Proceedings of the 13th North American Caribou Workshop
Winnipeg, Manitoba, Canada
25–28 October, 2010

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13th North American
Caribou Workshop

Sustaining Caribou and their Landscapes
Knowledge to Action

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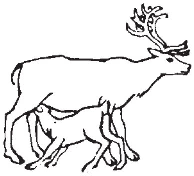

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Preface

The 13th North American Caribou Workshop which was held in Winnipeg, Manitoba, was a great success with more than 400 participants: people from Canada, the United States, Norway and Greenland, representatives from co-management and resource management boards across North America, First Nations, Inuit and Inuvialuit, governmental and non-governmental organisations, private companies, researchers, students and youth. The theme of the Workshop was *Sustaining Caribou and their Landscapes – Knowledge to Action* and the intent of the organizers was twofold: first, to provide participants with the opportunity to share scientific and traditional *knowledge* on different subspecies and ecotypes of *Rangifer* across the circumpolar North, the particularities of the different landscapes and land use management issues; second, to explore innovative ways to transfer knowledge to *action,* ensuring the long-term persistence of *Rangifer* throughout its range through the development of better governance structures, sound policies and effective communication.

The week began with several pre-conference seminars, including an Aboriginal Talking Circle facilitated by Walter Bayha (Délı̨nę First Nation) and Danny Beaulieu (Deninu Kue First Nation); a presentation on new statistical analysis to address correlation issues in habitat analysis organized by Nicola Koper (University of Manitoba); and a forum on the role of protected areas in the conservation of boreal caribou organized by Ron Thiessen (Canadian Parks and Wilderness Society).

The Aboriginal Talking Circle was remarkable both because of the large size of the audience (approximately 200 people packed the room in addition to the circle of invited speakers), and because it was the first forum of its kind in the history of the North American Caribou Workshop. Organized by Daniel Gladu (Centre for Indigenous Environmental Resources) and Deborah Simmons (University of Manitoba), and hosted by Albert Thorassie (Sayisi Dene First Nation), the Talking Circle provided an opportunity for aboriginal speakers to share experiences and ideas about caribou research and stewardship. The focus was on local or regional understandings of Aboriginal Traditional Knowledge about caribou, and how Aboriginal harvesting and stewardship practices relate to science-based research and management regimes. A number of key topics were identified during the day for more in-depth discussion at other Talking Circles later in the week.

As part of the main conference program, 75 abstracts were retained for oral presentations and 55 additional abstracts were presented in the form of posters. The conference began with a plenary session entitle *Knowledge and wisdom to assist with caribou management and land use planning efforts*; the session was chaired by Ovide Mercredi (current Chief of Misipawistik Cree Nation in Manitoba and former national chief of the Assembly of First Nations). This was followed by two symposia addressing key issues in barren-ground and woodland caribou management: *How does knowledge inform management decisions of barren-ground caribou?* chaired by Ron Thompson (Beverly and Qamanirjuaq Caribou Management Board) and *Innovative approaches to woodland caribou management*, chaired by Dennis Brennan (Manitoba Conservation).

The contributions of other participants were presented in different concurrent sessions on a wide range of topics on the biology and ecology of *Rangifer*, on approaches to management and conservation. The conference included a multi-media dimension, including telemetry data mapping demonstrations, a showing of the new film *EALÁT - People and reindeer in a changing climate*, and a presentation on the barren ground caribou sculpture by Peter Sawatzky. As well, there were opportunities to socialize at a banquet followed by a dance with entertainment by the local band Bullrush, and two interesting field trips. The conference concluded with a closing panel chaired by Ross Thompson, *Future directions for caribou research and management.*

The 13th North American Workshop brought together researchers and managers, Aboriginal peoples, politicians and advocates to remind us of the grandeur and complexity of the northern landscapes and the rapidly increasing amount of anthropogenic activities across the different regions. The unparalleled diversity of the contributions was reflective of an impressive commitment to sound *Rangifer* research and good management across nation and state boundaries – while also exposing the major challenges in such work. A key message emergent from the conference was that to be successful, caribou conservation and management require information from many different experiences and ways of knowing.

In conclusion, I would like to propose that to take advantage of the amount and wealth of information on the species – to understand how *Rangifer* will respond to a rapidly changing world and what can be done to ensure that animals continue to move freely across the North – we should strive for greater collaboration amongst disciplines in research and a greater involvement of the different knowledge communities in management.

And again, thank you to all who contributed to this most unique event.

Micheline Manseau

Western and Northern Service Centre Parks, Canada and Natural Resources Institute, University of Manitoba
Program Chair and Issue Editor for the Conference Proceedings

Organization

This workshop was organized by a steering committee chaired by Manitoba Conservation.

Workshop co-chairs:

- Jack Dubois, Director, Wildlife and Ecosystem Protection Branch, Manitoba Conservation
- Ron Missyabit, Director, Aboriginal Relations Branch, Manitoba Conservation

Coordinator:

- Kent Whaley, Regional Wildlife Manager, Manitoba Conservation

Committee chairs:

- Micheline Manseau, Ecosystem Scientist, Parks Canada and Associate Professor, Natural Resources Institute, University of Manitoba *(Program)*
- Dennis Brannen, Regional Caribou Biologist, Manitoba Conservation *(Program)*
- Bev Dubé, Executive Assistant, Manitoba Model Forest Inc. *(Registration and Financial)*
- Dale Cross, Regional Wildlife Biologist, Manitoba Conservation *(Sponsorship)*
- Vicki Trim, Regional Caribou Biologist, Manitoba Conservation *(Sponsorship)*
- Herman Dettman, Big Game Biologist, Manitoba Conservation *(Critical Path and Organizing Committee Secretary)*
- Christine Tymchak, Communications Specialist, Manitoba Conservation *(Advertising, Promotion and Venue)*
- Paul Galpern, PhD Candidate, Natural Resources Institute, University of Manitoba *(Website)*
- Fiona Scurrah, Senior Environmental Assessment Officer, Manitoba Hydro *(Social)*
- Ken Rebizant, Big Game Manager, Manitoba Conservation *(Volunteer)*
- Kelly Leavesley, Regional Wildlife Manager, Manitoba Conservation *(Field trip)*

Additional workshop organizing committee members:

- Trevor Barker, Wildlife Technician, Manitoba Conservation
- Matt Conrod, Forestry Modeling Specialist, Manitoba Conservation
- Vince Crichton, Manager of Game, Fur, and Problem Wildlife, Manitoba Conservation
- Jessica Elliott, Ecological Reserves and Protected Areas Specialist, Manitoba Conservation
- Brian Hagglund, Wildlife Allocations Manager, Manitoba Conservation
- Daryll Hedman, Regional Wildlife Manager, Manitoba Conservation
- Brian Joynt, Regional Wildlife Manager, Manitoba Conservation
- Stephen Petersen, Visiting Fellow, Department of Fisheries and Oceans
- Doug Schindler, Joro Consultants
- Deborah Simmons, Assistant Professor, Native Studies and Adjunct Professor, Natural Resources Institute, University of Manitoba
- Mark Ryckman, Population Ecologist, Manitoba Conservation
- Tony Viveiros, GIS Database Manager, Manitoba Conservation

Special thanks to Stephen Petersen and Paul Galpern for their work on the Conference Program and Carrie-Anne Lander for editorial work on the proceedings.

