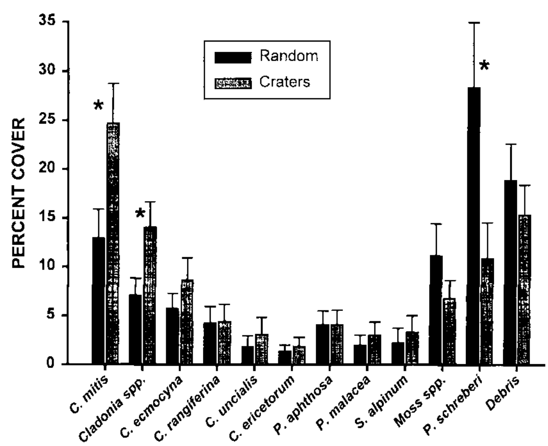

Fig. 3. Percent ground cover of lichens at random (n=255) and cratered (n=206) sites in forested locations. Vertical lines represenr a half widrh of a Bonferroni-corrected 95% confidence interval and asterisks designate statistically significant differences between corresponding sites.

Table 1. Lichen and moss species and groups identified at terrestrial feeding and random sites; classification is based on ease and reliability of field identification, and frequency of occurrence in north-central British Columbia (Dec 1996-Apr 1998).

Ground Cover	Description	Location
Cladina mitis	Distinct lichen class.	Forest/Alpine
Cladina rangiferina	Distinct lichen class.	Forest/Alpine
Cetraria islandica	Distinct lichen class.	Alpine
Cetraria ericetorum	Distinct lichen class.	Forest
Cetraria nivalis	Distinct lichen class.	Alpine
Cetraria cucullata	Distinct lichen class.	Alpine
Peltigera aphthosa	Distinct lichen class.	Forest
Peltigera malacea	Distinct lichen class.	Forest
Cladonia uncialis	Distinct lichen class.	Forest
Cladonia spp.	Composite class consisting of rarely found and unidentified *Cladonia* species; composite of *C. uncialis, C. ecmocyna, C. gracilis, C. cenotea, C. chlorophaea, C. cornuta, C. crispata, C. deformis, C. fimbriata, C. multiformis, C. pyxidata,* and *C. sulphurina.*	Forest/Alpine
Cladonia ecmocyna	Composite class consisting of *C. ecmocyna* with a lesser component of *Cladonia gracilis* (J. Marsh, pers. comm.).	Forest
Stereocaulon alpinum	Composite class consisting primarily of *S. alpinum* with a small component of *S. glareosum, S. tomentosum,* and *S. paschale* (J. Marsh, pers. comm.).	Forest/Alpine
Thamnolia spp.	Composite class consisting of *T. vermicularis* and *T. subuliformis.*	Alpine
Lichen spp.	Composite class consisting of unidentified lichen species.	Alpine
Peltigera spp.	Composite class consisting of *P. aphthosa* and *P. malacea.*	Alpine
Cladina stellaris	Rate and omitted from analysis.	Forest
Nephroma arcticum	Rare and omitted from analysis.	Forest
Solorina crocea	Rare and omitted from analysis.	Forest
Dactylina arctica	Rare and omitted from analysis.	Alpine
Pleurozium schreberi	Composite class consisting primarily of *P. schreberi* with a lesser component of *Hylocomium splendens* and *Ptilium crista-castrensis.*	Forest
Moss spp.	Composite class consisting of unidentifiable or rare moss species and liverworts.	Forest/Alpine

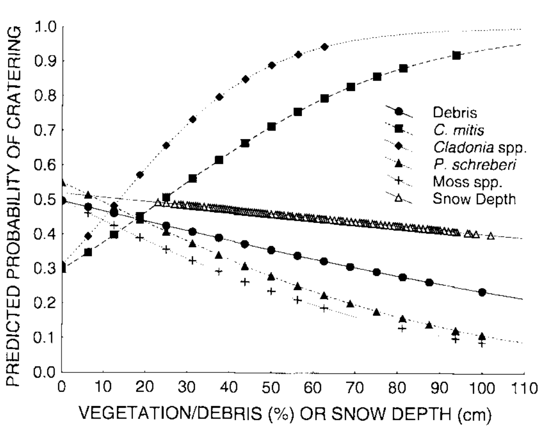

Fig. 4. Predicted probabiliry of caribou cratering at terrestrial foresr sites relative to the percent cover of vegetation or debris (measured in units of 6.25% cover) and snow depth (cm). Symbols illustrate the tange of data collected in this study.

ing, 251 random) sites in the forest and 136 sites (70 feeding, 66 random) in the alpine. Nine distinct species of *Cladina, Cladonia, Cetraria,* and *Peltigera* lichens and 8 composite groupings of lichen and moss types were regularly observed at alpine and forested terrestrial feeding sites (Table 1). *Cladina stellaris, Nephroma arcticum, Solorina crocea,* and *Dactylina arctica* were also noted, but because they occurred at <10 feeding sites and could not be easily grouped with anothet lichen species, they were excluded from the analysis. *Bryoria* spp. were the dominant atboreal lichens.

Feeding Sites in Forest Locations

Average snow depths at cratered sites ranged from 23-97 cm and at random sites ftom 27-102 cm. Average snow hardness at cratered and random sites ranged from 0.27-3.19 g/cm^2 and 0.25-4.2 g/cm^2

Table 2. Summary ofi multiple logisric regression model derived using the Wald backward elimination procedure for terresrtial and arboreal feeding sites in forested locations in north-central British Columbia (Dec 1996-Apr 1998).

TERRESTRIAL FEEDING SITES (n=460; model χ^2=128.576, df=6, P<0.001)

Variables Retained in Model	B	SE	P	Odds Ratio
Moss spp.	-0.030	0.011	0.007	-3.0%
Debris	-0.026	0.008	0.002	-2.5%
Pleurozium schreberi	-0.023	0.006	<0.001	-2.3%
Snow Depth	-0.021	0.007	0.002	-2.0%
Cladina mitis	0.024	0.008	0.003	+2.4%
Cladonia spp.	0.042	0.011	<0.001	+4.3%
Constant	1.173	0.565	0.040	
Variables Excluded From Model				
Canopy Closure			0.289	
Snow Hardness			0.174	
Snow Density			0.325	
Cladina rangiferina			0.165	
Cladonia ecmocyna			0.155	
Cladonia uncialis			0.961	
Cetraria ericetorum			0.996	
Stereocaulon alpinum			0.862	
Peltigera aphthosa			0.456	
Peltigera malacea			0.642	

ARBOREAL FEEDING SITES (n=356; model χ^2=17.009, df=1, P<0.001)

Variable	B	SE	P	Odds Ratio
Bryoria spp. (g/1-2 m)	0.095	0.026	<0.001	+9.9%
Constant	-1.183	0.145	<0.001	

and snow density from 5-46.97 g/cm^3 and 6.25 - 40 g/cm^3, respectively.

Percent cover of all of the lichen species was greater at cratered sites, but non-overlapping confidence intervals revealed differences only for *Cladina mitis* and *Cladonia* spp. (Fig. 3). At cratered sites *C. mitis* and *Cladonia* spp. averaged 24.7% (standard error of the mean ±1.40) and 14.0% (±0.90), respectively, relative to 12.9% (±1.04) and 7.1% (±0.60) at random sites. In contrast, random sites had a greater percent cover of mosses and debris than crater sites. *Pleurozium schreberi* was the only non-lichen variable to differ significantly, having an average percent cover of 10.6% (±1.25) and 26.2% (±2.19) for cratered and random sites, respectively. Canopy closute ranged from an average of 27.1% (±1.85) at cratered sites to 28.8% (±1.61) at random sites.

The multiple logistic regression model used to describe site selection of terrestrial feeding sites in the forest, cotrectly classified 71.2% of the cases as cratered or random sites and explained 20.2% (R^2_L=0.202) of the between feeding site variation (Table 2). Snow depth, percent cover of debris, *C. mitis, Cladonia* spp., and the two moss classes significantly contributed to the statistical differentiation of cratered and random sites (Fig. 4). *Cladonia* spp. had the highest odds ratio at +4.3% and the greatest influence on the selection of cratering sites by caribou (Table 2, Fig. 4). Snow depth had the least influence on selection of a feeding site; in this case, the odds ratio implies that a 1 cm increase in snow depth will reduce the likelihood that a caribou will crater by 2% (Table 2, Fig. 4).

Although tolerance scores for each variable in the model were greatet than 0.20, several of the variables wete significantly bivariate correlated. *Cladina*

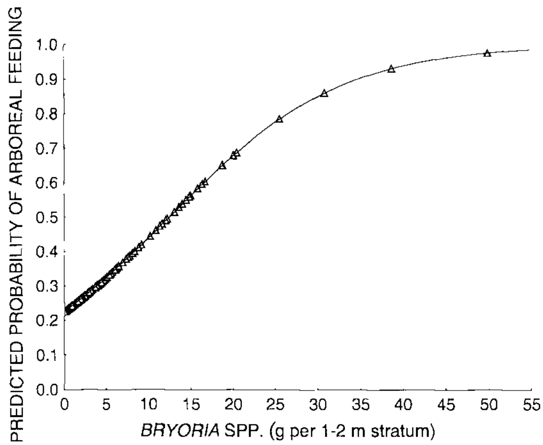

Fig. 5. Predicted probability of caribou choosing an arboreal feeding sire relarive to the grams of *Bryoria* spp. within the 1-2 m stratum above the snow. Symbols illustrate the range of data collected in this study.

mitis was negatively cotrelated with debris (r=-0.227), *P. schreberi* (r=- 0.403), and moss spp. (r=-0.155), and *Cladonia* spp. was correlated with *P schreberi* (r=- 0.370). This indicates that there may not be a direct relationship between site selection and the presence or absence of these moss and lichen species.

When choosing to browse arboreal lichen, caribou selected those trees with a greater biomass of *Bryoria* spp. than found in randomly available trees. On average, selected trees had 4.9 g (±0.74) in the 1-2 m stratum versus 2.3 g (±0.24) for random trees. *Pinus contorta* was the dominant tree species at both selected (81%) and random sites (90%). The simple logistic regression model indicated that the amount of *Bryoria* spp. was a meaningful predictor of what trees caribou chose to browse (Table 2, Fig. 5). The model accounted for only a small amount of the variation between feeding and random sites (R^2_L=0.039); however, 72.2% of the cases were correctly classified as feeding or random sites. The odds ratio indicated that a 1 g inctease in the amount of *Bryoria* spp. would increase the likelihood of a caribou foraging by 9.9%. There was a significant, but weak linear relationship between tree diameter and arboreal lichen abundance (F=17.495, df=250, P<0.001, R^2=0.066).

Feeding Sites in Alpine Locations

Average snow depth per quadrat ranged from 3-37 and 0-69 cm, and snow hardness between 0.54-28.89 and 0-30.38 g/cm^2 for cratered and random sites, tespectively. Percent cover of lichen classes was typically greater at cratered sites, but not sig-

Table 3. Summary of multiple logistic tegression model derived using the Wald backwatd elimination procedure for terrestrial feeding sires in alpine locations in north-central Brirish Columbia (Dec 1996-Apr 1998).

TERRESTRIAL FEEDING SITES (n=136; model χ^2=58.748, df=9, P<0.001)

Variables Retained in Model	B	SE	P	Odds Ratio
Cetraria islandica	-0.106	0.062	0.085	-10.1%
Snow Depth	-0.071	0.023	0.002	-6.8%
Stereocaulon alpinum	0.036	0.015	0.014	+3.7%
Cetraria nivalis	0.060	0.026	0.022	+6.2%
Snow Hardness	0.064	0.040	0.112	+6.6%
Cladina mitis	0.087	0.023	<0.001	+9.1%
Cetraria cucullata	0.095	0.033	0.004	+10.0%
Cladina rangiferina	0.159	0.052	0.002	+17.2%
Thamnolia spp.	0.240	0.119	0.044	+27.1%
Constant	-1.888	0.699	0.007	
Variables Excluded From Model				
Debris			0.626	
Cladonia spp.			0.146	
Peltigera spp.			0.900	
Lichen spp.			0.464	
Moss spp.			0.700	
Poaceae			0.216	

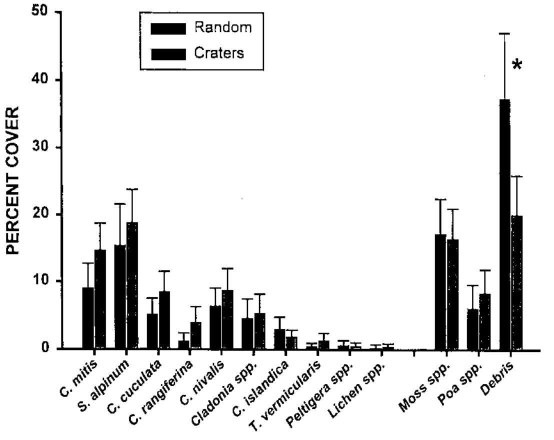

Fig. 6. Percent ground cover of lichens ar random (n=66) and cratered (n=70) sites in alpine locations. Vertical lines represenr a half widrh of a Bonferroni-corrected 95% confidence interval and asterisks designate statistically significant differences berween corresponding sires.

nificantly so, with *C. mitis, Stereocaulon alpinum,* and *Cladina rangiferina* demonstrating the largest differences (Fig. 6). Debris was the only variable to illustrate a significant difference in percent cover, being more prominent at random (mean=37.3%±3.30) than cratered sites (mean=20.0%±1.99).

The multiple logistic regression model used to describe site selection of tettestrial feeding sites in the alpine accounted for 31% of the between site variation, and correctly classified 76.5% of the cratered and random sites (Table 3). Statistically

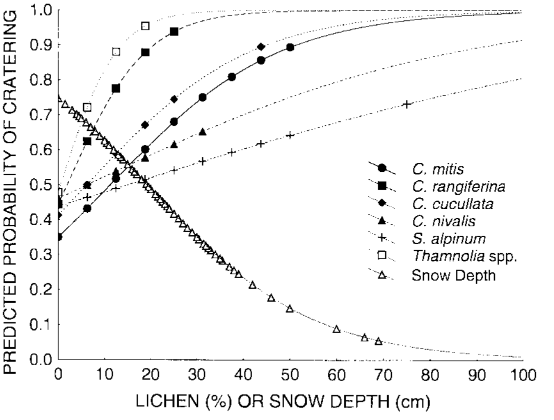

Fig. 7. Predicted probability of caribou cratering at alpine sites relative to the percent cover of vegetation or debris (measured in units of 6.25% cover) and snow depth (cm). Symbols illustrate the range of data collected in this study.

significant variables were snow depth, percent cover of *C. mitis, C. rangiferina, Cetraria cucullata, Cetraria nivalis, Thamnolia* spp., and *S. alpinum* (Fig. 7). *Thamnolia* spp. had the highest odds tatio at +27.1% and the greatest influence on the selection of feeding sites followed by *C. rangiferina,* and *C. cucullata* at +17.2 and + 10%, respectively (Table 3, Fig. 7). *Cladina mitis* and *C. rangiferina* (r= + 0.171) and *C. rangiferina* and *C. nivalis* (r=- 0.239) were the only significant bivariate correlations for variables identified as important by the logistic regression model. Most cover types were highly correlated with debris, with the highest correlation occurring with *S. alpinum* (r=- 0.453).

Discussion

Past studies have found that most continental populations of caribou and reindeer (*R. t. tarandus*) forage primarily on fruticose lichens throughout the winter (Pegau, 1968; Helle & Saastamoinen, 1979; White & Trudell, 1980; Klein, 1982; Boertje, 1984; Skogland, 1984; Cichowski, 1993; Terry, 1994), and that snow conditions may restrict access to this food source (Laperriere & Lent, 1977; Skogland, 1978; Duquette, 1988; Brown & Theberge, 1990). However, with few exceptions (e.g., Bergerud, 1974; Thing, 1984; Frid, 1998), most investigators failed to classify forage beyond food type or genus or to consider the interaction between snow conditions and forage selection. Furthermore, the lack of comparison control sites has frequently resulted in the analysis of forage availability as opposed to selection by the animals. We attempted to improve upon these studies by investigating the influence of lichen species in combination with the limiting effects of snow on the fine scale selection of feeding sites in forested and alpine areas.

Selection of Feeding Sites by Caribou

Using data collected over two years across a broad geographic area, we developed statistically significant models to predict the selection by woodland caribou of terrestrial and arboreal feeding sites in forested locations, and terrestrial feeding sites in alpine areas. All three of the models had relatively low explanatory power (R^2_L) indicating that the independent variables (i.e., ground cover and snow condition) captured only a small proportion of the differences between selected and random sites. We believe that this is a consequence of four sources of error in our sampling design and analysis. First, it is likely that we did not recognise, measure, or include all of the variables that are important to the cognitive processes that caribou use when choosing where to feed. For instance, we allowed the backward elimination procedure to determine the most parsimonious model. This excluded certain variables that contributed relatively little new statistical information, but which may have been of some impottance to explaining ovetall differences between the selected and random sites. It is also possible that model aptness was affected by aggregate variables, such as *Cladonia* spp., which may have masked or confounded individual lichen species that were highly selected or avoided by caribou. Frid (1998) identified a similar limitation within his study of crater site selection by woodland caribou.