Pre-workshop seminars:

- Daniel Gladu, Centre for Indigenous Environmental Resources
- Nicola Koper, Natural Resources Institute, University of Manitoba
- Ron Theissen, Canadian Parks and Wilderness Society

Opening ceremony: Peter Sawatzky, a well known Manitoba artist, presented his work including the Fairmont Hotel sculpture, "Seal River Crossing", which portrays barren-ground caribou crossing the Seal River in northern Manitoba.

Plenary Session:

Ovide Mercredi (Chair), Walter Bayha, Chris Johnson, Philip D. McLoughlin

Session Chairs:

Dennis Brannen, Matt Carlson, Vince Crichton, Paul Galpern, Kelly Leavesley, Stephen Petersen, Charles Powell, Don Russell, Deborah Simmons, Ross Thompson, Vicki Trim, Doug Urquhart, Stephen Virc, Tony Viveiros, Bill Watkins, Kent Whaley, Bob White.

Closing Panel:

Ron Missyabit (Chair), Jack Dubois Anne Gunn, Micheline Manseau, John B. Zoe, Fiona Scurrah, Stephen Virc.

Issue Editor:

Micheline Manseau, Western and Northern Service Centre, Parks Canada and Natural Resources Institute, University of Manitoba

Issue Associate Editors:

Deborah Simmons, Native Studies and Natural Resources Institute, University of Manitoba
Dennis Brannen, Vince Crichton, Mark Ryckman and Jessica Elliott, Manitoba Conservation.

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Pre-conference Event

Talking Circle

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Overview by the Aboriginal Talking Circle Coordinating Team

Aboriginal talking circle: Aboriginal perspectives on caribou conservation

Deborah Simmons, Walter Bayha, Danny Beaulieu, Daniel Gladu, & Micheline Manseau

Correspondance: Deborah Simmons, University of Manitoba, 4915-48 St, Unit 23, Yellowknife, NT X1A 3S4 (simmons@cc.umanitoba.ca).

The 13th North American Caribou Workshop in 2010 was the venue for a remarkable forum of Aboriginal knowledge holders in which experiences and ideas about caribou research and stewardship were shared in a Talking Circle format. Facilitated by Danny Beaulieu (Denesųłıné/Deninu Kųę First Nation) and Walter Bayha (Délı̨nęgotı̨nę/Délı̨nę First Nation), the Aboriginal Talking Circle took place over a full day as well as a half day, totalling more than ten hours. At least thirty-six Aboriginal people contributed to the discussion, representing thirty organisations and nearly as many First Nation, Inuit and Métis nations. Delegates converged from a geographical area spanning caribou ranges in six provinces and all three territories of northern Canada.

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Coordination of the forum was led by Daniel Gladu of the Center for Indigenous Environmental Research (CIER). A key to the success of the event was the establishment of a planning team well beforehand, providing an opportunity for interested participants to provide input into the design of the forum. The Talking Circle format was settled on as a culturally appropriate way for Aboriginal people to share, synthesize and create new knowledge across cultures[1]. The proceedings were audio recorded, so it was possible to preserve and transcribe the knowledge shared. Each participant signed a consent form that defined the protocols for using the materials respectfully.

Members of the Talking Circle planning team (Micheline Manseau and Deborah Simmons) also participated in overall planning of the conference program, as well as editing of conference proceedings. This was critical in ensuring that guidance was fully conveyed about appropriate ways of situating Talking Circle within the conference, and providing other venues for Aboriginal participation and leadership at the conference.

The central location of the event was a major advantage, since it both symbolically showed the significance of the role of Aboriginal people at the conference as a whole, and facilitated the flow of participants and audience to and from other sessions. Contributions by Aboriginal speakers and audience members to presentations and discussions in other sessions often showed linkages with issues raised at the Talking Circle. Talking Circle participants (Walter Bayha and John B. Zoe) were invited to contribute to the opening and closing plenary sessions, further underlining the meaning and value of Aboriginal perspectives and providing a way for the conference as a whole to become aware of key messages leading into and following from the Talking Circles. The flexible and oral nature of the Talking Circle process allowed individuals to progressively develop narratives over several iterations. For several individuals who were also scheduled to present in formal symposia and panels (Walter Bayha, John B. Zoe, Joseph Judas and Danny Beaulieu), this made it possible for more fully

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[1] *For a discussion of Talking Circles in indigenous research methodologies, see McGregor, Bayha, & Simmons, 2010.*

Fig. 1. This map, created during the Aboriginal Talking Circle, shows the geographical spread of the participating speakers across Canada.

developed narratives to be woven together as papers for publication in the present conference proceedings.

There was a spiritual and historical aspect to the Talking Circle[2]. The sessions were framed by prayer, spoken by elders Albert Boucher (Łutselk'e Dene First Nation) and Moses Bignell (Opaskwayak Cree Nation). Ceremonial tobacco was passed, and the final prayer by Moses included a tobacco teaching. Danny Beaulieu introduced the ceremonial aspect of the Talking Circle with a story about the history of the Talking Stick.

The initial two rounds of the Talking Circle required a full day to complete. This relaxed pace allowed for a gradual process of relationship-building among the broad spectrum of Aboriginal nations, while providing a scoping of key issues in caribou research and stewardship. During the first round, speakers briefly introduced themselves. A projected Google Earth map allowed each person to map the traditional territory, caribou habitat and cultures that they had inherited from their ancestors in relation to all the others represented in the circle (Fig. 1). By the second round, participants had some understanding of the other members of the circle, so were comfortable to share a key story illustrating an interest or concern; this round was completed by the end of the first day. The third round allowed for some work in synthesis, reflection and analysis by participants, crystallizing where there was consensus, or where issues required further discussion or research.

There was general consensus that stories are an important means of preserving and sharing knowledge about caribou. There was also an emphasis on the role of language as a carrier of knowledge and meaning about caribou ecology, people's relationship with caribou, and the spiritual dimension of this relationship. At the same time, it was acknowledged that there are new challenges to be faced in interpreting Aboriginal knowledge in the context of environmental and social change. Through their stories, Talking Circle speakers all asserted the responsibilities of Aboriginal peoples as both knowledge holders and stewards of caribou; frustration was often expressed about the ways in which this role has been usurped by federal, provincial and territorial governments in the guise of science-based decision-making.

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[2] *For an overview of the spiritual dimension in indigenous ways of knowing, see Willson, 2008.*

One observation made by many in the circle was that the youth who are the future caribou stewards were for the most part absent from the discussion. The small number of youth who did participate were much appreciated by the older speakers, and remarks were often directed to them. An important lesson learned from the 2010 Aboriginal Talking Circle is that youth need to be part of the creation of new knowledge about caribou in order for traditional knowledge to remain alive and be carried into the future.

References

McGregor, Deborah, Walter Bayha, & Deborah Simmons. 2010. "Our Responsibility to Keep the Land Alive": Voices of Northern Indigenous Researchers. – *Pimatisiwin: A Journal of Aboriginal and Indigenous Community Health* 8 (1): 101-123.

Willson, Shawn. 2008. *Research is Ceremony: Indigenous Research Methods.* Black Point, NS and Winnipeg, MB: Fernwood Publishing.

Talking Circle Protocol

The following protocol was distributed to participants and audience at the Aboriginal Talking Circle.

"When you put your knowledge in a circle, it's not yours anymore, it's shared by everyone."
Douglas Cardinal

This forum will be facilitated according to a Talking Circle protocol. Talking Circles vary depending on who is leading the gathering, the purpose, and who is participating. This circle represents the voices of all participants from north, south, east and west, coming together to share stories about their relationships with caribou.

This Aboriginal forum is arranged in two rings according to the four directions. The inner ring is the Talking Circle where one Aboriginal guest from each participating nation is invited to sit. This person will be supported by neighbours and collaborators in the second ring. People in the outer ring are observers who are invited to listen throughout the day.

The Talking Stick in this circle is being used for the first time. Facilitators Walter Bayha (Délı̨nęgotı̨nę) and Danny Beaulieu (Denesųłıné) are responsible for guiding the circle, and will be stewards of the Talking Stick. The Talking Stick is a symbol of respect for the thoughts and stories of each person participating in the circle.

Whoever is holding the stick is welcome to speak, or they can decide to keep silent and pass the stick to the next person. All stories are respected equally, and there is understanding that stories are told without interruption. At the same time, speakers respect that all members of the circle need to have time to speak. The facilitators will signal if there is a need to think about time and the stories of others waiting to be shared.

Danny Beaulieu's Talking Stick Story

About twelve or fifteen years ago, a good friend named Jim Bourque walked from Yellowknife to Fort Providence, and later walked from Hay River to Fort Smith, a total of about seven hundred kilometres over the two trips. During the first journey, he got to Mosquito Hill near Behchokǫ̀, a hundred kilometres from Yellowknife. That hill is pretty steep. So he walked off into the ditch and cut himself a willow. He used that stick to walk the rest of his journey.

Eventually Jim gave the stick to the woman who became my partner, Susan Fleck, who is now Director of Wildlife for the Government of the Northwest Territories. She told me the story of the stick one day when I was about to throw it out. I carved the bark off it, and saw that it was a diamond willow. I made this talking stick with the bottom end of Jim's cane and an eagle feather, to facilitate a traditional justice workshop with the wildlife officers in the Northwest Territories.

Jim Bourque was a trapper, a hunter, and he became a wildlife officer. He was also the president of the Metis Nation at one time. He became the Deputy Minister of Natural Resources in the Northwest Territories. He was well known for his respect and support for Aboriginal hunters and trappers as stewards of the wildlife.

So this stick has history and value to some of the people in this circle. The only rule is that only the person who is holding this stick speaks. Nobody is going to start arguing, there will be no cross-talk in the circle.

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Special Communication

A giant step forward: Notes from the Aboriginal Talking Circle[1]

John B. Zoe

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I think for many First Nations and Aboriginal peoples in general, caribou are the foundation of their language, culture, and way of life in the areas that they live in. These are rooted in the landscape and knowledge accumulated over the centuries. Life was about co-existing with the animals in their habitat, and the relationship was spiritual.

Although caribou is a species of great importance to us, governments have failed to achieve balanced and sustainable development. Linked to this is a failure to engage with the Aboriginal inhabitants of this land in land management.

We know that governments have continually refused to recognize the original owners' knowledge of the land. At the same time they have used imported laws to encroach on natural resources. It is because of this history that many Aboriginal people have come to this conference with some scepticism about whether dialogue will make a difference.

But it was interesting and meaningful, I think, that in the Aboriginal Talking Circle we were using a talking stick that actually belonged to an Aboriginal person, the late Jim Bourque, who was a Deputy Minister of Renewable Resources in the Northwest Territories. He passed on many years ago, in 1996.

Many of the Aboriginal delegates are also survivors of residential schools who were denied their identities. Even so, we possess a deeply rooted strength to talk about the pressures affecting the woodland and barren-ground caribou. Many of the activities that threaten the existence of caribou were mentioned, such as development in mining, hydro development roads, deforestation, oil and gas development, tourism, and also the interventions of well-meaning preservation groups.

The Talking Circle is also about looking for Aboriginal perspectives on how traditional knowledge could be used to ensure that caribou continue to live on the lands intended for them. The Talking Circle provided many answers, but it will take time to peel away the layers of distrust, struggles, and identity theft before we get to the real core of the meaningful contributions that can be made to a forum like this.

We know that the North American Caribou Workshops have had a long history of holding an exchange of information every second year by the researchers that are knowledgeable in the field. But I came to understand that this 13th gathering marks the first time there has been large contingent of Aboriginal people taking part in it. This is a major step for the NACW as well as a giant step for the Aboriginal people who have participated and shared what they can in the short time that is provided in this forum.

It is also a big step to team up in learning how science can be integrated with traditional knowledge towards the continual survival of the caribou and its habitat. In the Aboriginal world as well as any other society, tradition is important. Tradition is what

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[1] *The following text is adapted from the closing plenary presentation by John B. Zoe, who shared a perspective on key messages from the Aboriginal Talking Circles.*

makes people remember sources of knowledge, and the tradition of learning and listening is an important source. We have to find some ways of ensuring that a tradition is established of inviting people that have potential traditional knowledge to the forum, so that we're actually creating knowledge together.

In the end it's about how as a society we can coexist with caribou in the complex, challenging, and evolving world that we live in today. In the end it's about trying to find some ways to affect policy, especially in the sharing of traditional knowledge. The concept of traditional knowledge has been slapped around over a number of years. But we need to find some way of applying it and experimenting with it seriously to try to make it a part of a bigger picture. Because like the art work that my friend Doug Urquhart presented earlier, it has a lot of a lot of meaning.

We can be sitting around the table in co-management processes, but it's no use if our special knowledge isn't recognized and used. One of the things that I've heard from elders is that we've been living with the caribou for centuries, and we have stories of how animals and people emerged from one another. So we as traditional knowledge holders are really the voices for the caribou. One of the things that were really emphasized in the Talking Circle was that all information should be used as a source of knowledge about how we can move forward. This is something that we're doing for future generations, not only on the traditional knowledge side but on the scientific. It's the collaboration and how we work together that really sets the stage for the next generation. So if there's habitat encroachment or other threats to the caribou in the future, at least we will have examples of how we're dealing with it today – if we're successful. I'm sure we will be.

One priority is to ensure that the next caribou forum has a similar Talking Circle event. I'm sure that the Aboriginal people that participated in this forum will be further strengthened knowing that we can bring some really knowledgeable people to the next forum. Máhsi cho.