Second, although we are confident in our ability to identify feeding sites, it is possible that some sites were incorrectly classified. Caribou may have ctatered but not fed at certain terrestrial sites, or trees may have been incorrectly classified as browsed when they were not. Sampling error also may have been introduced by classifying out random sites as non-selected sites when in actuality caribou did not make a choice, but passed by that location for reasons not directly related to a fotaging decision (e.g., satiation, minor disturbance). Furthermore, because caribou remain in an area for some period of time, our random samples may contain a proportion of sites that would have been cratered at a later date. To reduce this source of error, we should have chosen random sites where it could be confitmed that a caribou had made a decision not to ctater, such as unexcavated sniffing holes (e.g., Helle, 1984). Because snow conditions often made the identification of sniffing sites difficult, this approach was abandoned in favour of sampling random locations along the tracks.

Third, we assumed that the lichens temaining at a sampled feeding site were representative of the pte-cratering lichen cover, although the foraging and digging actions of caribou may have resulted in our underestimating the percent cover of lichen at feeding sites. To minimise this bias, we chose percent cover, as opposed to biomass, as out measure of relative lichen availability. Caribou rarely cropped the entire lichen thalus, thus using a point ftame with 6.25% inctements we were able to accurately and precisely measure percent cover by species at feeding sites.

Fourth, selection strategies of the caribou may have changed during or between winters, confounding the importance of individual variables. For example, nuttitional requirements may vary over time or abundance of lichen species may vary spatially, resulting in tempotally variable selection patterns. This, and the sources of error listed above did not invalidate our results, but rather forced us to test a mote conservative model (which may have decreased the likelihood of obtaining significant differences).

Influence of Vegetation on Feeding Site Selection

Numerous conclusions, in some cases contradictory, have been reported by researchers using field studies or cafeteria-type experiments to investigate preference and selection of lichen species by caribou and reindeer (see DesMeules & Heyland, 1969). Bergerud & Nolan (1970) concluded that comparing food lists between areas or populations is of little value because caribou are adapted to eat most species of plants and, therefore, localised studies reflect only what is available rather than universal selection criteria by *Rangifer*. We also recognise that there may be inter-population variability, but feel that our results placed in the cor text of other works add to the understanding of the similarities and plasticity in foraging habits of these animals.

Our data indicate that northern woodland caribou select cratering sites based on the percent cover of several lichen species. In most cases our results agree with other studies. Fot example, *C. mitis* is commonly reported as being preferred or selected by caribou and reindeer (Helle & Saastamoinen, 1979; Helle, 1984; Lance & Mills, 1996). Cafeteria-type experiments have concluded that caribou (*R. t. caribou*) pteferred a mixture of *C. stellaris, C. mitis,* and *Cladonia uncialis,* followed by *C. rangiferina, Cetraria islandica,* and *Stereocaulon* spp. (DesMeules & Heyland, 1969); and that reindeer exhibited a preference for *C. stellaris, C. rangiferina, Stereocaulon paschale, Cetraria richardsonii,* and *Peltigera aphthosa,* in that order (Holleman & Luick, 1977). Analysis of faecal samples from the Porcupine caribou herd (*R. t. granti*) indicated that their winter diet consisted predominantly of *Cladonia* and *Cladina* spp., followed by *Stereocaulon, Cetraria* and *Peltigera* spp.; the proportions of these species, however, may have been more related to availability than to selection (Russell *et al*, 1993). Danell *et al.* (1994) assigned high preference rankings to *Cladina arbuscula,* which is morphologically indistinguishable from *C.*

mitis, C. rangiferina, and *S. paschale* and a low ranking to *P. schreberi.* Research by Frid (1998) in the southern Yukon is the most comparable to outs in method and species designation. He reported that the probability of a woodland caribou digging a crater increased as the percent cover of *Cladonia* spp., *C. mitis, C. cucullata,* and *C. islandica* increased, but the amount of *C. rangiferina, C. nivalis, Peltigera* spp., and *Stereocaulon* spp. had no effect. With a few exceptions, mostly being the lichens selected in the alpine, those results are in accordance with the findings of our study.

Through our conclusions we do not infer causal relationships between feeding site selection and the importance of individual lichen and moss species. We emphasise this *caveat* because of the high correlations between several of the significant lichen and moss species. Fot example, where the model shows a strong effect for lichen and mosses at forested sites, caribou may be selecting for lichens or may be avoiding mosses; the statistical importance of one may be the product of the presence or absence of the other. *Pleurozium schreberi* may be an important discriminating variable only because it occurs where *C. mitis* and *Cladonia* spp. are not found, not because caribou avoid sites where it is found. High negative correlations likely occur because these species of moss and lichen have distinct light and moisture requirements and, therefore, grow in different locations (Robinson *et al.,* 1989; Ahti & Oksanen, 1990).

Interpretation of our results is complicated by the inconsistencies in selected lichen species across forested and alpine sites. Most notably, *C. rangiferina* and *S. alpinum,* which were important discriminating variables at alpine sites, wete not selected, even though available, by caribou at fotested sites. Our results from the forested sites agree with most of the above cited studies that have shown that these species, especially *Stereocaulon* spp., are relatively less palatable. This discrepancy suggests that depending on location, forest or alpine, animals may have different foraging sttategies.

We observed that the majority of the lichens found in forested areas appeared more vigorous and occurred in greater abundance than those in the alpine (Figs. 3 & 6; C. J. Johnson, unpubl.). Furthermore, at alpine sites clumps of lichen were more unevenly distributed, being separated by bate areas of rock or debris, as reflected by the high negative correlation between debris and *S. alpinum.* Caribou in the less productive alpine areas may be less selective, taking advantage of those sites with the greatest amount of lichen regardless of palatability. The use of a larger number of species and less palatable yet more prevalent lichens, such as *S. alpinum,* may be an adaptation to a less productive environment where foraging decisions are based largely on availability. This is consistent with the hypothesis of Bergerud & Nolan (1970) that caribou are adaptive and flexible in the forage species they select.

In our study area, woodland caribou in the forest fed on both terrestrial and arboreal lichens; although, based on feeding site frequency, it appeared that cratering is the predominant activity (C. J. Johnson, unpubl.). Comparable findings were reported for our study animals by Wood (1996) and for other woodland caribou populations (Cichowski, 1993). Selection of arboreal lichen may increase following some threshold in accessibility or availability of tetrestrial lichen (Bergerud, 1974; Sulkava & Helle, 1975; Helle & Saastamoinen, 1979; Helle, 1984; Vandal & Barrette, 1985).

Our study animals selected trees, principally *P. contorta,* that supported the greatest biomass of arboreal lichen. Across the transects we sampled, which occutred mainly in *P. contorta* or mixed *P. contorta - P. glauca* x *P. engelmannii* stands, the predominant epiphyte was *Bryoria* spp. with only trace amounts of *Alectoria sarmentosa. Bryoria* spp. has been reported as a highly palatable food type (Danell *et al.,* 1994) and studies of the mountain caribou ecotype have revealed preference for this lichen group ovet other alectorioid species (Rominger & Robbins, 1996). The lack of a strong linear relationship between amount of lichen within the 1-2 m stratum and tree diameter suggests that lichen gtowth and the selection of arboreal feeding sites is related to factors other than tree size.

Influence of Snow Conditions and Canopy Closure on Site Selection

Although caribou are well adapted to deep snow environments (Telfer & Kelsall, 1984), snow can hinder both the accessibility and detection of forage. Previous studies identified the threshold depth for crateting by caribou and reindeer to range from 50-80 cm (Formozov, 1946; Pruitt, 1959; Statdom, 1975; LaPerriere & Lent, 1977; Helle & Saastamoinen, 1979; Darby & Pruitt, 1984), although craters as deep as 123 cm have been reported (Brown & Theberge, 1990). The ability to crater is also influenced by other snow conditions including hardness and ice layers (Formozov, 1946; Skogland, 1978; Helle & Tarvainen, 1984; Adamczewski *et al.,* 1988; Brown & Theberge, 1990). Bergerud & Nolan (1970) concluded that Newfoundland caribou could not smell terrestrial lichens under snow exceeding 25 cm in depth, but Helle (1984) reported that reindeer in Finland detected lichens through a snow thickness of 91 cm. Over our two-year study period, the maximum crater depths we observed were 97 and 50 cm for forested and alpine sites, respectively.

Canopy closure increases snow interception and correspondingly reduces snow depth and the effott necessary to expose lichens (Schaefer, 1996). Across the range of the Wolverine herd, canopy closure did not affect the selection of cratering sites. In contrast, Cichowski (1993) and Lance & Mills (1996) found that ctatering occurred most often in forested areas with more open canopies. In both cases, however, there was an interaction with the presence of terrestrial lichen suggesting that open canopy stands were more productive. Our analysis used a moosehorn coverscope as opposed to a visual estimate of canopy closure (Cichowski, 1993; Lance & Mills, 1996). The latter estimates closure of a much larger portion of the canopy (i.e., scale of the stand) than the coverscope (i.e., scale of the feeding site). This likely accounts for the differences between our results and other studies.

If a caribou attempted to forage optimally by expending as little enetgy as possible when cratet-ing, then selection of sites with shallower, softet, and less dense snow would be expected as long as the additional search time did not exceed the cost of finding more accessible lichens (Fancy & White, 1985). In agreement with this ptemise, LaPerriere & Lent (1977) found snow depths and hardness to be less in feeding areas relative to adjacent unctatered areas. At the individual feeding sites we surveyed, caribou appeared to partially meet these criteria by selecting locations to crater where snow depths were shallower than tandom sites. The greatest effect, as indicated by the odds ratio and univariate logistic plots (Fig. 4, 7), was in the alpine where because of uneven topography and drifting snow, we observed snow depths to be much more variable. Neither snow hardness nor density appeared to influence crater site selection. In other studies, Frid (1998) found no effect of snow depth or penetrability on crater site selection, but attributed this to the relatively low snow depths of his study area (mean=31.5 cm, standard deviation=5.8). Cichowski (1993) found that crater sites had greater snow depths, but reduced penetrability when compared to random sites. Duquette (1988) studying the Porcupine herd, reported that snow depths were deeper along migration trails than within adjacent feeding areas, and snow hardness did not diffet between the two areas.

Management Implications

Our research suggests that particular scale-specific habitat characteristics may be important to manage for, or consider during an assessment of the winter range of the northern woodland caribou of British Columbia. Forested areas should be managed to contain terrestrial lichen mats with a high percent covet of *C. mitis, Cladonia* spp., and a high biomass of arboreal lichen (*Bryoria* spp.). *Cladina mitis, C. rangiferina, C. cucullata, C. nivalis, S. alpinum,* and *Thamnolia* spp. are important species that should be considered when assessing and managing alpine areas. Because snow may limit access to forage, and restrict use to specific areas of the range, snow depths should be considered in conjunction with the availability of lichens when assessing the suitability and availability of caribou winter range.

Our results describe selection of foraging sites by caribou at one explicitly defined scale, the individual feeding site. However, the relationship between an organism and its environment is often complicated by multiscale influences. Factors from both finer and broader scales may act in unison to elicit responses that may not be detected by measurements designed to record responses at one particular scale. To accommodate the tecording and understanding of these interactions, a multiscale hierarchical approach should be pursued (Senft *et al.,* 1987; Kotliar & Wiens, 1990; Wiens *et al.,* 1993). This study was designed to measure just one of many scales that may be televant to how caribou perceive and respond to their environment (Johnson, 1980). The results and conclusions must, therefore, be viewed within the context of other scale-sensitive influences on movement and distribution across the landscape (e.g., large scale distribution of snow, habitat patch configuration, predation risk) which are necessary considerations when managing the wintet range of woodland caribou (Cumming, 1992). We are currently investigating the affects of those influences on the foraging behaviour, movements, and distribution of woodland caribou at stand and landscape scales.

Acknowledgements

We thank our field technicians M. Wolowicz and G. Keddie, the pilots of Northern Mountain Helicopters, and rhe numerous volunteers whose assistance made this study possible. We extend our appreciation to A. Frid who graciously shared unpublished data and thoughts on study design and statistical analysis as well as M. Gillingham and B. Zumbo who provided sratistical advice and aided wirh graphics. We also acknowledge J. Marsh who shared her knowledge of the distribution and abundance of lichens in the Germansen Lake area. A. Frid and B. Griffith provided helpful commenrs on earlier versions of this manuscript. This study was funded by Forest Renewal British Columbia, a Grant-in-aid from the Boone and Crockett Club, a British Columbia Ministry of Environment, Lands, and Parks Environmental Scholarship, and a University of Northern British Columbia Natural Resources and Environmental Scholarship.

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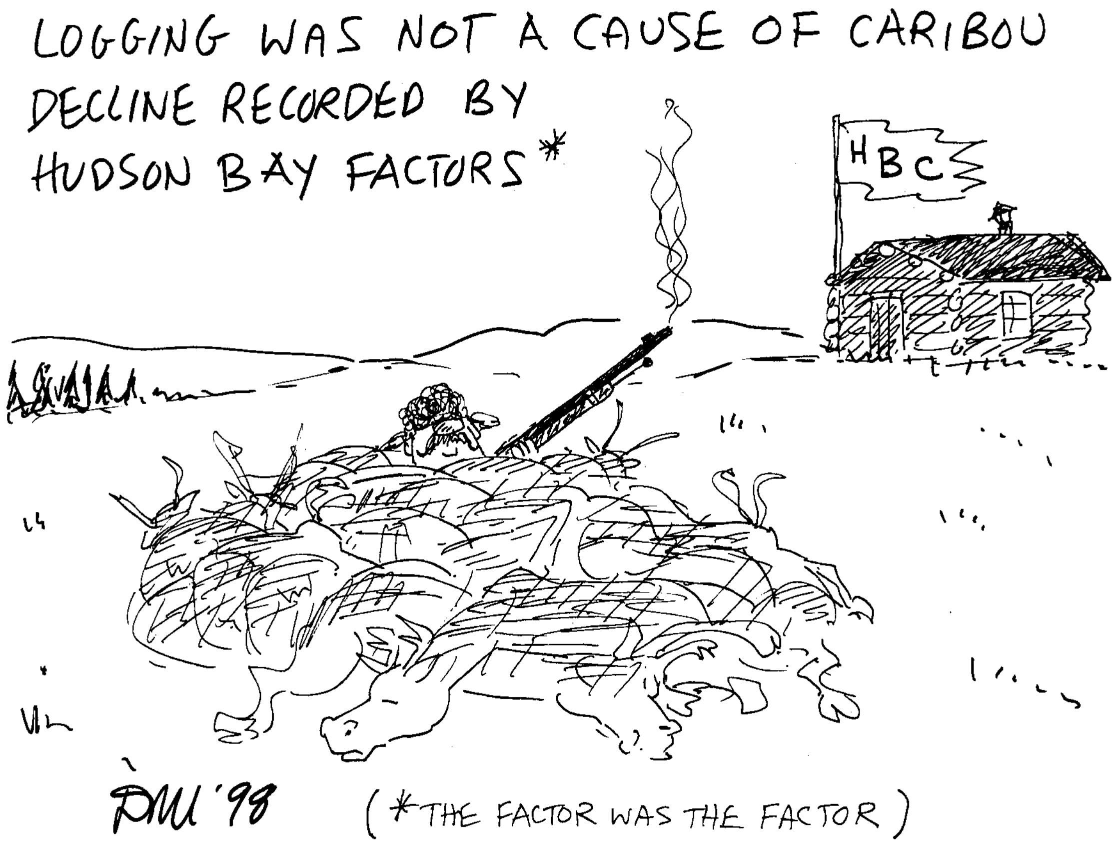

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Woodland caribou range occupancy in northwestern Ontario: past and present

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Abstract: A zone of continuous woodland caribou (*Rangifer tarandus caribou*) distribution is defined for northwestern Ontario. This zone establishes a benchmark for measuring the success of future management of habitat and conservation of populations. Inventory of key winter, summer and calving habitats reaffirms the concept of a dynamic mosaic of habitat tracts that supports caribou across the landscape. The historical range recession leading to this current distribution has been associated with resource development, fire and hunting activities over the past 150 years, and numerous attempts at conservation over the last 70 years. The decline was apparently phased according ro several periods of development activity: i) early exploitation in the early to mid-1800s; ii) isolation and extirpation of southern populations due to rapid changes in forest use and access between 1890 and 1930; and iii) further loss of the southernmost herds due to foresr harvesting of previously inaccessible areas since the 1950s. Lessons learned from history supporr current conservation measures to manage caribou across broad landscapes, protect southern herds, maintain caribou habitat as part of continuous range, mainrain large contiguous rracts of older forest and ensure connectivity between habitat components.

Key words: caribou, development, forest management, habitat, history, populations, wildlife.

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Introduction

The status of woodland caribou (*Rangifer tarandus caribou*) in northwestern Ontario has been debated widely because information on population size and range occupancy is inadequate. Kelsall (1984) suggested that caribou were secure in local areas in Manitoba, Ontario and Quebec, but considered the southeastern Manitoba, Slate Islands, Pukaskwa and Lake Nipigon populations threatened. He considered Ontario's woodland caribou part of the "vulnerable" western Canada population. This recommendation was based on various estimates of the population size or status of caribou in Ontario by de Vos & Peterson (1951), Cringen (1957), Banfield (1961), and Simkin (1965). Recent estimates of population size (Cumming, 1998) suggest that the provincial population is relatively stable, but that, based on numbers and threats, forest-dwelling woodland caribou should be considered "threatened" (Cumming, 1997). Population estimates for forest-dwelling woodland caribou are difficult to obtain, imprecise and unreliable (Thomas, 1998). We believe this to be ttue in the forests currently used for commercial purposes in northwestern Ontario.

Although teliable population estimates are lacking, it is clear that caribou range in the Lake Superior - northwestern Ontario area has become more restricted since the mid 1800s. Cringen (1957) documents the extirpation of caribou in Minnesota, Michigan and Wisconsin and suggested that caribou had disappeared from 30 000 square miles (76 800 square km) of range west of Lake Superior. A more detailed account of current distribution and historical recession of woodland caribou range in Ontario was provided by de Vos & Peterson (1951). These declines in the Lake-Superior - northwestern Ontario area coincide with general trends observed across North America (Cringen, 1957; Bergerud, 1974; Cochrane, 1996; Mallory & Hillis, 1998). Range recession maps suggest a gradual recession in Ontario caribou range over the last century (Darby & Duquette, 1986; Darby *et al.*, 1989; Cumming & Beange, 1993).

Apparent decline in the numbers and distribution of caribou in Ontario has resulted in a history of management actions, starting with closure of the hunting season for caribou in 1929. Since then, caribou management has been supplemented by widespread caribou survey work conducted in the 1950s (Simkin, 1965), and broad habitat assessment (Ahti & Hepburn, 1976). Initial attempts at caribou policy development began in the 1970s and 1980s (Darby *et al.*, 1989), although there is no provincial caribou policy at this time. Forest management guidelines were developed in the 1990s (Racey *et al.*, 1991; Racey & Armstrong, 1996) but it is too early to evaluate long-term effectiveness of these guidelines. Debate continues over appropriate management strategies and has led to demands for better information about current range utilization, better understanding of how and why caribou suffered this historical decline and what the implications may be for survival of caribou in the commercial forest of northwestern Ontario.

In northwestern Ontario, the current management objective is to halt the northward recession of caribou range and maintain range occupancy (OMNR, 1998). We suggest that achievement of this objective over the long term may be evaluated by monitoring change in range occupancy rather than by population estimates. This paper looks at the current and past distribution of woodland caribou in northwestern Ontario, and describes ecological, social and economic factors associated with the historic decline in range. Improved understanding of the nature of past range recession will support development of management strategies to avoid future range loss.

Materials and methods

Study Area

The study area included all of northwestern Ontario within the currently licensed commercial forest (Fig. 1). This forest includes the Lac Seul Uplands,

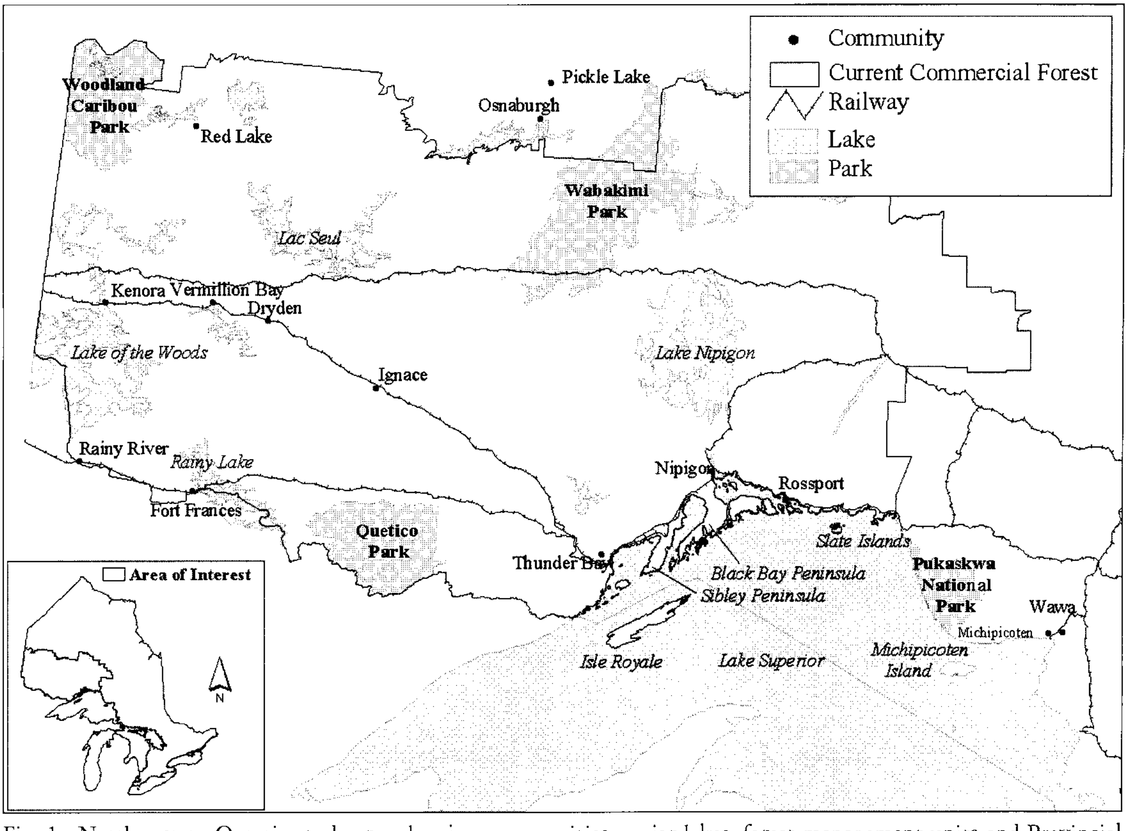

Fig. 1. Northwestern Ontario study area showing communities, major lakes, forest management units and Provincial Parks referenced in text.

Lake of the Woods, Rainy River, Thunder Bay - Quetico, Lake Nipigon and a small portion of the Big Trout Lake ecoregions of the Boreal Shield ecozone (Ecological Stratification Working Group, 1995). Woodland caribou are considered native to the entire study area. This area has had a long human development history; it was occupied by paleo-Indian cultures and later by the Ojibway and Cree peoples, followed by European exploration in the late 17th century. Development of northwestern Ontatio was driven by the fur trade until the mid 19th century, and more recently by forest, mining, transportation, agriculture, tourism and recreation industries.

Current Range Occupancy

Current range occupancy was defined by reliable observations of caribou activity since 1990. Presence of caribou within cells of a 10 km UTM grid was recorded. Caribou presence data were obtained from a variety of sources including surveys of caribou winter habitat and calving sites between 1988 and 1997 (Timmermann, 1998a; b) incidental sightings during regular early winter moose (*Alces alces*) surveys (Bisset, 1991), reports to Ontario Ministry of Natural Resources (OMNR) staff from forest workers, anglers, hunrers, trappers, tourism operators and naturalists, and location data from a concurrent habitat use study (Hillary, 1998) involving 25 caribou (19 females, 6 males) fitted with Argos Satellite collars between 1995 and 1998.

Historic Range Occupancy

Historic range occupancy was determined on the basis of the most recent record of caribou presence within UTM grid cells. Evidence was obtained from archeological studies of late pre-historic and early historic (1600-1800) periods, fur trade diaries, land survey records and railway construction records. Other historical documents that made reference to observations of woodland caribou and which provided relatively specific geographical locations were also used. Old Department of Lands and Forests (pre-1972), and OMNR (post-1972) wildlife survey information and internal correspondence was used to identify and verify areas and times of previous occupancy.

Regional Habitat Map

A regional map was produced to depict the nature of seasonal habitat use within current occupied range. Significant areas of winter, summer and calving habitats currently used within the study area, and the main directions of travel between them were mapped. Data for this map were assembled from the same wide vatiety of sources used to map current range occupancy. Winter habitat surveys were conducted by OMNR staff in late winter (February-March) and occasionally earlier in winter. Areas of high concentrations of caribou tracks were delineated and recorded as winter habitat. Where surveys of the same areas spanned multiple yeats, the areas used in all years were considered in delineating winter habitat tracts (Timmermann, 1998a).

Some summer and calving habitat was identified through incidental observations from forest workers, trappers, anglers, hunters, naturalists and tourist operators. Areas with significant, observed summer use by caribou were considered summer habitat. A general area, lake, group of islands or wetland complex was considered used for calving if cows and calves were observed there during the May - June post-calving period, or if evidence (e.g. recent calf tracks) was observed in the vicinity during those same time periods. In addition, since the early 1990s, calving surveys of high potential lakes have been conducted to determine if specific lakes contain islands, peninsulas or shorelines used for calving (Timmermann, 1998b). Only a small portion of the overall caribou range has been surveyed for calving areas. Aerial monitoring of caribou and caribou tracks during the fall and spring, combined with recorded movements of 25 radio-collared caribou were also used to delineate habitats and some major travel routes between habitats.

Chronology of Caribou Decline

A general description of the chronology and circumstances surrounding the decline of caribou in northwestern Ontario was generated after reviewing available data and records from a wide array of common and obscure sources, and examining circumstances and data associated with five geographic case studies. Substantial interpretation was required to understand some historical written accounts with vague references to general locations. Some parts of the study area had no historical information on caribou.

Results

Range Occupancy

The plotting of current (1990-1997) records of woodland caribou occurrence revealed that caribou

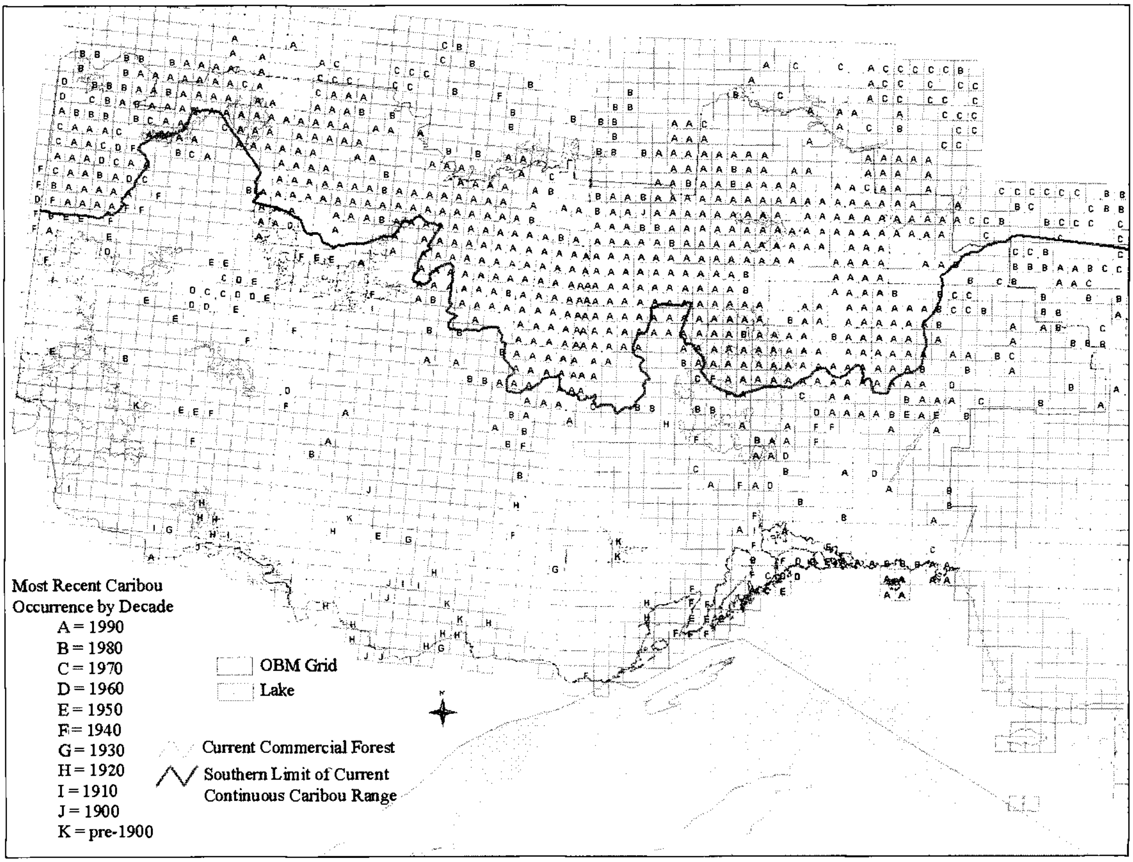

Fig. 2. Woodland caribou range occupancy map identifying locations of most recent caribou observations by decade. The southern boundary of the zone of continuous distribution and woodland caribou range occupancy map identifying locations of most tecent caribou observations by decade. Observations ate recorded on 10 km UTM grid.

distribution is essentially continuous across northwestern Ontario (Fig. 2). From these data, a southern limit of continuous caribou distribution could be distinguished and delineated. Isolated populations south of this area exist on some of the islands and adjacent shore of Lake Superior. The majority of the recent inventory work has been focused on areas near the southern range limit, and within the commercial forest. The lack of recent data near the northern boundary of the study area reflects less complete caribou inventory effort.

Regional Recession in Caribou Range

Plotting the decade of most recent caribou occurrence revealed the extent of caribou range recession over the past century (Fig. 2). While historical data were sparse, a pattern is evident. Several discrete clusters of caribou habitat spanned the southern edge of the study area, just north of the Canada-USA border, at sometime in the period between the early 1900s and the 1920-30s. Historical records show that for the same period of time, many of the areas with no evidence of use wete heavily disturbed by fire, human development and logging. Caribou persisted along the shoreline of western Lake Superior until the 1950s, and until the 1970s in the Black Bay area. More recent occurrences in the 1940s, 1950s and 1960s were scattered across the region midway between the Canada-USA border and the current southern range limit. A significant cluster of activity south of the current range limir persisted into the 1970s, and occasional recent sightings are scattered immediately south of the range limit in several areas particularly in the eastern portions of the study area. The following case histories represent data describing the context for occupancy and eventual decline of caribou in these southern habitats.

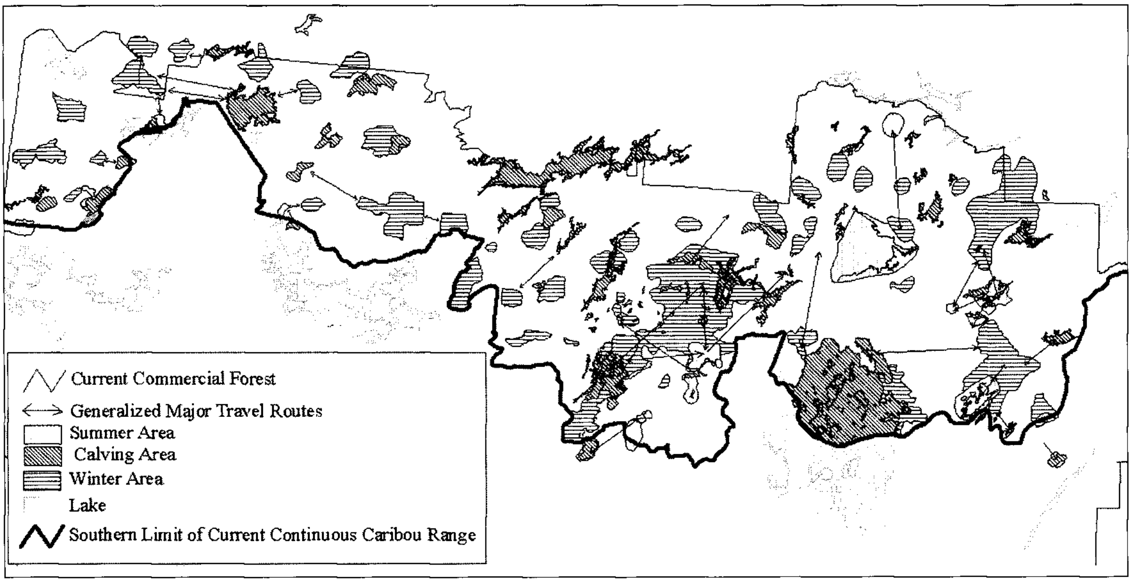

Fig. 3. Coarse mapping of woodland caribou winter habitat utilization and major calving areas for the current commercial forest of northwestern Ontario.

Regional Habitat Map

Regionally significant caribou seasonal habitats are spaced relatively evenly across the northern landscape (Fig. 3). Calving areas are generally widely dispersed, with some considered of greater value from a strategic petspective. The pattern of habitat use suggests concentrated caribou activity within the broader fabric of the continuous range distribution shown in Fig. 2. The absence of latge gaps between used habitats combined with the telatively continuous nature of range occupancy does not suggest the presence of discrete herds.