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Plenary Session

Knowledge and wisdom to assist with caribou management and land use planning efforts

What are the different ways of thinking about the land, how are the recent advancements in landscape and population analysis contributing to our efforts, is the concept of landscape disturbance thresholds a useful concept?

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Using Indigenous stories in caribou co-management[1]

Walter Bayha

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Introduction

I was so happy when I learned I was going to be Chair of the Sahtu Renewable Resources Board (SRRB) and would be able to spend more time talking to people about wildlife. The SRRB is a co-management board, developed like others in the Northwest Territories (NWT) through the comprehensive land claims which were settled in 1993 in the Sahtu Region. The co-management board is a public institution. Half of the appointees are nominated by federal and territorial governments, and half by the aboriginal government. The board members do not represent the governments that nominated them; the board is not a political body. In order to make good decisions, institutions like ours have to be left alone, without political influence. The people who developed the land claims were very wise in setting the boards up like that.

People often think co-management is the answer to challenges in management. Yes, the co-management boards have powers. They have powers that are protected by the Constitution. We make decisions, but they're subject to change or modification, or maybe even rejected in some places. Although the co-management board is structured so that it is the main body that would make the decisions on wildlife in the Sahtu, the ultimate power over wildlife is not in the hands of the co-management board. The ultimate decision-maker is the Government of the NWT's Minister responsible for wildlife. But the only time the SRRB's decisions can be reversed is if they made a huge error in law or in process.

Co-management is a new beast. We haven't really seen it work to its full potential. The co-management board is a powerful institution, but it faces immense challenges. Our society is so complex today. You have the pro-development people, the people that are in the middle, the people that don't want development. They don't behave much different than people behave in the south. I have a son that's 12, 13 years old now. Probably he doesn't behave any different than kids in Toronto – more so today than any other time of our lives because of technology, the internet, television.

Dual lives: Harvesting and law in Dene Territory

The Sahtu Region where I live and work is a huge area. It's approximately 283 000 square kilometers. It is dynamic and diverse. We have mountains, boreal forest, tundra. We also have the biggest lake within the boundaries of Canada, Great Bear Lake.

For many years I used to be a wildlife officer. Here's the kind of things that happened to me when I became a game officer. I came back in May. In the NWT prior to the 1980s, we still had a law called the Migratory Birds Convention Act that prevented

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[1] *This paper is adapted from the author's plenary presentation at NACW, as well as the Barren-Ground Caribou Symposium presentation entitled "Barren-ground caribou management in the Sahtu region: bridging traditional knowledge and science," and contributions to the NACW Aboriginal Talking Circles.*

Aboriginal people from hunting in the spring. At least in the NWT, May is the spring. But my people hunted anyway. I hunted, we hunted, and May has always been the time that we hunt migratory birds, that is what we eat in May.

So I came home in May in a brand spanking new uniform. I wanted to see my mom. I hadn’t seen my mom for a while. I knew she was around because I could smell the geese boiling. Boy, you know, with the wind blowing towards me I could smell the geese cooking five hundred yards away. She didn’t know I was coming, but somehow through the window she noticed me coming in. So I came in and I hugged my mom and I said, “Mom, where’s the geese?” She said, “No geese. Don’t have any geese.”

I said, “What do you mean, Mom? I know, I smell it. We eat geese all the time.”

“No, no, no,” she said. “You can’t eat geese.” See, right off the bat, the uniform. I can’t eat. I’m a Dene, I want to eat geese. She says no, you can’t do that.

I remember those days very well. The priest spent a lot of time in our homes, the Hudson Bay people, and certainly the police. I was taught not to ask questions. But I should have asked, “Grandfather, how come you behave different when the RCMP and the priest are around?” Because they lived dual lives. They behaved the way the RCMP wanted them to behave. The way the priest wanted them to behave. This is the way the Dene people are. They try to respect and respond to people. And then they are themselves when these people were not around.

So people would hide who they really are when I was around in my uniform, even though I was Dene. But when I asked them if they knew anything about the Wildlife Act, or the Migratory Birds Convention Act, or the Environmental Protection Act, they would say, “No, why should I? They’re not my laws. They belong to somebody else.”

We used to deal with wastage a lot. So I thought, my people had ways of dealing with this. I asked the question, how did they deal with that in the past? How did they do that before contact? So one year I got some money to do some clean-up. At the same time I was talking to people and trying to understand how my people, the people of the Sahtu, Sahtúgot’ı̨nę is what we call ourselves, how they dealt with wastage. Well, by the time the project was over I learned that they didn’t have any waste. All the waste we found was cans, things that didn’t deteriorate. With aboriginal people prior to contact they didn’t have any waste. They used everything. Whatever was left was scattered by animals and disappeared. I’d never really thought about that at the beginning, when I first asked that question.

It really scared me the first time I had to deal with a grizzly bear. I was just a brand new game officer working with a guide, and we were trying to scare the bear away from my grandfather George Blondin’s camp. That was the first time I had to do that. When I grew up I didn’t have to scare bears away. My grandfather had taught me, if there’s a bear, you go somewhere else. It was midnight, it was cold, I think it was late October. I could hear the grizzly bear chew and crack solid bones. You know, femur of caribou. You could hear it two miles away. I said, gee, maybe I shouldn’t go over there. I should leave him alone. When I resigned from the Wildlife Service I said, I’m never going to shoot another bear again unless I’m going to eat it. And I think that’s one of the reasons I have a journey today. A journey to become a human being, a true Dene.

Becoming Dene

One day my dream would be to write a policy in my own language and let somebody else interpret. I think my days of interpreting are going down steadily. I’d rather just talk my language these days and leave it at that. As an officer I used to do a lot of judging. I was trained to do that. After I left the Wildlife Service, my wife said to me, “How come you don’t ask those questions anymore?” I said, “I don’t have to. I don’t need to. I just want to be a Dene, like the wildlife out there. Continue being a human being.”

As a Dene person I’m taught to listen, to respect people, especially in learning centres because those are like my grandfather. I was taught never to ask questions. I don’t, out of respect. We don’t do that today anymore. The first thing I learned in school was the word “why.” I can think right back when I was growing up as a small child there was no word “why” or “what for.” I had to learn very quickly that if I’m going to be a human being in the future, then I’m going to have to start behaving so that my people will live.

Our history is written on the land, in the placenames and the stories, in the language. It’s so important. Our people are disappearing very quickly. The place I come from, the Sahtu Region, I think they only have maybe three or four hundred people that speak the language. And unless you speak the language, you will not fully understand the stories. I’m always searching for stories. That’s where our knowledge comes from. That’s how knowledge in my area is passed on.

William Sewi was quite a storyteller. I remember him from when I was a young boy, because he spent a lot of time with my grandfather. I used to listen to

Fig. 1. Meeting of caribou and wolves. Credit: Alfred Masuzumi.

his stories many, many, many years ago. But when I went to school, when I started going to college and spending a lot of time in the south, I really didn't think about these stories anymore.