Case History 1: (1830s Ungulate Drought)

Caribou populations appeated to reach a temporary low point during the early 1820s to 1840s. The decline seemed to be widespread, but no obvious explanation for the synchronous widespread ungulate "drought" is evident. This occurred before the advent of latge-scale forest harvesting, railway construction, or development of agricultute in the tegion. Fritz and Suffling (1993) attributed low caribou and moose populations and harvests in the vicinity of Osnaburgh House from 1820 to 1860 to large-scale wildfire activity that created a butned area of approximately 250 km in length. This rarity of ungulates was also documented in the vicinity of Fort William and the west end of Lake Superior (Haldane, 1824), and the scarcity of caribou in the Kaministiquia River valley was corroborated by Murray (1849). Cochrane (1996) identified several references to low abundance of caribou between Fort William and Lake of the Woods in 1822, Mille Lac in 1824, and between Fort William and Fond du Lac in 1831. Lytwyn (1986) suggested over-hunting was a factor in caribou declines as early as the late 1700s.

These references support the understanding that caribou were an important part of the northwestern Ontario fauna in the early 1800s, an important food for native peoples, used in trade, yet inexplicably uncommon during that period. They also suggest that factors othet than logging may influence decline of ungulates across broad areas.

Case History 2: (Lake of the Woods - Northwestern Minnesota)

Caribou once occupied most of the landscape surrounding Lake of the Woods when De Noyen became the first white man to visit in 1688 (Mead, 1981). This area was relatively unique in that by 1890 it appears to have supported four ungulate species: white-tailed deer (*Odocoileus virginianus*), moose, caribou and elk (*Cervus canadensis*), and all four were used by natives and Europeans as food and even a trophy hunt (Brown, 1890-1893). Sawmilling industries started to increase pressure on forest resources, especially pine ecosystems, aftet 1879 and harvesting further increased following the development of pulp mills in Fort Frances in 1914 and Kenora in 1922 (Mead, 1981). Archaeological data from the Hudson's Bay Company Whitefish Bay Post shows that caribou were consistently used as food until 1895, when white-tailed deet became the primaty ungulate used (Pets. comm. P. Reid, Regional Archeologist, Kenora) This shift in use coincides with the increase in logging activity and a probable improvement in habitat quality for white-tailed deer. By 1927 most forest area surveyed east of Lake of the Woods had been cut over or burned (Phillips & Benner, 1926; van Nostrand, 1927). Large amounts of burned area were also common in the vicinity of Rainy River in the mid to late 1890s (Niven 1890; 1892; 1894; 1895).

In Minnesota and Southwestern Manitoba, caribou declined more slowly. These areas contain vast bog and fen complexes which may have provided refuge from predators and hunting pressure, as well as providing habitat that was not in industrial demand. Beginning in 1932, major efforts were made ro preserve caribou in northern Minnesota, including establishment of the Red Lake Game Pteserve, resettlement of homesteaders, blocking of drainage ditches, introduction of beaver (*Castor canadensis*), wolf (*Canis lupus*) control, intensified enforcement, and the blasting of wallows (Berg 1992). Nevertheless, Fashingbauer (1965) noted that by 1937 the last native band of woodland caribou consisted of three cows occupying the muskeg area known as the "Big Bog" between upper Red Lake and Lake of the Woods. Manweiler (1939; 1941) noted that agricultutal development along Rainy River isolated this population, and interrupted their traditional migratory route between calving islands in northwestern Ontario and winter habitat in northwestern Minnesota. Caribou reintroduction efforts begun in 1938 failed to produce a viable self-sustaining population (Bergerud & Mercer, 1989).

Very rare sightings of individual caribou or small groups persisted east of Lake of the Woods until 1961 (internal OMNR correspondence, 1961). These observations were later attributed to movement of animals from farther north. Caribou populations petsisted northeast of Lake of the Woods (Cliff and Clay Lake) until 1977 and north of Lake of the Woods until the ptesent (Umphreville Lake) (OMNR data).

The decline of caribou in the vicinity of Lake of the Woods is consistent with cumulative impacts of hunting ptessure, habitat alteration by fite and logging, isolation from contiguous range, range expansion by white-tailed deet with increased exposure to the parasitic brainworm *Parelaphostrongylus tenuis,* and increased predation (caribou were protected in Minnesota and Ontario when the final decline and disappearance occurred).

Case history 3: Boundary Waters - Quetico

Woodland caribou resided in the vicinity of the current Quetico Provincial Park and the Minnesota Boundaty Watets Canoe Area until approximately 1930. Sewell (1888) noted that much of the area east of the present Quetico boundary was burned over in a great fire, but that caribou were still abundant west of Bitchu Lake. Likewise large fires were also prevalent to the west, in the vicinity of Rainy Lake (Niven 1892; 1895). The northern portion of Quetico was one of the major east-west canoe and trade routes prior to construction of the Canadian Pacific Railway (CPR) in the 1870s. Logging fot white (*Pinus strobus*) and red pine (*P. resinosa*) and other sawlogs became big business in rhe area that became the park in 1908, and continued along most of the waterways beyond the 1930s . Large fires also altered the habitat in 1910, 1917, and 1929. Hunting was active throughout the country until 1929 as caribou slowly diminished.

Woodland caribou sightings between 1900 and 1930 became less and less common as the cumulative impact of habitat alteration, hunting and changing wildlife composition became mote apparent. The fites of 1929 and 1930 seemed to be followed by an influx of white-tailed deer (Pers. comm. B. Soini & A. Primeau); deer range expansion was widespread across northwestern Ontario ar that time.

It appears as if the caribou in the vicinity of Quetico Park became isolated from continuous range as early as 1900 due to wildfire, consttuction of the railway and hunting along access corridors associated with canoe routes and the railways. Once it became isolated, it was only a matter of time until the population declined as a result of continued hunting from settlers, travelers, and commercial hunters supplying the logging camps. Habitat loss resulting from further fires and logging, the influx of white-tailed deer and the associated risk of brain worm and predators eliminated caribou from this area around 1930.

Case History 4: (North Shore of Superior)

On the notth shore of Lake Superior, hunting pressure was heavy as early as the late 1700s (Lytwyn, 1986). Cochrane (1996) describes the decline of caribou on Isle Royale, and the shores of Lake Superior. These researchers also document traditional use of woodland caribou by natives, use by settlers, miners and loggers, and the continued existence of caribou on the north shore of Lake Superior into the 1890s. At that time the tourist trade across the north shore (*e.g.* Pays Plat, Nipigon, Port Arthur) was becoming big business, and caribou were widely advertised in travel brochures as a game species and a general attraction. The north shore CPR Line provided economical access to opportunities for resource development, tourism and settlement.

By 1919 logging operations began on the Sibley Peninsula, leading to an increase in the occuttence of white-tailed deer. A 1924 land grant to settlers at Pass Lake created habitat disturbance at the north end of the Peninsula, severing any landscape connection with the northern mainland. Similar harvesting and land settlement was occurring in the vicinity of Nipigon. By the 1930s caribou were still noted as an attraction for tourists, although hunting for caribou was not allowed. By 1950 deer and moose were common across the Sibley Peninsula, Black Bay Peninsula and St Ignace Island. Occasional sightings of caribou occurred on the Black Bay Peninsula, the islands off Rossport, the mainland between Rossport and Wawa and the isolated population on the Slate Islands. At this time caribou also occurred east of Long Lake and along the eastern shores of Lake Nipigon, although population size is poorly documented. By 1972, caribou were more or less restricted to a remnant population on the Slate Islands and a 1.5 km wide strip of land along the Lake Supetior shoreline of Pukaskwa National Park (Bergerud, 1989), although infrequent observations inland continued. Habitat disturbance and access east of Long Lake and north of Tettace Bay, and the lack of consistent caribou observations in that area during the last 20 years has led to the conclusion that the caribou on the north shote are now an "isolated" population.

Case History 5: Cliff Lake

The decline of catibou at Cliff and Clay Lake is the latest and probably best documented of range recession events (Brousseau, 1979). This area was home to an observed 36 caribou during the winter of 1966-67, when recommendations were made to conserve and maintain a natural habitat for this species (Hansson, 1967). At that time, the area inhabited by caribou was largely undisturbed by roads and logging. Wolf hunting was a widesptead practice at that time, with 254 gray wolves bountied in Depattment of Lands and Forests Kenora District during 1968 (OMNR file data). Some poaching occurred - two hunters were convicted of illegally killing a caribou from this herd in October of 1967 (OMNR file data).

Correspondence from local offices identified the value of the commercial timber under existing license and questioned; "are the aesthetic and scientific values sufficient to protect and save them and their range?" (internal OMNR correspondence). The corporate response was that any remnant herd was valuable, public attitudes toward non-game were shifting, and staff should examine alternate areas where equally good timber could be obtained (internal OMNR correspondence). Planning took place between 1967 and 1969, access development and logging began in 1970 and continued until 1982. The caribou population in the survey area declined from 32 in 1972 to 12 in 1978 (Brousseau, 1979). Although some caribou continued to use rocky jack pine-dominated ridges neighboring the study area these animals also soon disappeared. Apparent increases in white-tailed deet, wolf activity and human activity all coincided with the decline of caribou. Caribou activity located west of the Cliff Lake study area also disappeared during the same time frame as the decline within the Cliff Lake study area (Pers. comm. D. Anderson, OMNR).

Discussion

Caribou Range Occupancy

The zone of continuous distribution of caribou in northwestern Ontario (Fig. 2) is supported by discrete seasonal habitats distributed across that zone (Fig. 3). Most of these seasonal habitats are associated with large tracts of older forest embedded in a landscape distutbed by fire and logging. This concept is an important principle upon which the northwestern Ontario caribou habitat management strategy (Racey *et al.*, 1991; OMNR, 1999) is based. It implies the need fot a landscape-level habitat management strategy predicated upon a dynamic, shifting mosaic; this concept is substantially different from defining and managing discrete hetds or protecting only cuttently used habitat tracts. Caribou habitats within the zone of continuous distribution are dependent in part on land capability and in part on current suitability. Many of these

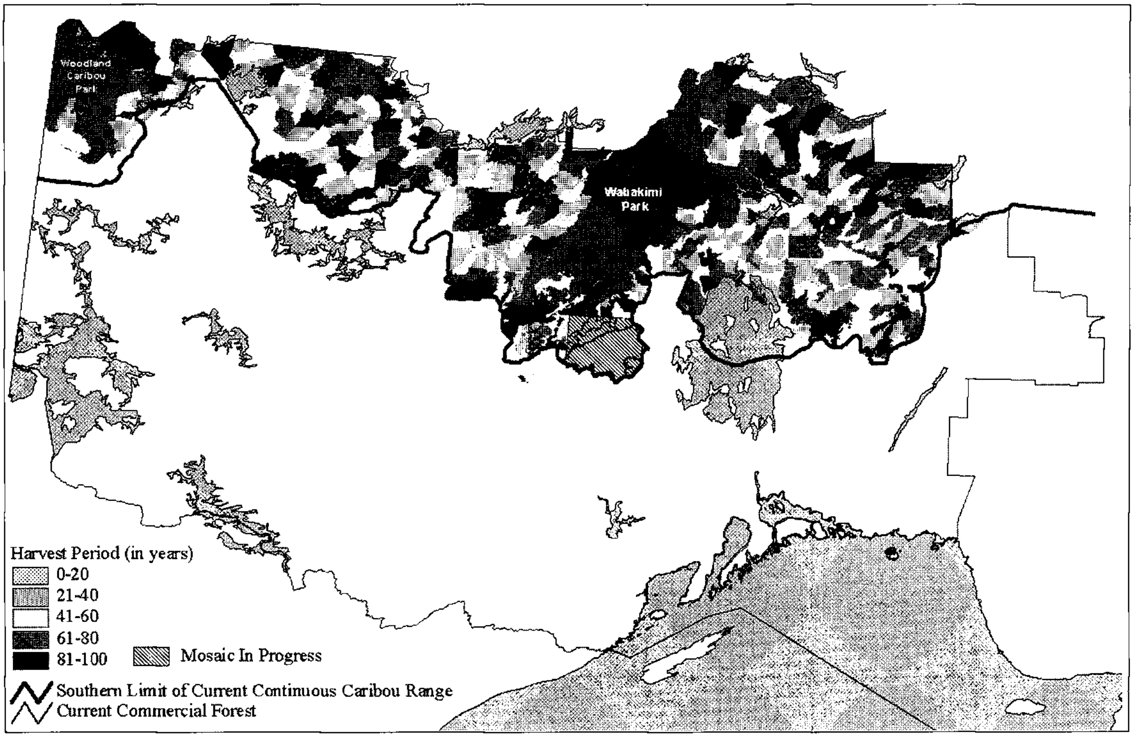

Fig. 4. Existing caribou habitat management mosaic for northwestern Ontario identifying the large tracts of forest that will be rerained or allocated at various times to provide for a continuous supply of caribou winter and year round habitat (OMNR 1998).

used habitats may persist for a period of time until a disturbance takes place, at which time other habitats will need to be available. There is a strong resemblance between the natural habitat mosaic cteated primarily by wildfire (Fig. 3) and the mosaic planning process (Fig. 4) (OMNR, 1999), which is intended to provide guidance for the sequencing and spacing of large harvest blocks in order to ensure futute habitat supply and availability in a managed landscape. It is postulated that a similar relationship between continuous tange and discrete high value habitats existed across northwestern Ontario in the late 19th and early 20th centuries.

Recession of Caribou Range in Northwestern Ontario.
The lessons from historical data and case studies suggest that caribou decline had several phases. There was an initial period of early exploitation when caribou were taken as encountered, usually for food or trade. As northwestern Ontario was developed, access, wildfire and forest harvest led to isolation and fragmentation of southern populations. These populations later became depleted due to continued habitat alteration, hunting and disease. Mechanization in forest management activities, access development and the advent of road hauling of logs opened up previously inaccessible areas leading to decline of previously isolated populations. Since 1960 a steady northward progression of timber harvest has led to a more systematic recession of caribou range. The majority of early range recession was apparently not "gradual". This recession involved a series of "collapses" of relatively isolated populations, and not a gradual recession as could be inferred by maps of range recession (e.g. Darby *et al.*, 1989).

Caribou hunting by both natives and Europeans was a fact across northwestern Ontario throughout the 1800s, and when caribou were in low abundance in the 1820s to 1840s severe hardship was encounteted by residents.

Fragmentation and alteration of habitat was assisted as early as 1855 by development of the Sault Ste Marie locks. This permitted development of a widespread, export-based sawmill industry and led, in part, to the development of the railroad from

Thunder Bay through Dryden to Kenora in the late 1870s (Bray & Epp, 1984). By 1880, sawmilling activity was abundant in the vicinity of Thunder Bay, Fort Frances, Kenora, Dryden, and Nipigon, with much of the activity centred on waterways. Another significant factor was the burning of large areas of land west of Thunder Bay (Sewell, 1888; 1890), in the vicinity of Rainy Lake (Niven, 1890; 1892; 1894), and a large fire (140 km long) between Vermillion Bay and Ignace in 1882 (Wice, 1967). By 1900, this created sevetal relatively isolated groups of woodland caribou across the southern portion of northwestern Ontario. These groups were located along the north shore of Lake Superior and the Lake Superior islands including Isle Royale, in the general location of Quetico Provincial Park, and in the vicinity of Lake of the Woods and northern Minnesota.

The northwestern Ontario economy boomed from 1900-1920 with settlement and agricultural development in the vicinity of Dryden, Rainy River and Thunder Bay. It was supported primarily by the development and growth of a pulp industty that was much less "discriminating" on the size and species of trees used than the sawmill industry (Bray & Epp, 1984). A strong tourism industry based on rail travel distributed food and trophy hunters across the north shore of Lake Superior (Bray & Epp, 1984). It is conceivable that as early as 1920-1930 the southern boundary of the continuous distribution of caribou may not have been unlike the distribution map produced by deVos & Peterson (1951). This map suggested that caribou existed in the areas south and west of Lac Seul (Cliff Lake area), across to Lake Nipigon, and with scattered occurrence east of Lake Nipigon to the Lake Superior shoreline and islands to Pukaskwa National Park. Although caribou existed below that line, these animals were isolated in fragmented landscape patches as discussed in case studies 2 and 3. Habitat alteration due to timber harvest was occurring along most water-accessible areas, hunting was still widespread, and human-caused and natural fire continued to play a significant role in depleting mature forest areas. In the 1920s white-tailed deer range was expanding along with a presumed increase in predators in the Lake of the Woods area (Voigt *et al.*, 1992). Brainworm associated with white-tailed deer may have been a contributing factor to widespread decline. By 1929, when the hunting season for caribou was closed, the caribou in the southerly part of the study area may already have been doomed due to the cumulative direct and indirect impacts of human activity, with the exception of the animals along rhe north shore of Lake Superior.

The 1930s-1950s brought a mining boom to many areas in northwestern Ontario, and roads followed the development of mining communities. The 1950s brought forestry mechanization, automation, and road hauling and new areas that were previously remote began to be opened up to timber harvest. This was driven in large part by the need of the forest industry to have a year-round supply of wood and to avoid the seasonal and unreliable nature of river drives. The mainland areas north of Lake Superior, west of Lake Nipigon and in the Cliff Lake area became vulnerable at that time, and caribou declined accordingly. In the last 20 years, a number of timber companies accessed and harvested areas that overlap the southern boundary of the current zone of continuous distribution. Harvest has been creeping northward in a relatively systematic manner until the first approximation of the northwestern Ontario caribou habitat management strategy was introduced in the early 1990s. Caribou habitat continues to be under pressure from forest management in many of the southerly porrions of this zone of continuous distribution and caution is advised if caribou are to be maintained (Cumming, 1992). History suggests it would be undesirable to isolate and protect components of the landscape independent of a comprehensive landscape management approach.

Management Implications

No single factor identified in the case studies can be cited as the cause of decline. In all cases, the cumulative impact of early hunting, timber harvest, habitat alteration, disease, shifts in range of white tailed deer and moose, shifts in predator-prey balance, wildfire, construction of road and rail access corridors and land clearing for agriculture, have contributed to the decline of caribou in northwestern Ontario. Multiple factors appear to interact to the detriment of woodland caribou, stemming primarily from the access and exploitation of natural resources. Clearly, thoughtful resource management strategies that consider broad landscape impacts are required to halt the decline of caribou, particularly for the forest-dwelling ecotype. The lessons from the case studies do not support a catibou management approach focused on individually defined and geographically discrete caribou herds. Given the history of caribou range loss, managing only at the local level could readily lead to habitat fragmentation and eventual isolation and extirpation of local populations. A holistic approach to managing forested landscapes is advocated, where all aspects of fotest health are addressed: forest structure (size of disturbances and habitat ttacts and how they are distributed on the landscape), forest composition (age class structure, ttee species representation, and stand composition) and ecosystem function (predator-prey relationships, habitat value, food availability, refuge *etc.*). Range occupancy may only be maintained by implementing a comprehensive ecosystem-based approach that modifies social and economic needs to operate within the bounds of maintaining boreal forest health.

This historical review of caribou range recession demonstrates the value of range occupancy data for tracking change in status of woodland caribou. Such data are particularly valuable when population estimates are difficult to obtain and unreliable, as they are for caribou.

It is cleat that a successful caribou conservation program will require consideration of both population and habitat management strategies, and managers must recognize that the two interact. Woodland caribou habitat management is a very complex issue, requiring both long-term temporal perspectives and large-scale spatial petspectives in order to address requirements for specific food, shelter and movement habitats, as well as habitats that provide a high probability of avoiding predators. Our information on biological tequirements and limitations is incomplete and examination of historical information allows us to better understand the current status of caribou, and to make future projections. However, habitat should not be managed without considering the implications fot populations. Population dynamics are an important consideration in caribou survival, given the sensitive balance between ptedator and prey numbers (Bergerud, 1985; Seip, 1992; Thomas, 1992). Hunting and subsistence use were probably significant factors in at least some of the early extirpations and range recessions of caribou, and the impact of changing incidence of predators and disease cannot be under-estimated.

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Brief communication

Habitat selection and use by muskoxen and reindeer in western Alaska: a preliminary report

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Due to their specific physiological and morphological adaptations to survival in the arctic, muskoxen and reindeer/caribou have evolved different foraging strategies and habitat preferences which are believed to keep competition at a low level (Klein, 1986; Schaefer *et al.,* 1996). On the Seward Peninsula in western Alaska, open herding of reindeer has provided cash income and a food supply for native people since their introduction in the late 1800s. Following introduction of muskoxen in 1971 and 1980, some teindeer herders have developed concerns about possible competition for forage with reindeer or antagonistic behavioral interactions between muskoxen and reindeer that might displace reindeer from feeding sites.

This study addresses those concerns with the following objectives: 1) to characterize muskox and reindeer habitat at different scales of selection (range, feeding sites, feeding craters, diet), to identify overlap and factors driving forage selection at each level for each species, and to understand implications for possible competition between the two species, and 2) to assess behavioral interactions between muskoxen and reindeer.

The study area encompasses the reindeer range of herder Herbie Karmun on the northwestern Seward Peninsula, between Kugruk River in the east, the mouth of Goodhope River in the westand Imuruk Lake to the south. Approximately 2500 reindeer and 150-200 muskoxen occupy the range year round. Feeding sites of both species were sampled and marked in March and April of 1996 (n=15 for muskoxen; 14 for reindeer) and 1997 (n=14 for muskoxen, 12 for reindeer). On a 30X30 m sample grid 10 random spots which characterize feeding sites, and 10 randomly chosen craters were sampled for snow depth and integtated snow hardness using a Rammsonde penettometer (Skogland, 1978). The amount of above-snow vegetation (graminoids, shrubs or hummock) was recorded at each sample point. A composite fecal sample from 10 pellet groups was collected at feeding sites (n=16 for muskoxen in 1996, 15 for muskoxen in 1997, 13 for reindeer in 1996 and 13 for reindeer in 1997). Sites wete telocated in summer when the vegetation cover was assessed using a 16-point sample frame. Since the exact availability of habitat during late winter is not known for either species, range was defined as the area within a radius of one mile surrounding feeding sites, a margin wide enough to generally include neighboring feeding sites. Within this atea, control plots (n=10 for muskoxen in 1996, 10 for muskoxen in 1997, five for reindeer in 1996 and eight for reindeer in 1997) were sampled in the manner described above.

Data from both yeats were combined for the analysis. Snow data were analyzed separately by year. Fecal samples were analyzed by microhistological analysis. In order to assess their relative importance for the selection at each level, all variables were analyzed together by stepwise logistic regression. Multivariate analysis of variance (MANOVA) was used to detect differences based on species (muskoxen *vs.* reindeer) and use (used *vs.* available) at the diet, crater and feeding site levels, where the respective next highest level provided data for availability. Analysis is still in progress and all results are preliminary. While muskoxen fed almost exclusively on exposed upland habitats dominated by lichen/*Dryas*/communities, teindeer used a wider variety of habitats, feeding also on tussock and tussock/ shrub tundra along slopes and in valleys. Decreasing snow depth appears to be the most important indicator for the selection of feeding sites and craters for both species. Snow hardness is also selected against by both species, but more clearly so at the cratet level than at the feeding site level. For muskoxen, the amount of above-snow graminoids was also a strong indicator of crater selection. Vegetation cover of range plots does not diffet greatly for muskoxen and reindeer. Muskox feeding sites have a higher occurrence of lichens and a lower occurrence of sedges and standing dead than reindeer feeding sites, while at the crater level the trend is reversed, with muskox ctaters higher in sedges and standing dead and teindeer craters higher in lichen. Reindeer diets were dominated by lichens (53.0±1.8%) while muskox diets were dominated by sedges, lichens and moss (26.9±1.8%; 23.0±1.4%; 19.9±1.9%), respectively.

These values reflect diet composition after adjusting for differential digestibilities of fotage classes (Boertje, 1981). While both species select for lichens and against sedges and standing dead at the feeding site level, diffetences in selection become more evident at lower levels of selection and reach their clearest separation at the diet level, with reindeer selecting strongly for lichens and muskoxen for sedges and to a lesser degree for mosses and lichens. Shrubs and willows are selected against by both species at all levels. Few direct behavioral interactions between muskoxen and reindeer were observed. Though muskoxen were occasionally frightened by reindeer running frantically from insect harassment, all other encounters were of a benign nature, with neithet species appearing to be distutbed by the presence of the other. Complete analysis of the data will help to further quantify the degree of resource use overlap between muskoxen and reindeer at different levels of selection and its implications fot competition.

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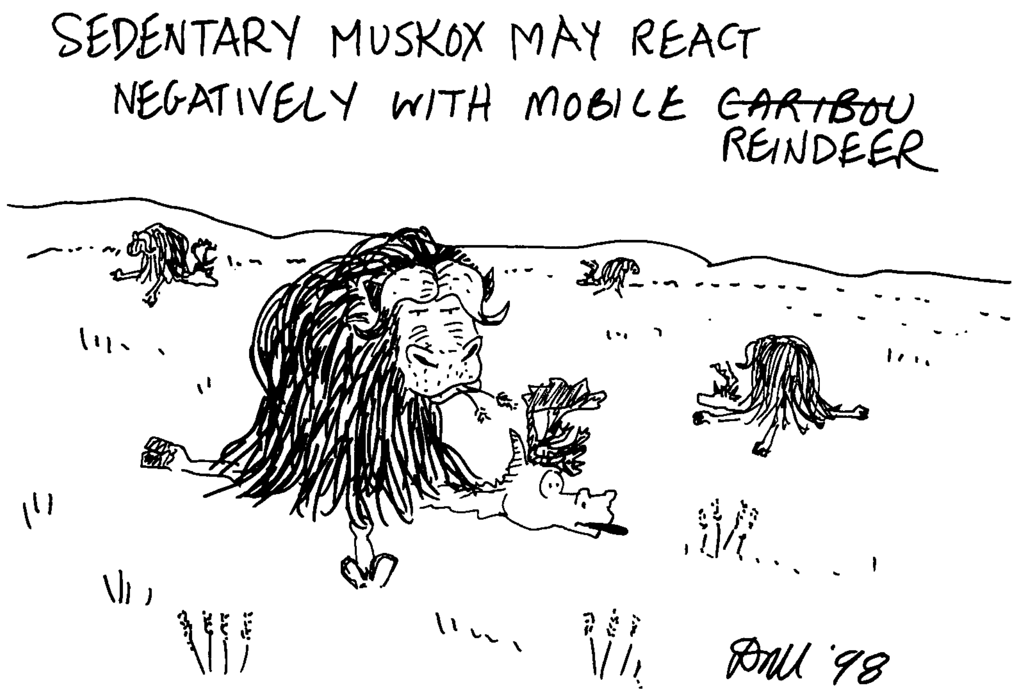

The Eight North American Caribou Workshop,
Whitehorse, Yukon, Canada,
20–24 April, 1998.

Brief communication

Landscape-level considerations in the management ofı forest-dwelling woodland caribou (*Rangifer tarandus caribou*) in northwestern Ontario

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Abstract: Forest-dwelling woodland caribou (*Rangifer tarandus caribou*) are disrributed widely across northwestern Ontario, although their range has receded significantly during the 19[th] and 20[th] centuries. Despite this continuous range occupancy, thete is a clear mosaic of high value habirats used by caribou, separated by lower-use habitats. Radio-collating data illustrate the large scale ar which woodland caribou use the range (i.e. 100's to 1000's of sq. km/year). This mosaic of habitat use is a reflection of habitat conditions and landscape patterns created by wildfire wirhin the boreal forest. As forest management and other human development extend further into woodland caribou range, rhe continued presence of caribou in the boreal forest will be dependent upon the continuation of forest landscape patterns similar to those which occurred with wildfire. "Mosaics" of scheduled harvesr and deferred tracts intended to emulate natural fire patterns are in place for all Forest Management Units within caribou range.

Key words: forest management, landscape pattern, habitat management, caribou conservation.

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Introduction

Woodland caribou range has receded northward during the last century and a half, and this range recession appears to be relatively permanent. Management efforts are underway in northwestern Ontatio to ensure no furthet range recession, and to maintain catibou use of currently occupied tange. Management activities are being directed at the landscape level, because that is the scale at which woodland caribou in northwestern Ontario appear to be using their habitat.

The plotting of tecent (1990s) observations of woodland caribou occurrence, without consideration of the degree of use, by 100 km^2 U.T.M. cells indicates that caribou occurrence is almost continuous within their range. The exceptions relate to isolated populations that still exist on some islands and mainland portions of eastetn Lake Superior.

Natural Disturbance Patterns

Caribou in northwestern Ontario occur within the boteal forest. This area has historically been subjected to a number of natural disturbances such as wildfire, blowdown, and insect infestations. These areas vary in size from very small to very large (i.e. 1000's of km^2). However, the dominant landscape pattern is most often determined by the large wildfires that periodically occur within the boreal forest. While woodland caribou typically frequent mature forests and habitually use traditional habitats, they have also had to deal with major, abrupt changes in forest structute, composition and function periodically caused by these large wildfires.

The broad scale at which caribou use the landscape, including their movements between seasonal habitats and theit occupation of large areas even within one season, have allowed caribou to adapt to the changing habitat conditions caused by these periodic wildfires, and to find new areas with both suitable habitat conditions and low ptedatot densities.

Caribou Habitat Utilization

Despite their broad occupation of the landscape, areas of significant woodland caribou habitat can be delineated. Field staff were able to identify significant areas of winter habitat, calving habitat, and summer habitat, as well as basic movement patterns, based upon known information on:

- areas where caribou are more abundant during that season, and/or
- areas where caribou would predictably be present during that season.

This information was obtained from winter aerial surveys, summer surveys of lakes and islands, incidental reports from the public, and data from an ARGOS radio-collaring study. Major wintering areas were primarily areas of mature, sparsely stocked coniferous forest. Summer and calving habitats were focused on eithet shoreline/island habitat, or peatland areas with upland islands within them.

This significant caribou habitat is dispersed discontinuously across the forested landscape of northwestern Ontario, often separated by many km from other similarly classified habitat. This information supports the concept of range occupancy at the landscape level, while emphasizing that some areas are of greater value and use than others at any particular time.

Caribou Collaring Study

A number of woodland caribou across northwestern Ontatio have been equipped with ARGOS satellite radio-collars as part of a co-operative research project with Laurentian University, in order to obtain information on caribou habitat use that would be of value to forest management planning. Twenty-one collars have been placed on a number of different catibou (more than 21, as collars have been refurbished and replaced on new animals periodically). Data from this small set of animals ovet a two year period porttays the broad landscape utilization pattern of caribou - information from these animals alone covers much of the area of continuous caribou distribution neat the southern range boundary.

Information from two specific collated animals (#24135, #1616) further portrays the broad scale of habitat use by individual animals. Caribou 24135 spent considerable time within Wabakimi Provincial Park, a 892 000 ha park based in part on caribou habitat values, but also spent a considerable portion of its life cycle outside of this patk. Movements of this caribou spanned a distance of over 90 km. Caribou 1616 similarly moved within an area approximately 80 km in diameter, and spent time both in Woodland Caribou Park (a park of 450 000 ha) and in the adjacent managed forest. These observations support the concept that caribou habitat cannot be managed solely within parks and protected areas, no matter how large, but must also considerable appropriate management of the adjacent landbase.

Caribou Habitat Management - The "Mosaic" Approach

The southern range of woodland caribou in northwestern Ontatio occupies both provincial parks and forest management units. These forest management units ate licensed for timber harvesting, and the expectation is that the entire unit will be harvested over a rotation period. A regional approach has been taken to caribou habitat management, so that caribou habitat requirements are considered during the development of forest management plans both within each management unit, as well as being coordinated across adjacent management units. Caribou habitat "mosaics" were developed to ensure long-range habitat supply in units scheduled for timber harvesting. These mosaics disperse timber harvesting across the landscape in a pattern somewhat similar to that created by wildfire, maintaining large tracts (100 km^2+) of mature conifer-dominated habitat and similarly allowing timber harvest in large ttacts of timber to provide for the provision of future habitat.

The development and implementation of these caribou habitat mosaics requires both a landscape perspective (i.e. across several management units), as well as long-term planning (i.e. over the rotation age of the forest - usually 100 yeats). Mosaic development includes consideration of current habitat use, habitat capability and suitability, operational harvesting concerns, forest age, composition and sttucture, and the existing degree of forest disturbance on the landscape.

Challenges

There are several major challenges associated with the implementation of the regional habitat management and conservation strategy for forest-dwelling woodland caribou.

While this approach emulates natural disturbance patterns more closely than traditional timber harvesting approaches, it is still only an initial approximation of natural disturbance patterns, and does not by itself address associated natural processes. Considerations such as forest succession and future forest condition must also be addressed during the development of operational forest prescriptions.

i) The potential for a change in forest composition to a higher hardwood component at the landscape-level is of significant concern from a caribou habitat perspective.

ii) The creation of major forest access road networks has no natural parallel, and these roads have indirect effects such as increased and permanent edge, enhanced predator access, continued human presence, etc. To optimize the probability for continued caribou range occupancy, access must be carefully planned and managed.

iii) There are operational limitations to the forest industry's ability to make the transition to a more dispersed harvesting pattern, and there are also implications to the available wood supply that lead to lower harvest levels. Any approach that attempts to manage on an ecosystem-based approach by spatially directing timber harvest will have similar effects.

iv) The caribou habitat mosaic requires long-term planning of forest harvest and renewal, but at the same time it must be subject to periodic review during each planning cycle (five years). Changes in forest disturbance, caribou information and new science will all be considered during the periodic review and refinement of these habitat mosaics.

v) Taking a landscape approach to caribou management is controversial, particularly when it means the creation of large disturbance patches as well as the deferral of large, mature tracts from harvesting. However, if logging is to occur within caribou range within the boreal forest of northwestern Ontario, it appears important that the logging disturbance patterns approximate as closely as possible those created by natural conditions.