George Blondin is another grandfather of mine who taught me many things. He is one of the few people who made me understand that you have to break protocol, even if you love your people, so that you can survive in the future. George used to tell me that he wasn't going to write stuff down. The elders and his forefathers didn't want to do that. But he when he became older he did begin to write. One of the books that he wrote was *When the World Was New.* I think the other one was probably even harder for him to write, it was called *Trail of the Spirit.* These books had a lot to do with traditional "medicine power" and our Dene spirituality. George broke a lot of protocols with his elders and that was a huge decision for him. Those kinds of decisions make things easier for me to talk to an audience like this, interpreting the stories in new ways for the present context.

Story of a meeting

William Sewi tells this story. William is an elder who died probably 10 years ago. I've been listening to a recording of his story. It's too bad that I couldn't let you listen to the original recording of the story and then you can tell me what you think about it. But I have to translate it. In preparation for this conference, I played the recording for the Délı̨nę Renewable Resources Council members, and we discussed the meaning of the story. William uses terms that I don't even recognize. The story goes on for about half an hour. It's about caribou and wolves, when the world was new. William talks as if the caribou tells us that the animal relationship with the land was the same as the relationship people have with the land.

The way William tells the story goes back thousands of years. He authenticates it. He said this is the truth. We must tell it that way. It is real. It happened when the world was new. He tells us where the gathering took place, using a traditional placename, ʔenake Túé – which I believe may be the lake known in English as Dismal Lake[2]. Then he relates this place all to the earth and the universe, where it fits in the ecosystem – the relationships among living things. William spends a couple of minutes just explaining how the story is the absolute truth that he knows. I think that gives you an idea about how oral knowledge is passed on. This is how they do it.

The story goes like this: The caribou and the wolves had a gathering because there was an issue. When the caribou came to the land, the wolves didn't appreciate that. They wanted to stop the caribou from coming to this land. They wanted the caribou to leave the land and the earth. After the wolves had their say, the caribou took their turn. They said, "We've come to this earth as food, and nothing else. We are a very good source of food for you wolves on this earth." And then they said, "Is there a reason somebody doesn't want us here?"

This meeting went on and on and on. There were probably other animals at the meeting. There are different ways they tell the story. Eventually one of the wolves spoke out and supported the caribou. He said, "What they are saying is true. They tell the truth. They're food for us. They're food for us in the future." He stood up and all the other wolves stood up and supported him. And they all said, "The caribou tell the truth. They are food for Dene, food for the animals that feed on them."

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[2] *George Douglas gave the English name to this lake. The Dene name means "one with two parkas," likely referring to Qitirmiut (Copper Inuit) who followed the caribou from the arctic coast.*

The Dene have the greatest respect for harvesters, and for food. The story is telling us the meaning of the relationship between the wolves as harvesters, and caribou as their food.

My grandfather taught me that you start developing relationships with everything from the day you're born. Even prior to that, while you're still in your mother, you start developing relationships with things. You learn. You begin to see what happens. You begin to see things that are talking to you, because everything has to be alive for us to have relationships. Whenever you want to meet something, whenever you want to build a relation or start one you say hi, hello. The Dene people do it by giving something. I've learned that very well as a child.

There is the big relationship with caribou and wolves. I'm sure as biologists and wildlife managers we're all aware of that. I knew that from the day that I first ate caribou.

At first the wolves didn't want to have anything to do with the caribou. You see that so often today. The new initiative. Or maybe something that's different. New knowledge systems. People hesitate. They dismiss things. If it's not in the learning systems that we have, the universities and all of the learning systems that we have, we dismiss them. I did that. I'm talking about myself. I used to dismiss a lot of these things and not think very much about it because I never really, I guess the knowledge system that I was involved in did that.

It took me about 32 years to understand what my grandfather was talking about. When I was a young man, my grandfather said, "You're not going to listen to me in the future, you're not going to use these things in the future." And he's right. I didn't. It's only when I turned about 50 when I asked the question, "Who is a Dene? What is a Dene?"

But after listening, the wolves changed their minds. The wolves changed their minds. They realized that the caribou are their source of survival, their source of wealth. In ancient times, the amount of fat, prime meat, fish, would determine how rich a Dene person was.

This story could apply to so many issues we are faced with today, and how they might be resolved. If we're going to survive, then we have to do things very differently in the future. At the meeting in William's story, all the stakeholders have a fair share of input before final decisions are made. I think we strive to accomplish that with our co-management system in the NWT. We have hearings, and make decisions based on consensus. Lots of people are questioning, "Is it the right road we're on?" But I haven't seen another management system that tries so hard to support all the stakeholders to have a voice in the process.

When I started working with the wildlife service, one of the things I realized right away with my people is that they learn things from caribou by observing. There's no other way. I can't go up to a caribou and ask him, you know, how do you feel today or what do you think about all this development? You have to watch, observe, note behaviour. Our people have been doing that for thousands of years. Where do you find the caribou? In the stories, on the land. And in observing caribou, we learn something about what it means to be Dene.

There is an island called ʔek'a Du. Every year, some bulls always stop there. For some reason they don't follow the rest of the herd in their yearly migration to the calving grounds. They stay there all summer. If they don't get hunted by the Dene people then they continue on south in the fall time to join the rest of the herd. There's something special about these caribou that stay there, there's something special about the island, it must provide some kind of habitat that's not available elsewhere. People shoot those caribou in August when they're very fat. On that island I've seen big bulls with maybe two inches of fat. And so, ʔek'a Du means Fat Island. But it also means a place of wealth. In the old days, even though Dene didn't have money, if he had a lot of fat he was considered well off. Fat animals, prime, good to eat, he's rich. So the name of that island speaks not only to caribou ecology, but also to the nature of Dene well-being.

During our Aboriginal Talking Circle at this conference, I was really trying hard to get stories from everybody. We had many different First Nations there and they all had stories. They identified their story and they knew about that story. I'm going to try to use this method in the way I do things as Chair of the SRRB, the way I do things in the communities.

We have to pass a lot of this information on to our young people. One of the reasons I'm doing this is because I want to pass those stories on. We don't have time like in the days of my grandfather. If I had my way I'd be out back on the Johnny Hoe area trapping with my grandchildren, and leave the rest of the world to somebody else.

From stories to policy

Our new co-management system is created by law and gives Dene rights to participate in decision-making, but it doesn't tell you what you're going to do tomorrow.

We never have enough time. Here I'm talking to a lot of people and it's still not going to be enough time to try to be comfortable with bringing knowledge back to your communities. The stories are one way of preserving the knowledge. As we gradually learn the meaning of the stories over time, we bring the knowledge alive in the present. In this way, our stories can become our policies for wise wildlife management again.

But it's not quite that simple. As a young game officer, and even when I became Chair of the SRRB, I was naïve, thinking that things would be simple if I went back to my people and this is the way they do things, we'll just write it up and we'll put it in law and it will work. I'm thinking, boy, here's my chance to talk about traditional knowledge, develop policies, all these beautiful things that I'm dreaming about. Well, it didn't work. I'm still trying.