Conclusions

The continued presence of woodland caribou within the managed forest is clearly a conservation biology issue, and requires significant adjustments to forest management practices. Given that woodland caribou use the forest at a landscape level, management practices must also be addressed at this level, as well as at the more site-specific level (e.g. protection of individual calving sites). The emulation of natural wildfire patterns appears to hold the best promise for maintaining current caribou range, while recognizing that local considerations, ecological processes and related impacts such as the predator-prey balance must also be addressed.

Continued monitoring of caribou habitat use and range occupancy will be necessary to determine the long-term success of this strategy.

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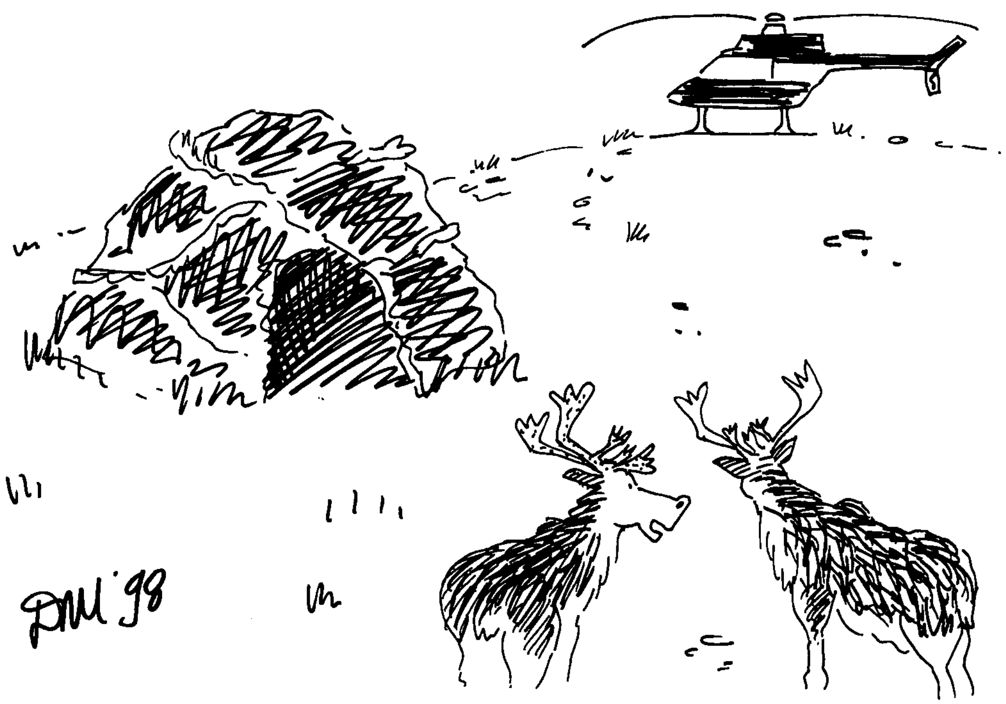
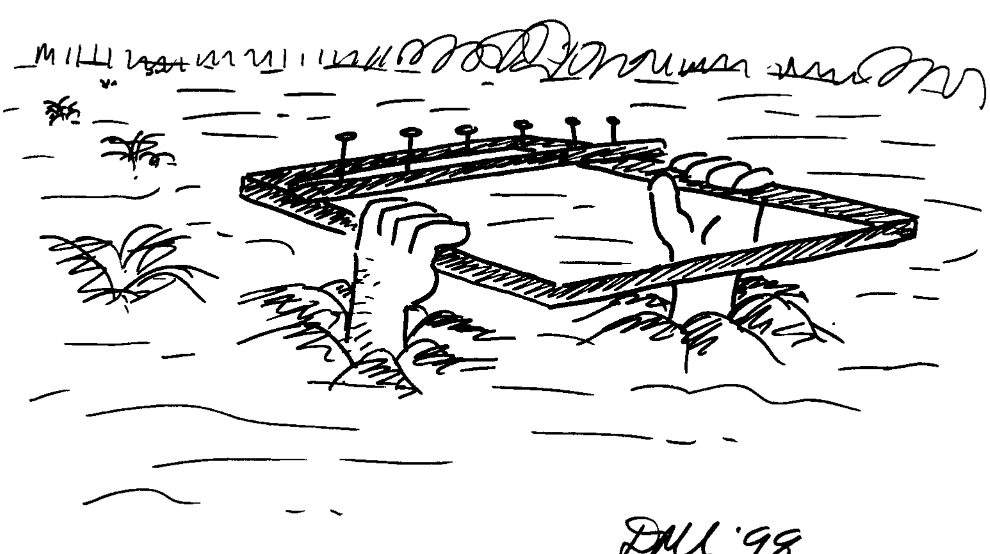
HUMANS ARE CHANGING RAPIDLY! MAYBE WE SHOULD STUDY THEM?!'



ACCESSIBILITY RATHER THAN RANDOMNESS DETERMINED CHOICE OF STUDY PLOTS



The ebb and flow of caribou in the high Arctic

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Abstract: Caribou (and reindeer), *Rangifer tarandus,* show a broad range of adaprability to varying habitats throughout the distribution of the species, from the southern limits of the boreal and taiga forests and intermounrain regions of North America and Eurasia to the northernmost lands in the Arctic. The caribou and reindeer and the muskox, *Ovibos moschatus* are the only two ungulate species adapted to life in rhe high Arctic. In the high Arctic however, caribou and reindeer live close to the limits of their adaptabilty to the extreme conditions present there and their populations are characterized by wide fluctuations, often culminating in local extirpation. Although the muskox may be somewhat better equipped to survive the climatic and associated vegetational extremes of the high Arctic, the extremely efficienr locomotive ability of caribou has enabled them to become established, during at least some portions of the Holocene, on virtually all of the high arctic islands, as well as the insular-like ice free portions of all of Greenland. Their often transitory presence in these extreme habitats appears tied to past periods of climatic change as well as short term climatic extremes. However, the arrival and successful establishment of caribou on rhe extremely remote arctic islands of Svalbard and Franz Josef Land 5000 and 4000 years ago respectively, required favorable climatic conditions for establishment and growth of forage plants, a population source from which they derived, and conditions permitting their long distance travel across the pack ice. The presence and dynamics of caribou on rhe Severnaya Semlya and New Siberian archipelagos have been the product of seeding by the large migratory herds on the adjacent mainland, favorable ice conditions in the straits separating them from the mainland, suitable climatic conditions on the islands, and the frequency of disruptions in their freedom to return to the mainland. Of crirical importance to the establishment and persistence of populations of caribou in rhese marginal habitats at such high latitudes has been the absence or low density of predators, including humans, and freedom from the physiological stresses of insecr parasitism and harassment common at lower latitudes. If the current patterns of global climate change continue, with greatest changes occurring in the Arctic, caribou in the high Arctic can be expected to respond through major distributional and population changes in relation to the regional variations that characterize arctic climate.

Permafrost, lichen, and woodland caribou: late-winter habitat use in relation to forage availability

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Abstract: Factors such as fotage abundance and predation risk may influence an animal's habitat use patterns at a number of different scales. On a large scale, woodland caribou (*Rangifer tarandus caribou*) in north-eastern Alberta have been shown to restrict their movements to within large peatland complexes during winter. It has been suggested that avoidance of upland habitats may be influenced by predation risk. No study has been done on finer scale habitat use within these peatland complexes. The purpose of this study was to determine if late-winter habitat use within the peatland complex is related to the abundance of *Cladina* lichen. Ir was hypothesised that peatland classes containing permafrost would have the greatest *Cladina* abundance and, therefore, be selected by caribou for feeding. We also predicted that telemetry locations would be closer to high forage areas than is expected by chance. Average *Cladina* ground cover was quantified for ten wetland types during the summer of 1997. Feeding sites were located by backtracking during the late-winter period from mid-January ro the end of March, 1997. The wetland class for each feeding sire location was derived from a digital wetland inventory using a GIS (Geographic Informarion System). The telemetry data analysed in this study was collecred during late-winter in 1995, 1996, and 1997. A corresponding set of random points was generated for each year. The distance to the closest habitat polygon with high forage abundance was calculated for telemetry and random points using a GIS. Vegetation analysis produced two habitat categories: 1) 'high' *Cladina* treed peatlands; and 2) 'low' *Cladina* open peatlands and non-peat wetlands. Contrary to our hypothesis, peatland classes containing permafrost did not have significantly higher *Cladina* abundance than other treed peatlands. Feeding site analysis did, however, show almost exclusive use of high *Cladina* habitats for feeding. In all years, telemetry locations were closer to high *Cladina* habitats than were random points. The distribution of high forage habitat within the peatland complex appears to be related to the pattern of habitat use. Future habitat use analysis will include a number of factors such as tree cover, habitat patch size, and stand age.

Crater site selection by woodland caribou of the Southern Lakes herd, Yukon: differential effects of congeneric lichen species

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Abstract: Caribou foraging during winter on snow-buried terrestrial lichens must locate resources by scenr and access them by digging craters. Previous research found that caribou select crater sites where the relative abundance of certain lichen genera is greater, and avoid cratering at sites where these genera are scarcer or absent. I expanded on previous research by proposing that congeneric lichens species have differential effects on crater site selection, and tested my hypothesis with data collected by snow-tracking woodland caribou in the Southetn Lakes Region, Yukon. Results supported my hypothesis. Cratering probability increased as the percent cover of *Cladina mitis* became gteater, but the percent cover of its close relative *Cladina rangiferina* had no effect. Similarly, cratering probability increased as the percent covers of *Cetraria islandica* and *Ce. cuculata* became grearer, but was unaffected by the percent cover of their close relative *Ce. nivalis.* The effects of *Ce. islandica* and *Ce. cuculata* are noteworthy because these species were as scarce as any taxa that did not affect cratet site selection (their maximum % covers were, respectively, 5% and 22%, and their 75% quartile % cover was 0). In addition to testing my hypothesis, I found rhat cratering probability increased as the percent cover of *Cladonia* sp. became greater, but was unaffected by the percent covers of *Peltigera* sp. and *Stereocaulon* sp. (field personnel could not identify these genera to species). Crater site selection was unaffected by variability in snow depth or penetrarion, which was not surprising given the shallow snowpack of the study area (mean and srandard deviation snow depth=31.5 (5.8) cm). I found almost no cotrelations among the percent covers of each lichen taxa, suggesting that the number of cratets a caribou must dig, and thus the atea it needs to search, will increase with the numbet of lichen species it is searching for. My results suggest that management decisions based on the distriburion of lichen genera, rather than species, could underestimate the amount of land that should be protected to ensure the long-term persistence of a caribou population. Also, protecting areas where *Ce. islandica, Ce. cuculata, Cladina mitis* and *Cladonia* sp. are abundant likely will contribute towards conserving the Southern Lakes herd, which is endangered partly because of habitat loss. Research needed to refine conservation recommendations includes comparative nutritional analysis of lichen species, addtessing the effects of species of *Cladonia* on cratering probability, and landscape-level analysis of foraging decisions and of lichen distributions.

Development and application of animal borne global positioning system (GPS) technology on woodland caribou

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Abstract: In 1996, a cooperative research and development project was initiated by Manitoba Hydro in cooperation with the Manitoba Model Forest (MBMF), Manitoba Natural Resources (MNR), the Univetsity of Manitoba Natural Resources Institute (MNRI), and TAEM Consultants. The research involves the testing of Global Positioning System (GPS) collars and mapping systems which have the potential to significantly enhance the efficiency of environmental and resource planning and mitigation. To date, over 8000 woodland caribou relocations have been logged and mapped into a Geographic Informarion System, and plotted on habitat maps of various scale and precision. Preliminary observations include; the identification of travel corridors between summer and winter range, habitat selection during various seasons, movement in relation to human disturbance, access and hydro lines. Ongoing testing of the system components is currently underway with future analysis being planned.

Seasonal range use and demography of the South Nahanni woodland caribou herd, southern Mackenzie Mountains, NWT and Yukon

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Abstract: Investigations of woodland caribou (*Rangifer tarandus caribou*) were conducred from March 1995-March 1998 to provide informarion on seasonal range use and demography of the South Nahanni herd (SNH) locared in the southern Mackenzie Mountains of the Northwest Territories and Yukon. Parks Canada developed and sponsored the three-year baseline study to address the concerns of local First Nations, encourage collaboration with Territorial wildlife agencies and acquire an enhanced understanding of the little known SNH. The Yukon Department of Renewable Resources provided technical support from rhe outset and in 1996/97 contributed funds for fall composition surveys.

To define seasonal herd range and movements, twenty-five adult female caribou were radio-collared on late winter range in March 1995 and relocated five rimes annually. These locations showed that the SNH inhabits a traditional winter range of approximately 4000 km-sq within and adjacent to Nahanni National Park Reserve. The herd is more dispersed in other seasons and its overall range covers approximately 16 000 km-sq located principally within the uppet South Nahanni Watershed of the Selwyn/Logan/Mackenzie Mountains. The majority of the SNH was found to migrate off winter range to calving, post calving, and fall rur areas northwest of the Ragged Range between the South Nahanni River and the NWT/Yukon Terrirorial Border.

A popularion census has yet to be conducted but is estimated to number 2000-3000 caribou (R. Farnell, Yukon Renewable Resources, pers. comm.). Annual survival of radio-collared adulr females averaged 0.81 during 1996 and 1997. The sex and age composition of the SNH was estimated from aerial surveys in October, 1995-1997. The adult sex ratio of adult males to females at that time avetaged 39:100 (range 32.0-47.0) and the calf:cow ratio averaged 21:100 (range 17.1-25.6). The calf:cow ratios over the three-year srudy period point to low recruitment and possibly an unstable or declining population. Both resident and guided non-resident hunters harvest the SNH but the extent of this harvest is not well known. Analyses of diet from fecal samples and snow depth/density resulrs from late winter crater surveys indicate that winter forage is not a limiting factor for the SNH.

Data collected thus far provides insighr inro the herd's identity, seasonal range use and demographic ttend but requires additional study for effecrive and informed management. The GNWT Department of Resources, Wildlife and Economic Development has committed to take a lead role in the further study and management of the SNH. Proposed srudy efforts include a detailed harvesr analysis and stratified population census on late winter range in 1999.

Status and conservation of forest-dwelling caribou in Canada

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Abstract: The World Wildlife Fund Canada believes that the conservation of foresr-dwelling woodland caribou in Canada may be promoted by the production of a national map showing their range occupancy and sratus across the country. The 'draft' map presented is a compilation of data collected for each provincial jurisdiction from available sources. This 'besr-estimate' representation highlights significant gaps. The mapping project undertaken by Northwestern Ontario is referenced as a case study of an excellent mapping strategy. Could this be the basis for a consistent approach to mapping the entire Canadian range of forest-dwelling caribou? The role of caribou as an indicator of boreal ecosystem health is raised. The importance of protected areas is visited along with the need for connecting corridors between protected areas and careful habitat management of the intervening landscape. Finally, the need for a national strategy of conservation is proposed and discussion regarding the formulation of this strategy is promoted. In this regard consideration is given to the best way of achieving consistency of approach while leaving latitude for adaptations to meet ecological variations.

Postglacial caribou remains preserved in snow patch in southern Yukon

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Abstract: In September, 1997 the first author noted a large concenttation of caribou (*Rangifer* sp.) fecal pellers and a caribou antler on a permanent snow patch in the Kusawa Lake area of southwest Yukon. There is little recorded local or traditional knowledge of caribou occurring in the area in the last 100 years (O'Donaghue, 1996). The snow patch is at 1830 m above sea level in a north facing alpine basin. It is estimated to be about 750 m long and 300 m wide and 3-10 m thick. The site provided the opportunity to investigate long term ecological changes that affect caribou distribution in southwest Yukon. Fecal pellet samples were collected from 18 surface sites around the snow patch. Several faunal samples, including a jawbone, long bone and small clump of hair were also recovered. An ice coring auger was used to obtain buried fecal matetial, to determine the age of the accumulation. Also tecovered at the site on the edge of the ice patch was the shaft of prehistoric wooden dart. Fecal, bone and hair samples were sent for DNA fingerprinting to the Universiry of Alberta ro confirm the samples to species. Fecal samples were sent to the Washington State Universiry for analysis of plant fragmenrs. Fecal caribou matetial recovered from approximately 1.6 m below the surface and a small portion of the wooden dart were sent to Isotrace Laboratories at the University of Toronto for AMS radiocarbon dating. An age of 2450 BP ± 50 years was obrained for the fecal material and the darr was dared at 4360 BP ± 50 years. These dates indicate that the formation of this alpine ice patch may coincide with a mid-Holocene cooling trend and that aboriginal Yukon huntets have been harvesting animals, presumably caribou, at this location for at least 4000 yeats. The dart fragment appears ro represent one of the few organic examples of atlatl technology (short spear propelled by a throwing board) ever found in Canada. These results indicate that the site offers a rare opporrunity to explore a number of questions regarding implications of climate change on caribou populations, prehistoric ecology of large caribou populations and high elevation archaeological sites. The site will be further investigated over rhe next couple of years after an interdisciplinary srudy design is developed.

Seasonal distribution and important habitats of Beverly and Qamanirjuaq caribou

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Abstract: The Beverly and Qamanirjuaq Caribou Management Board initiated a project in 1996 to identify areas of imporrant habitat for the Beverly and Qamanirjuaq caribou herds, and to produce documents and maps which will help the Board and orhers assess rhe potential effects of proposed land use activities on these caribou and their habitat. This work is being conducted with the support of Wildlife Habitat Canada and the Northwest Territoties Department of Resources, Wildlife, and Economic Development. The first tasks undertaken by the authot were: to compile available scientific information on the distribution and movements of the Beverly and Qamanirjuaq caribou herds; to enter rhese data into a geographic informarion system (GIS); and to produce maps of seasonal caribou ranges. Approximately 400 data layers have been incorporated into the GIS to date, including information from government surveys conducted between 1957 and 1994, locations of satellite-collared caribou from 1993 to 1997 (n=1793), and sites used by Beverly and Qamanirjuaq caribou to cross warer bodies (n=120). Furthet information from surveys conducted before 1966 will be added to the cuttent database, and traditional knowledge on caribou distribution and movements will be mapped when it becomes available. The Board is also preparing guidelines for assessing potential impacts of land use activities that could negatively affect Beverly and Qamanirjuaq caribou and their habitat. The tefetence materials produced by this project (e.g., reports, maps, CD-ROM) will make a large amounr of previously inaccessible information available to a wide audience, including the Board, government agencies, Aboriginal resource management boards, land use planning boards, industry, and the public. This information will assist efforts to ensute that adequate consideration is given to requirements for caribou conservarion across the range of Beverly and Qamanirjuaq caribou during land use planning, protected areas planning, and appraisal of the potential environmental impacts of land use activities.

Other papers

The following paper by Don Miller was presented, submitted, reviewed and accepted by the editors of the 7th North American Catibou Conference in Thunder Bay, Ontario. Revisions arrived too late to be included in those proceedings. We have included them in these proceedings as a courtesy to the Thunder Bay organizers.

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Lichens, wildfire, and caribou on the taiga ecosystem of northcentral Canada

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Abstract: Terrestrial lichens are unique organisms that are pioneers on bare sand and rock, survive desiccation and reproduce both sexually and asexually. They compete poorly with dense, aggressive vascular flora. Wildfires require organic marter as fuels, are the driving force in perpetuation of the Taiga Ecosystem in a heterogeneous environment and, if left alone, are self controlling. Caribou wintering on the Taiga are dependenr on: (1) a terricolous lichen forage supply for most of the winter, (2) a heterogeneous environment to cope with predators and the changing nival environment, and (3) natural wildfires to supply these needs. Wildfire control on the Taiga winter range is not tecommended as a management tool for barren-ground caribou.

Key words: caribou management, forage use, forest fire, *Rangifer*, snow cover, winter range.

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Introduction

Science is a search for ttuth, but it cettainly has been difficult to identify what is fact and what is fiction in the controversial subject of forest fires, lichens, and wintering barren-ground caribou on the taiga of northcentral Canada (see Viereck & Schandelmier, 1980). There was nothing wrong with the otiginal suggestion that forest fires on the taiga may have contributed to a rapid decline of caribou populations in northcentral Canada in the middle of the twentieth century (Banfield, 1954), and it certainly was proper to assign a range ecologist to the job of studying the relationship of forest fires on the taiga and the effect on declining caribou populations (Scotter, 1964; 1965; 1970). When Scotter reported an increase of forest fires in the taiga duting the middle of the present century compared with the previous century, and it's influence on the preferred lichen forage supply of caribou (Scotter 1964; 1966), there appeared to be a plausible cause for the population decline. Howevet, it was later reported that Scotter's hypothesis was incorrect because the method used to age forest stands on the taiga winter range of the Beverly caribou population was biased to recent forest fires (Johnson & Rowe, 1975). Johnson & Rowe reported that forest fires in the wintet range of the Beverly caribou population wete mostly caused by lightning and had not increased in recent years as a result of human caused fires, as proposed by Scottet (1964). They concluded that the carrying capacity of this winter range of the Beverly caribou population was much the same as it had been for centuries.

The barren-ground caribou populations in Canada continued to decline through the 1950s and had not shown any improvement by the middle of the 1960s despite an intense and costly wolf control program and a much reduced annual harvest of caribou by northern residents. In otdet to find some answers to why these catibou populations weten't responding to management efforts an intensive research program was initiated in 1966 on the Kaminuriak caribou population (renamed in 1989 the Qamanirjuaq caribou population). Four separate biological studies wete conducted simultaneously and cooperatively between 1966 to 1969 on this one caribou population that calves in the vicinity of Kaminuriak Lake, Northwest Territories and usually winters in the taiga of northwestern Manitoba, nottheastern Saskatchewan and southern Northwest Territories (Millet & Robertson, 1967). One of these four studies was on the taiga winter range relationships which revealed that caribou utilized a wide variety of habitats and winter forages associated with the changing winter seasons and nival characteristics on the taiga of northcentral Canada (Miller, 1974). Formosov (1946) and Nazimovich (1955) had reported similar nival characteristics on the taiga in Russia. Miller (1976a) reported that wildfires on the taiga were essential to maintain a heterogeneous environment (mosaic of environments in Heinselman, 1973) in which catibou could find suitable forage and escape habitat during any nival conditions they may be subjected to on the taiga duting winter.

At the conclusion of the Kaminuriak caribou population study, Millet was given the assignment by his employer, the Canadian Wildlife Service, to study the taiga winter range relationships of the adjacent Beverly caribou population with emphasis on the influence of wildfires. This paper includes both the second taiga winter range study, which was reported as a dissertation (Miller, 1976b) and summarized at the second International Reindeer/ Caribou Symposium (Miller, 1980); and the initial study of the Kaminuriak caribou population (Miller, 1974; 1976a). Essentially the results of these two winter range studies agreed with extensive studies in Alaska of barren-ground caribou (Skoog, 1968) and in Newfoundland of woodland caribou (Bergerud, 1971; 1972) that wildfires in the taiga did not appear to influence these particular caribou populations.

Duting the mid and late 1970s there were a number of important papers published on the incidence of forest fires and on the existing terricolous fruticose lichen flora in the taiga and adjacent transition zone (between taiga and tundta) in North America (Rowe & Scotter, 1973; Viereck, 1973; Johnson & Rowe, 1975; Makinow & Kershaw, 1976; Kershaw, 1977; Johnson, 1979, and others). A review paper by Kelsall *et al.* (1977) on the effects of fire made particular reference to northern Canada, and one by Viereck & Schandelmeier (1980) in Alaska and adjacent Canada. Klein (1982) in a review paper entitled, "Fire, Lichens and Caribou," concluded that there were long term benefits from fire on the taiga and short term consequences. Bunnell *et al.* (1975) reported on a computer simulation study involving Canadian Wildlife Service caribou biologists who had studied or were studying batten-ground caribou populations in northcentral Canada. They concluded that an increase of forest fires by five times the normal 1 percent per annum would have "little effect on the population."

In 1979, however, a reported 1 1/4 million hectares were burned in the taiga and adjacent transition zone of northcentral Canada and the caribou users requested forest fire control to protect the barren-ground caribou's winter range (Thomas *et al.*, 1996). As a response to this request another study was initiated on the taiga winter range of the Beverly caribou population in 1982-1986. As a result of this study a forest fire control program was proposed specifically for the taiga and transition area winter range of the Beverly and Qamanirjuag caribou populations (Thomas, 1994).

The scorching of the large acreage on the taiga and the transition zone winter range of the Beverly caribou Population, as reported in 1979, is not unusual for this area (Johnson & Rowe, 1975). In some summers, practically nothing is burned in this particular winter range area and the combination of these light burn years with the large burns of other years, like in 1979, average out to about one percent scorched annually (Wein & MacLean, 1983).

This paper attempts to show that these wildfires are an essential component in terrestrial lichen dominance of the ground cover in much of the taiga. Also using data collected in the 1960s and early 1970s on the taiga of northcentral Canada, it shows how wildfires vary between years, what portion of areas within the margin of the burned areas actually was ignited, and what role wildfires play in the perpetuation of tetrestrial lichens. Finally, also using field observations in the 1960s and early 1970s during the various winter seasons barren-ground caribou inhabit the taiga, it will be shown how caribou utilized both the burned and unburned habitats feeding on terrestrial lichens, arboreal lichen and non-lichen forage supplies in response to a continuously changing nival environment. The paper attempts to show how a successful wildfire control program in the taiga of northcentral Canada, as proposed by Thomas (1994), would ultimately teduce rather than increase the carrying capacity for wintering barren-ground caribou. And finally the paper concludes with a proposal that caribou managers need to monitor the effects of human population increase and activities in the taiga that can seriously threaten wintering caribou. Wildfire may briefly change how caribou use the taiga but people and their activities will eventually determine what portion of the taiga will be available for winter use by caribou.

Lichen Ecology

Lichens are unique organisms that dominate the ground flora in much of the taiga, especially on xeric, sandy soils. Most of the uplands in the taiga and transition zone of northcentral Canada is composed of a xeric, well-drained, pure sand mantel. (Ritchie, 1962; Argus, 1966) They are pioneer organisms that are in a symbiotic relationship between a fungal (mycobiont) and one or more algal (photobiont) components (Hale, Jr., 1967; Nash, 1996). The primary characteristic of lichens that permits them to dominate the ground flora in the taiga is that they can survive severe desiccation which destroys vascular flora and most other bryophytes.

Lichens dominate the ground flora in much of the taiga until an accumulation of organic matter with its moisture retention characteristics occurs on the surface of the sandy soils. This retention of water in the accumulated organic matter permits vascular plants to become established and thrive at the expense of the lichen flora.

Lichen woodland is what has often been referred to as the sparsely treed taiga stands on upland sites of black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*), eithet alone or in combinations, with a dominant ground cover of lichens. These are the lichen woodlands in the taiga that are important caribou feeding sites, in mid-winter especially. However, these are not the only sites where lichens grow in dense mats. They grow on hummocks in the lowland muskegs and also grow on the slopes and tops of eskers, which are often sparsely treed by white bitch (*Betula papyrifera*). These esket sites may be fed on all wintet, but especially the south exposed slopes and open tops are utilized by foraging caribou in late winter and spring when the sun begins to melt snow on exposed sites (Miller, 1974). Bare patches also appear in the snow cover on windswept openings and in feeding craters, previously excavated by caribou. The north and east slopes ate usually still unavailable for foraging at this time because of deep, drifted snow.

How do terricolous, fruticose lichens recover from disturbances like caribou cratering, foraging and trampling activity? Lichens are well adapted to this kind of caribou activity in the presence of a snow cover because of their characteristic of growing new podegia when fragmented or dislodged (see Webb, 1998). This is exceedingly important because it permits lichens to not only sutvive caribou feeding activity in winter, and man's foot steps when the lichens are dry and brittle in summer, but to become established on favorable substrate when transported by wind and water or by mammals, birds and insects.

Another characteristic about lichens that is of major importance to caribou-besides taste, nutrition and abundance - is the species or groups of species available for foraging. This involves the successional sequence following disturbance, such as wildfire. There are many wildlife biologists, ecologists and lichenologists who have reported on this subject, and many are good for areas studied. The best general description of the lichen flota in my opinion is by Ahti (1977), who has numerous publications on caribou range in North America (Ahti, 1959a; b; 1964; Ahti & Hepburn, 1967) and reindeer ranges in Scandinavia (Ahti, 1961a; b; Ahti *et al.*, 1968). Following is his general sequence of this lichen succession in the "Boreal Coniferous Zone" (Ahti, 1977) or taiga. (Ahti does not accept *Cladina* as a true genus and therefore uses *Cladonia*):

1. Bare soil stage, 1-3 years after fire.
2. Crustose lichen stage, 3-10 years after fire; *Lecidea oligotropha, L. uliginosa* and *L. granulosa dominant.*
3. Cup lichen stage, 10-30 (-50) years after fire; *Cladonia* subgen. *Cladonia* dominant (e.g. *C. cornuta* var. *cornuta*, *C. gracilis* var. *dilata, C. crispata, C. gonecha*)
4. First reindeer lichen stage, 30 (-50) -80 (-120) years after fire; *Cladonia* mitis, *C. arbuscula, C. rangiferina* and *C. uncialis* dominant.
5. Second reindeer lichen stage 80 (120) or more years aftet fire; *Cladonia stellaris* dominant.

Since I have included this lichen successional sequence verbatim from Ahti (1977, p. 165), I must also give his following statement:

"It should be noted that the timetable of this succession is greatly dependent upon the moisture regime and the climatic position of the stand, and different rates of succession may be encountered side by side (Jalas & Valpas, 1962)."

He also comments on "somewhat mesic lichen forests (recognized by a thicker humus layer)" that "there may be a stage of very dense, young forest, when lichens are temporarily in decline and even absent, although they appear again when the climax is approached." Ahti also states, in the same publication, that there is "...a *Stereocaulon paschale* stage in some continental areas, such as western Lapland (Ahti, 1961a) and northern Manitoba (Ritchie, 1959), but its ecological background is not well understood." This lichen species is discussed later under the heading of Caribou, Lichen and Non-lichen Forage Relationships.

Table 1. Area burned during a 16-year interval in northcentral Saskatchewan and during 12 years in northwestern Manitoba as determined from colored aerial photographs compared with previous panchromaric aerial photographs.

	Hectares land surface interpreted	Hectares burned	Years of aerial photography (# of years)	Annual burn (%)	Number of fires
Saskatchewan	575 687	63 411	1955 & 1972 (16)	0.7	41
Manitoba	982 701	19 230	1955 & 1967 (12)	0.2	47

The only othet characteristic of lichens that I want to discuss here is theit dominance of the ground flora as long as the moisture holding capacity of the substrate remains poor. When moisture holding organic material accumulates on the ground surface and within the lichen community - with time-leaf drop, decayed branch litter, wind blown debris, and animal droppings - othet btyophytes and vascular plants begin to invade and expand. Lichens lose their competitive advantage when the moisture holding capacity increases and usually do not again gain dominance until a major disturbance such as fire (wild or otherwise).

Forest Fires on the Taiga

The taiga winter range of caribou in northcentral Canada has evolved in the presence of lightning-caused wildfires. Johnson & Rowe (1975) in a study of fire on the subarctic wintering ground of the Beverly caribou population reported that 87% of the fires were started by lightning and burned 99% of the total atea burned. They reported that the recent burn rate of about 1.0% annually (fire rotation period of 110 years) is similar to historical times, and that fire is necessary to maintain this fire-dependent ecosystem. Viereck (1973) had reported the same reason for a vegetation mosaic in the taiga of Alaska as resulting primarily from past wildfires in the taiga of Alaska, more populated than northcentral Canada. Viereck commented on a 30 year period of fires from 1940-1969 that less than 30% were caused by lightning, but 78% of the acreage burned were from lightning fires. Both Johnson & Rowe (1975) and Viereck (1973) commented on the major acreage burned in the taiga as a result of a few large fire years that occur only occasionally over a span of low to moderate burn years.

In order to determine the actual area burned in a sample area of the taiga winter range of the Kaminuriak caribou population in northwestern Manitoba I had an area of 12 106 km² commercially photographed in 1967 with color positive film (Miller, 1976a). These colored aerial photographs were interpreted as stereo-pairs and compared with available black and white stereo-pairs photographed in 1955 (Table 1, from Miller, 1976b). A total of 19 230 hectares had burned in the 982 701 hectares, of land surface only, during the 12 year interval. The annual burn rate was slightly over 0.2%. This 12 year interval appeared to have covered a span of low fire years.

In a separate study of the taiga winter range, of the Beverly caribou population in northcentral Saskatchewan, I had a 7202 km² area commercially photographed in color and the stereo pairs were again interpreted and compared with the available 1955 black and white stereo pairs (Miller & Barnhard, 1973). The taiga in northcentral Saskatchewan included more upland portions compared with northwestern Manitoba (Table 2) and 63 411 hectares of the total land surface of 575 687 hectares had burned during the 16 year interval for an annual burn rate of 0.7 percent (Table 1). This burn rate, which only involves the land surface of the area photographed, agrees more closely to the burn rate of about 1.0 percent annually reported by Johnson & Rowe (1975) that included water surface areas. It is significant that 60 percent of the area burned in my study area between 1955 and 1972 occurred during a single year (one fire), which also agrees with observations reported by Johnson & Rowe (1975) and Viereck (1973). The 1970 fire

Table 2. Proportions of burns on uplands and lowlands relative to occurrence of these landforms in northcentral Saskatchewan and norrhwestern Manitoba as measured on colored aerial photographs.

	Uplands		Lowlands	
	Land surface %	Burned %	Land surface %	Burned %
Saskatchewan	80	78	20	22
Manitoba	55	67	45	33

Table 3. General caribou behavior and forage use relationships correlated with periodic changes in the snow cover on taiga ranges.