One of the reasons it's so difficult is because the Dene culture, their whole system, their worldview is different. It doesn't work the same way as the federal and territorial legal systems. Their laws are different. Imagine trying to take a set of laws, like even as simple as wastage, the same way that Dene people think about it, and stick it into the Wildlife Act. It won't work. We tried it. The federal/territorial legal systems don't allow for the existence of protocols that don't fit. The lawyers would say no, we can't do that.

Part of the challenge is that things have changed. In the Sahtu we talk about five communities, all kinds of different hunters: resident hunters, people that hunt from outside, and you have to sort all of that out. There's more and more information to include. So we need to have a process. You want to do good work and you want to include everybody's comments then things slow down. As information comes in everything slows down. Answers, making decisions is not as easy as it looks when you want to include all of the information that comes in. Decisions are made with papers in front of you, the information. Already you see the issues with our own aboriginal people. It's not easy for them to bring their oral history into the board rooms. It's not as easy as it seems.

This is why I'm so dedicated in trying to get these policies from stories. If those stories get in front of us, they could be included as part of the process, part of the information that we use in decision-making. That's so important.

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The 13th North American Caribou Workshop
Winnipeg, Manitoba, Canada
25–28 October, 2010

Thresholds or intractable complexity – Is there a middle ground for effective conservation and management of wild *Rangifer*?

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A disturbance threshold is an appealing idea for resource and conservation professionals focussed on the long-term persistence of wild *Rangifer*. If achievable, limits set on development can greatly simplify planning exercises at the scale of landscapes and tactical decisions at specific resource development sites. Contrarians state that the complexity of caribou-environment-human relations makes thresholds a naïve construct at best and at worst a science and management target that could impede effective conservation and management. Using examples from my research, I argue that the threshold concept has value, but that it should not be the end-point for understanding and managing the impacts of anthropogenic developments. Thresholds are valid when revealing the point at which small-scale development activities result in trivial impacts. However, the state of our science and the values at risk will prevent the meaningful application of thresholds to the understanding and maintenance of long-term population and distributional dynamics. In these cases, mechanistic and participatory approaches, although expensive and time consuming, are the best route to more effective conservation and management decisions. Thresholds are potentially one part of a larger discussion on how we manage the environment for *Rangifer*, not the stop point in a technical exercise designed to identify levels of development activities.

The 13th North American Caribou Workshop
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Uniting population and habitat analysis to better manage ungulate populations

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Long-term study of population demographics (survival and reproduction), combined with monitoring programs of movements and habitat use, allows us to link the environment that animals experience to their population dynamics. By an animal's "environment", I mean not only the habitat in which an animal is found, but also modifiers of habitat quality including important ecological processes such as competition, predation, and trends of disturbance and ecological succession. This information can be important for identifying "critical" habitat for species: components of habitat that can explain the greatest amount of variation in population growth under different ecological conditions. For example, we might be interested in identifying vegetation associations that can be expected to best promote survival and reproduction when a population is at its lowest (most critical) density. I present examples of such analyses for red deer, roe deer, and woodland caribou, and highlight applications for improving wildlife management.

The 13th North American Caribou Workshop
Winnipeg, Manitoba, Canada
25–28 October, 2010

Symposium

How does knowledge inform management decisions of barren-ground caribou

The 13th North American Caribou Workshop
Winnipeg, Manitoba, Canada
25–28 October, 2010

Barren-ground caribou management in the Sahtu Region: Bridging traditional knowledge and science

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The title of this symposium poses a question that until recently was very simple to answer in the Northwest Territories. In pre-colonial times, indigenous people used their stories and experience to maintain respectful relations with caribou so that they would continue to return as a food source every year. There were stories prohibiting the kind of control over caribou implied by the term “management.” Along with the arrival of the Federal and Territorial governments, scientists came to play an important role in establishing the core knowledge base for caribou conservation. Now following the land claims, the creation of co-management boards, and the establishment of traditional knowledge policies, decision-makers are required to draw upon both science and traditional knowledge. The Sahtu Renewable Resources Board initiated our first caribou traditional knowledge study in 2004, and established our traditional knowledge policy in 2008. However, we are finding that combining the two is not as simple as we had expected. There is a strong will to find a way to bridge Dene/Métis and scientific perspectives in a number of areas where we are finding differences. Dene/Métis harvesters and elders are aware that conditions for caribou stewardship are not the same as they once were. Climate has changed, habitat has changed, and our societies have changed. In this changing context, is traditional knowledge still relevant in the Sahtu Region? If so, how?

The 13th North American Caribou Workshop
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Co-management of the migratory caribou herds in northern Québec: The perspective of the Hunting, Fishing and Trapping Coordinating Committee

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Introduction

Aboriginal people have a long relationship with caribou, and caribou - especially the large migratory herds- cross aboriginal territories and jurisdictional boundaries. These two points are key to understanding the intricacies and complexities of managing caribou. Two of Canada's largest herds occur on the Ungava Peninsula. The peninsula stretches about a million square kilometres lying between James Bay, Hudson Bay, and the Labrador coast. Aboriginal people have been living and hunting caribou there for about 6000 years (Bergerud *et al.*, 2008).

Aside from small woodland caribou herds present in the southern portion of the territory (50th to 54th parallel), the Ungava Peninsula is the annual range of the Torngat Mountains herd, and two migratory tundra herds: the George River herd (GRH) and the Leaf River herd (LRH). Together the two herds once numbered one million animals (Couturier *et al.,* 2004). The annual ranges of the GRH and the LRH overlapped when the population was increasing and their ranges expanded in the late 1990's (Couturier *et al.*, 2009a; 2009b). The annual ranges of both herds are now separate -the range of the LRH has retracted from the southern limit of its winter range, and the GRH has moved in an easterly direction, with a majority of the range now in Labrador (Fig. 1).

The James Bay and Northern Quebec Agreement (JBNQA) (Anon., 1997) was signed in November, 1975 to facilitate the Province of Québec's plans to develop the La Grande hydro-electric complex in the James Bay area. It was hailed at the time as the first modern-day treaty in Canada between a government and one or more native peoples, and was to serve as a blueprint for agreements signed in subsequent years. The signatories of the JBNQA are the Crees of James Bay, the Inuit of Northern Québec, and the Governments of Québec and Canada. The territory described in the JBNQA (Fig. 2.1) and the Northeastern Quebec Agreement (NEQA) (Anon., undated) (Fig. 2.2), otherwise known as "the Territory", covers the greater part of Northern Québec. The JBNQA and NEQA touch on a variety of domains, including land regimes; local and regional governance; health and social services; education; the administration of justice; policing; and hunting, fishing and trapping rights, etc.