Season	Snow Condition	Movement*	Social behavior when foraging	Forage sites most used	Forage groups most utilized
Early winter	Shallow and soft, < 50 cm	M	Scattered in small bands, members (other than doe-fawn pairs) independent	River and lake shores Open canopy	Sedges, horsetails, lichens and shrubs
Mid-winter	Deep and soft, > 50 cm	M or S	Medium-sized bands, members dependent	Open conifer canopy close to tteeless areas	Terrestrial lichens and evergreen shrubs
Late-winter	(a) Deep, sun crust	S	Large bands, members dependent	Open and closed conifer canopy close to treeless areas	Arboreal lichens and deciduous shrubs
	(b) Depth diminishing, alternate crust and no crust condition	S	Medium-sized bands, membets dependent	Open canopy close to treeless areas	Terrestrial lichens and evergreen shrubs
Spring	Appearance of bare patches	M	Scattered in small bands, members independent	Open canopy on southern exposures	Terrestrial lichens and evergreen shrubs

* M=Mobile, bands migrating; S=Sedentary, bands not migrating.

that covered 38 404 hectares, included about 75% of the land area bounded by the periphery of the burn (Miller, 1980) and probably included some smaller areas that had burned between 1955 and 1972. This means that about 9601 hectares of land area within this 1970 burn remained as unburned islands (occlusions) within the periphery of the burn. These occlusions, which are a ready seed source for vegetation of the burned area and feeding sites of wintering caribou, are often included in the reported total area of the butn along with the water surface area when the periphery of the burn is used to calculate size of the burned area. In addition there is usually no distinction made in forest fire reports between upland and lowland areas burned. Lowland muskegs (bogs) and meadows (fens) often burn very superficially and are revegetated rapidly. The new growth of grass-like plants, forbs and shrubs on these burned sites is more nutritious forage, for a few years post fire, than the same forage plants on unburned sites. The favored mushroom forage of wintering caribou are also likely to be more abundant on recently burned than on unburned sites.

Caribou and Their Taiga Winter Range

The barren-ground caribou of northcentral Canada usually arrive on their taiga winter range in November or December and leave in late March or April (Kelsall, 1968). There is a complete snow cover on the taiga when they arrive and, except for portions of south-exposed banks and wind-swept esker and morraine ridge tops, there is a snow cover on their departure. During the eatly winter migration the caribou movements are not hindered by snow, they generally migrate over frozen lakes and rivers and freely move over treed and treeless terrain. As the snow depth reaches 50 centimeters (20 inches) in mid-winter the caribou mobility is restricted by snow (LaPerriere & Lent, 1977) and they travel more in single file when traveling inland from resting sites on frozen lakes and rivers to forage or move between lakes and rivers. Caribou forage in mid-winter close to their resting sites. As snow depths increase and drifts become deeper and more compact along lake and river shores caribou become more vulnerable to predation (Miller, 1975).

A sun crust forms in late winter, even in the major feeding sites of lichen woodlands, and caribou forage on deciduous trees and shrubs and arboral lichens above the snow cover as forage beneath the snow becomes unavailable (Table 3 from Miller, 1974: 753). Gradually, solar radiation during sunny days begins to expose bare ground, and forage plants on open south-facing banks, and windswept ridge tops as well as beneath the boles of exposed conifer trees. Caribou increasingly forage at these sites each sunny day. As the snow cover decreases and surface snow crusts soften with each sunny day, caribou start their migration from the taiga for their tundra calving grounds.

Caribou-Wildfire Interrelationships

Caribou use of recently burned sites differs from pre-burn use in response to changes in forage potential, covet and snow characteristics. During early winter, caribou migrate across these sites single file. In mid-winter, during deep, soft snow conditions, relatively sedentary bands use burns as treeless escape cover and as access to forage in adjacent unburned stands, probably in response to wolf harassment (Miller, 1975). It was apparent during my field work that unburned islands within burns also attract caribou as feeding sites in mid-winter and occasionally caribou feed in recent burns. Use of burned sites increases with time and vegetative recovery as these sites become mote useful as food sources. The rate at which terricolous lichens recover on burned sites varies according to many factors, such as severity of the burn, site characteristics, and weather, but generally good lichen standing crops appear in 30 to 40 years after the burn. Scotter (1968) showed that the appearance of usable stands of lichen standing crops was greatest between 31 to 50 years on his four taiga study areas in northcentral Canada. Bergerud (1971) reported that grazed lichen stands in Newfoundland were usually in stands 25 to 80 years after fire. I found that caribou had fed intensively on lichens in stands aged 35 to 166 years in northwestern Manitoba and northeastern Saskatchewan and 46 to 148 years in northcentral Saskatchewan (Miller, 1976a; b).

Caribou forage primarily on terricolous lichens on taiga winter ranges in northcentral Canada consuming living and dead portions of podetia, both ptimary and secondary rhalli of certain species, fruticose and foliose forms, and climax and sub-climax species. Large standing crop reserves of lichens are found on the taiga range of northwestern Manitoba and caribou damage to these reserves during a single winter are light (Miller, 1976a). Caribou and reindeer damage to terricolous lichen forage supplies occurs primarily through the action of trampling and pawing (Skoog, 1968; Pegau, 1968). Use of different portions of the taiga during a single winter (Miller, 1974) and between winters (Kelsall, 1968; Skoog, 1968) results in a form of natural rotation. Since light cropping of lichen pastures does not maintain lichen productivity (Skuncke, 1969), a fairly high stocking rate of caribou is desirable. Changes of snow depth, hardness and density (Pruitt, 1959), along with fluctuating ambient temperatures and wind velocities, help to disperse caribou over much of the taiga range within and between most winters. Even with high caribou stocking rates, it is unlikely that terricolous lichens could continue to dominate upland treed ranges without periodic disturbance by wildfires.

Under the present rate of wildfire occurrence, there is no justification for fire prevention and control for the expressed purpose of caribou management. *Cladina mitis,* probably the most important single lichen species utilized by caribou on the taiga of northcentral Canada, (Thomas *et al.,* 1996) is especially fire dependent (Ahti, 1959a).

Caribou, Lichen and Non-lichen Forage Relationships

Food habit studies of cratered sites, individual cratets and analyses of rumens collected during early, mid and late winter (Miller, 1976a) had shown that terrestrial lichens are an important forage of caribou on the taiga winter range, but lichens are by no means the only soutce of forage. Caribou can thrive without a winter forage supply of lichens according to reports in Alaska (Palmer, 1926; Murie, 1935; Skoog, 1968) and wild reindeer in Russia (Syroechkovskii, 1986). The use of non-lichen forage probably increases the digestibility of lichens (Scotter, 1964). Lichens alone have been listed repeatedly to be an insufficient forage to sustain caribou and reindeer for long periods of time (Druri, 1960; Ahti & Hepburn, 1967) although under protected conditions reindeer have been reported to do well on lichens alone (Palmer, 1926; Poijärvi, 1945). However, if for no other reason than abundance and availability, terrestrial lichens were the most predominant single source of forage utilized during the winter by both the Kaminuriak and Beverly caribou populations in northcentral Canada (Miller, 1976a; b). Thomas & Hervieux (1996) also reported tetricolous lichens to be the most important forage item of wintering barren-ground caribou from their rumen and crater samples collected during March in Northwest Territories and adjacent Saskatchewan. Russel *et al.* (1993) reported that terrestrial fruticose lichens also predominated in the winter diet of the Porcupine caribou herd in Canada.

Lichens of the *Cladina* group made up the bulk of the winter rumen contents and were also the most abundant found in the taiga winter range (Miller, 1976a; b). *C. mitis* and *C. stellaris* were the most abundant species in this branched group found at the study plots in northwestern Manitoba. Of the two species, *C. mitis* appears to be the most important as caribou forage (Scotter, 1965; Thomas *et al.*, 1996). Ahti (1959b) found this species in Newfoundland to be "a most abundant species owing to its rapid regeneration" and he believed it "to be the most impottant food-lichen of the caribou". *C. stellaris* on the other hand, is considered questionable as a preferred reindeer forage in Scandinavia and northwestern Manitoba (Scotter, 1965) while in certain areas of Russia (Kareev, 1968) it is "reindeer's main lichen fodder during winter".

There is a suggestion that *Stereocaulon* is a preferred caribou forage next to the *Cladina* branched group on the basis of its abundance in the wintet rumen samples and low occurrence on the taiga winter range. Although there is a possible bias in the rumen sample analysis data, in so far as *Stereocaulon* is easily recognized, the crater observations in April at Hara Lake, Saskatchewan, support the idea that it is an important late winter forage (Miller, 1976a). Steteocaulon recovers rapidly from caribou utilization ot mechanical disturbance at favorable sites. This lichen has a much higher protein content than *Cladonia* and *Cladina.* Kareev (1968) states that *Stereocaulon paschale* in Russia "is considered as a good fodder for young animals and, in certain cases, included among the fattening varieties of fodder plants".

The manner in which the terrestrial lichen forage is utilized by caribou is extremely important. Some investigators (Andreev, 1954; Scotter, 1964; Skoog, 1968; Pegau, 1968) suggest that the living portions of terrestrial lichens are nipped off by caribou and that the recovery from this utilization depends on the percent of the lichen tips removed. My observations do not agree with this (Millet, 1976a). During the early and mid-winter periods the entire lichen podetium, with the exception of the jelly-like layer, is plucked from the lichen community and ingested. This method of feeding on terrestrial lichens by caribou was observed at craters and was supported by rumen analysis findings. The dead portion of the lichen podetium and particularly the black portion of *C. rangiferina* is common in the rumens. Even the primary thallus, which is the portion of the lichen that is attached to the substrate, is common in the winter rumens. By utilizing the dead portion of the lichen podetium, as well as the living portion, the potential caribou lichen forage supply would increase by 100% (Scotter, 1963). During the latter part of the late winter period, however, caribou crop the top portions of lichens that are no longer protected by a snow covet and each night the exposed lichens become frozen to the substrate. Foraging at the snow free sites during early morning of sunny days permits caribou to remove the supple upper portions of lichen communities.

Arboreal lichens are also an important source of winter forage in the taiga winter range. In fact, in periods of extremely hard snow conditions during the early stages of the late winter period arboreal lichens may be very important. A number of investigators have reported that arboreal lichens are an important forage for caribou (Husrich, 1951; Banfield, 1954; Cringan, 1957; Scotter, 1971). Besides being more nutritious than the *Cladina* tetrestrial lichens the arboreal lichens no doubt help to retain a balanced rumen environment for the microorganisms during the period when terrestrial lichens are inaccessible. Scotter (1965) found arboreal lichens to be relatively abundant in the taiga winter range of northwestern Manitoba.

Grass-like plants are the major non-lichen forage utilized in the taiga winter range during the early winter period and are utilized during the late winter and spring as snow depths decrease. *Carex aquatilis* and *Equisetum fluviatile* are the primary grass-like plants utilized in northwestern Manitoba (Miller, 1974). *C. aquatilis* is the most abundant sedge in the "marshlands" of the area (Baldwin, 1953). This plant provides the richest reserves of "undersnow" green vegetation for reindeer in parts of Russia (Kareev, 1968) and is also considered especially important to caribou in Alaska (Skoog, 1968). *Equisetum* was reported as heavily utilized by wintering caribou at a site in northern Manitoba by Loughrey (1952), it is considered as heavily utilized in Alaska at all times of the year (Skoog, 1968) and as a good winter forage in parts of Russia (Aleksandrova & Andreev, 1964) where it is eaten when green as well as brown (Kareev, 1968). Russell *et al.* (1993) also reported caribou use of horsetails in certain habitats of wintering Porcupine caribou in Canada. Concerning the nutritious substances in *Equisetum* Aleksandrova & Andreev (1964) stated that "The ash is very rich in calcium, potassium, phosphorus and other elements of mineral nutrition". Baldwin (1953) listed *E. fluviatile* "as common and abundant on alluvium of the Cochtane River and silted bays of the larger lakes" in northwestern Manitoba.

In mid-winter and more often in late winter the major non-lichen forage items include evergreen leaves and deciduous stems. The leaves of *Vaccinium vitis-idaea* are the most utilized although large amounts of *V. myrtelloides, V. uliginosum* and *Ledum* spp. are also consumed. Scotter (1965) observed that the leaves were stripped from *V. vitis-idaea* in northern Saskatchewan and he thought that this may be an important source of protein in that caribou winter range. Skuncke (1963) attaches high significance to this plant as a winter forage for reindeer. Baldwin (1953) found *V. vitis-idaea* as one of the most common plants in the area he examined in northwestern Manitoba. Argus (1966) reported this plant as abundant in the area he studied in northeastern Saskatchewan. Kelsall (1960) believed that *Ledum groenlandicum* was actively sought by barren-ground caribou and Simkin (1965) reported that *L. groenlandicum* leaves were the most heavily used of the vascular plants in cratets dug by woodland caribou in Ontario. This plant is considered as "ubiquitous" in the taiga winter range by Scotter (1964; 1965) although I found that it was uncommon on well-dtained, sandy soils with little or no humus layer.

Deciduous stems make up a large portion of the non-lichen material found in rumens although differential digestion rates exaggerate the abundance of this forage (Bergerud & Russell, 1964). White birch and willow are browsed occasionally all wintet but especially during the petiod in late winter when a hard snow crust covers much of the inhabited range. Stems of *Salix* and *Betula* are listed as winter forage stems for caribou (Skoog, 1968) and reindeer (Herre, 1956; Andreev, 1954). Simkin (1965) listed that *Salix* sp. and *Alnus crispa* are utilized by woodland caribou in Ontario.

Mushrooms are another non-lichen winter forage which may be important in years of abundance. Entite, small mushrooms have been found in April caribou rumens and up to 10% of the contents in November rumens have been comprised of mushrooms (Miller, 1976a). Kareev (1968) states that reindeer in Russia "unerringly detect and dig out the snow covered shrunken and frozen mushrooms". He listed mushrooms as a valuable, nutritive and vitamin-rich fodder. Although mushrooms are not consumed by caribou in large quantities during the winter their high nutritional value (Latin, 1951) may be a very valuable supplement to a predominantly protein scarce, terrestrial lichen diet.

Discussion

I have attempted to show a relationship between wildfires and terrestrial lichen communities in the taiga ecosystem of northcentral Canada and how wintering barren-ground caribou benefit from each. It seemed from my data and observations that attempt to suppress wildfires on this taiga winter range as a caribou management tool (Thomas, 1994) was unwise. However, Thomas and BQCMB (1996: 345) explained "There is no justification for fire suppression based on the natural ecosystem, fire suppression capabilities, or caribou conservation," and that this proposed fire suppression model was "based strictly on the food and socio-economic requirements of local communities." This would appear to be a risky approach since Kelsall (1968) emphasized hunting mortality as the cause for the decline of barren-ground caribou in the middle of the present centuty, especially since the populations of indigenous people (caribou users) are increasing and expanding (Thomas, 1994). Perhaps a more long range approach would be to encompass the entire ecosystem instead of attempting to maximize a single species.

Although the vegetative environment on the taiga of northcentral Canada is relatively unchanged from what it has been for centuries there are indications that wintering caribou are being restricted from utilizing large portions of their former winter range by expanding human populations and activities in the taiga. In northern Manitoba, in particular, there has been a considerable amount of human activity since the late 1950s. Two modern mining communities have emerged, in the more southern portion of the caribou's former winter range at Lynn Lake and Thompson. In the more northern part of Manitoba, in the core area of the caribou's early winter migration, two settlements of indigenous people have appeated prior to 1982 at Lac Btochet and Tadoule Lake. The populations in the "user communities are doubling in 16-20 years" (Thomas, 1994) within the entire range of these barren-ground caribou populations. The influence of these human communities and activities in northern Manitoba, located in the path of early wintering caribou herd movements, may influence where these caribou spend the major portion of the winter.

Large wintering caribou populations require large units of uninterrupted range. Ordinarily these herds are on the move all winter and they are not known to utilize the same taiga range in successive winters. Some portions of the taiga are used infrequently, but this does not mean these ranges are less important to the population than mote frequently used areas. In an excellent publication on "Sensitive Habitats of the Porcupine caribou herd" (IPCB, 1993), the criteria used to assess the sensitive habitats was based on frequency of use. Therefore, this aspect of identifying critical, but little used habitats was not discussed. During unusual weather conditions, as occurred in the interior of Alaska in 1992 (Valkenberg *et al.,* 1996) two caribou populations wintered outside their normal range in black spruce north of Fairbanks. These occasionally-used portions of winter range may be essential to caribou populations.

The future challenge to caribou management and wildlife biologists is not how to increase the sustained yield of caribou (Thomas, 1994) or to favor optimal use of the range by caribou (Klein, 1982), but to identify and minimize the spatial conflicts between human and caribou populations. We need to recognize if and how caribou movements are being deflected and how best to hatmonize human and caribou spatial needs within both the caribou's winter and summer ranges. A start in this ditection is to read and digest Harrington (1996), who wrote about the human impacts on the George River caribou population. I would suggest, however, that Harrington's subsistence hunting comments need to be adjusted for taiga residents of northcentral Canada where communication, transportation and meat storage conditions have improved to both favor and encourage subsistence hunting. This means that some of Harrington's comments on commercial hunting need to be applied to existing conditions in northcentral Canada instead of his conclusion about subsistence hunting. Hopefully with a long term perspective and recognition of these dangers, caribou can be maintained both as a national resource and to meet the various needs of the tesident indigenous people.

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