Section 24 of the JBNQA establishes the Hunting, Fishing and Trapping Coordinating Committee (the HFTCC). The Naskapis from Schefferville negotiated

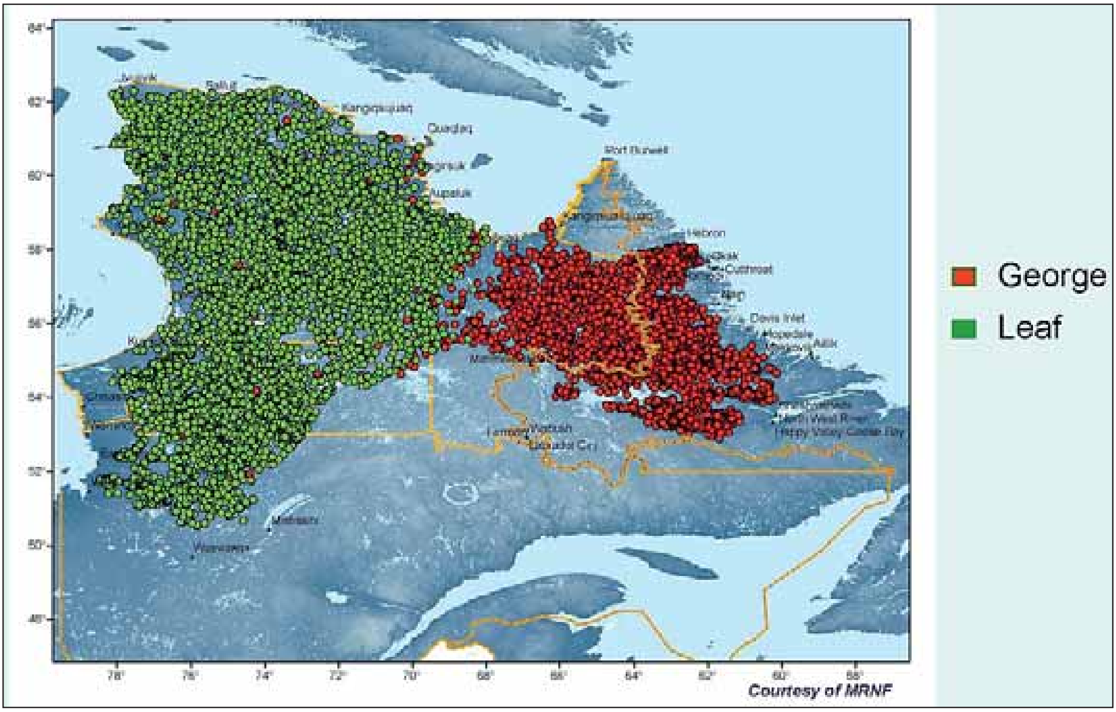

Fig. 1. Annual ranges of the George River and Leaf River herds in Quebec and Labrador between 2006 and 2009.

the NEQA, signed in 1978, and thereafter joined the HFTCC. As most explorations into the unknown, the HFTCC's make-up proved to present drawbacks that the design of later co-management boards attempted to correct. This paper's objective is to inform about this long-standing co-management committee, to summarize how it is involved in the current management of the GRH and LRH, and to reflect on the lessons drawn from its experience.

The hunting, fishing and trapping regime

The provisions of the JBNQA and NEQA establish three broad land categories in terms of tenure and governance, as well as hunting, fishing and trapping rights. Within Category I and II lands, the Native people have the exclusive right to hunt, fish, and trap; although they may authorise other people to hunt or fish within Category II lands. Within Category III lands - the greater part of the Territory - Québec residents are entitled to hunt and fish in accordance with provincial legislation and regulations concerning public lands. However, the beneficiaries of the Agreements enjoy the "Priority of Native Harvesting" (to be defined later in this paper) in Category III lands, as well as the exclusivity of trapping.

The JBNQA creates a Hunting, Fishing and Trapping Regime with specific rights for the beneficiaries of the Agreements. The Regime is subject to the principle of conservation, defined as "the pursuit of the optimum natural productivity of all living resources and the protection of the ecological systems of the Territory so as to protect endangered species and to ensure primarily the continuance of the traditional pursuits of the Native[1] people, and secondarily the satisfaction of the needs of non-Native people for sport hunting and fishing". This Regime applies fully in the "northern zone" (north of the 50th parallel) and it applies with certain exceptions in the "buffer zone". In the southern zone, the general rules concerning hunting and fishing apply, except that the Regime applies within Category I and II lands, trapping is exclusive to the beneficiaries, and only Cree tallymen, their families, and other beneficiaries of the Agreements authorised by them may harvest from the traplines located in this area.

The Hunting, Fishing and Trapping Regime applies to terrestrial mammals, freshwater and anadr-

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[1] *"Native" in this paper refers to the native parties to the JBNQA and NEQA (the Agreements), i.e., the Inuit, Crees, and Naskapis of Québec. "Non-Native" refers to all other groups, whether Aboriginal or non-Aboriginal, who are not signatories of the Agreements.*

Fig. 2.1. The territory area as set out in the James Bay and Northern Quebec Agreement signed in 1975, i.e. "the entire area of land contemplated by the 1912 Québec boundaries extension acts (…) and by the 1898 acts…".

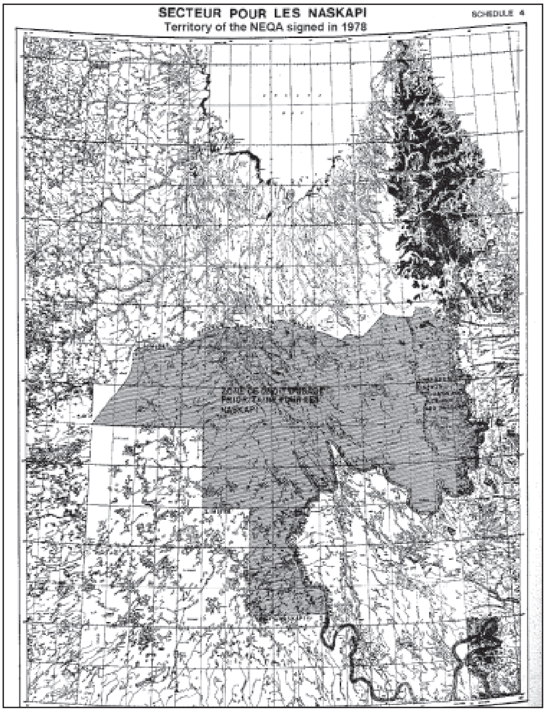

Fig. 2.2. The area of the Northeastern Qubec Agreement signed in 1978.

omous fish, migratory birds, and marine mammals[2]. The Regime grants the Cree, Inuit, and Naskapi beneficiaries the right to harvest any species of wildlife at anytime and anywhere in the Territory to meet their subsistence needs. The beneficiaries have the exclusive use of certain species (e.g., beaver, polar bear, sturgeon). While caribou is not a species exclusively reserved to them, they alone have the right to hunt this species for commercial purposes (i.e., to procure and sell caribou meat to non-beneficiaries of the Agreements.)

The Priority of Native harvesting is expressed as Guaranteed Levels of Harvesting (GLHs) negotiated for each species through the HFTCC. The GLHs are based on the results of Native Harvest Research studies (conducted to establish the levels of harvests that were current when the Agreements were signed). The concept of the Priority of Native harvesting is designed to ensure that no matter the quantities of wildlife available, a minimum number of animals of a given species (the number negotiated as a GLH) will be set aside for the beneficiaries before granting access to that species to non-beneficiaries. There are no provisions to monetarily, or otherwise, compensate the beneficiaries in times of scarcity of a given wildlife resource making it impossible for them to harvest the number of animals from that species corresponding to their GLH. The Inuit, Naskapis, and Crees have a total of 6200 caribou guaranteed to them as a minimum harvest of caribou (Inuit: 4547; Naskapis: 1030; Crees: 830).

The Hunting, Fishing and Trapping Coordinating Committee (HFTCC)

The HFTCC acts as an advisory body to the Governments and local and regional Native authorities on all hunting, fishing, and trapping matters. The responsible Québec or Federal government is obliged to consult the HFTCC and to strive to follow HFTCC advice. The governments, however, retain the ulti-

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[2] *There exists an as yet undefined degree of overlap between the HFTCC's mandate and those of the Nunavik Marine Region Wildlife Board (created under the Nunavik Inuit Land Claims Agreement signed December 1, 2006) and the Eeyou Marine Region Wildlife Board (outlined in the Agreement between the Crees of Eeyou Istchee and her Majesty the Queen in right of Canada concerning the Eeyou Marine Region initialled by the Negotiators on June 29, 2009).*

mate responsibility for the conservation and well-being of the Territory's wildlife. Seats on the HFTCC, and votes that each party can cast, are shared equally between the Native parties (Crees, Inuit, and Naskapi) and the governmental parties (Québec and Canada). The HFTCC has few binding legal powers. One such power is in establishing the Upper Limit of Kill for caribou (and moose, etc.) applicable to Natives and non-Natives across the Territory.

Harvesting the migratory caribou herds of the Québec–Labrador Peninsula

The annual range of the GRH straddles Québec and Labrador. In Labrador, the herd is hunted by the Innu, Inuit, and Métis of Labrador, by the residents of Newfoundland and Labrador, and by hunters from outside the province who retain the services of outfitters. No commercial hunts for the purposes of obtaining and selling caribou meat are currently authorised in Labrador.

In Québec, a sport-hunt by outfitters' clients targets the GRH in the fall in the easternmost part of Hunting Zone # 23. (Fig. 3). The province's sport-hunting regulations allow for a winter sport-hunt through outfitters but no outfitter is offering the service at present. In Hunting Zone # 24 there is a fall hunt reserved for the residents of Québec to hunt without guides. Although commercial caribou quotas were formerly allocated to the Naskapis to harvest animals from the GRH, the animals did not come close enough to Schefferville for it to ever be economically feasible for the Naskapis to carry out a commercial hunt.

The LRH is only harvested in Québec. In Zone 23, there is a fall sport-hunt for outfitters' clients. Commercial caribou quotas were formerly allocated to the Inuit, who succeeded in harvesting animals from the LRH. Due to concerns about that herd's numbers and condition, Québec has declined to renew the Inuit's commercial quota for the past few years. In Zone 22, there is a winter sport-hunt, for Québec-resident draw-winners in Zone 22 A and for outfitters' clients in Zone 22 B. No commercial hunt was ever held in the Cree area of interest as a result of a decision by the Grand Council of the Crees not to authorise the commercial harvesting of caribou in Eeyou Istchee.

Fig. 3. Game Hunting Zones established by the Government of Québec. Zones 16, 17, 22, 23, and 24 are within the JBNQA & NEQA territory.

Obtaining information on herd numbers and body condition

It was planned to survey both herds in summer 2010. The survey of the GRH was carried out jointly by the governments of Québec and Newfoundland and Labrador, with contributions from the Makivik Corporation and the Environmental Monitoring and Research Institute in July 2010. The planned survey of the LRH unfortunately could not be done in July 2010 due to conditions (scarcity of insects) which did not favour the caribou aggregating, which is essential for the photographic method. The Québec Government intends to try again in July 2011.

Recently, there has been more focus on caribou health, including investigations into the prevalence of parasites such as *Besnoitia*. There is a reported increase in predators such as wolves and black bear in the Territory. In addition, the Inuit are concerned that the caribou, who encounter musk-oxen in certain parts of Nunavik (the area inhabited predominantly by Inuit), are at a disadvantage when compelled to share their range with musk-oxen.

Management tools and measures

The HFTCC can establish an Upper Limit of Kill (ULK) for caribou for Natives and non-Natives in the Territory. The Committee started exercising that power in 1980–1981, when it set the ULK for sport-hunting at 3300. The members of the Québec party to the HFTCC were not entirely comfortable with the move because the limit set applied to non-Native hunting only. The Committee nevertheless continued to set ULKs applicable to sport-hunting each year until 1986–1987, increasing the limit of kill to reflect reported increases in caribou numbers. Given the high caribou numbers of the late '80s and the '90s, the HFTCC thereafter stopped setting ULKs for caribou.

The Native parties to the HFTCC had been pressing Québec to adopt a management plan for caribou since 1980. In 1986, Québec submitted a draft management plan for the GRH which the HFTCC commented on. At the time, there were concerns that the caribou, because of their high numbers, were over-grazing their ranges. Québec wished to intensify the hunting effort directed at the migratory herds and proposed that the beneficiaries be granted the right to harvest caribou (and a few other species) for commercial purposes. This feature was included in Québec's draft management plan. As discussions on commercialisation between Québec and the Native parties dragged on until 1993[3], Québec set aside its management plan and instead presented the HFTCC with a Tactical Plan (a document of lesser scope designed to be incorporated into the province's Big-Game Action Plan). The HFTCC reviewed the Tactical Plan and it was adopted in 1990. Work began again in 1998 to produce a joint Québec–HFTCC Management Plan for the GRH, LRH, and Torngat Mountains herd.

The joint management plan was adopted and implemented for the period 2004–2010, followed by a Monitoring Plan (Jean *et al.*, 2005) introduced in 2005. The joint Québec–HFTCC 2004-2010 management plan included a small section on Traditional Ecological Knowledge, and highlighted the desirability of co-ordination with Newfoundland and Labrador for the management of the GRH and the Torngat Mountains herd. Although no formal arrangement is in place between the governments of Québec and Newfoundland and Labrador , the HFTCC has been informed that the biologists and managers of the two provinces have developed an informal working relationship .

Under the scenario of declining caribou populations, the management measures set forth in the 2004–2010 Management Plan indicated the following actions:

1. Stop commercial harvesting;
2. Reduce bag limits for sport-hunting (including down to 0 if caribou numbers are insufficient to allow both a sport and a subsistence hunt at Guaranteed Levels of Harvesting);
3. Reduce the subsistence hunt to the Guaranteed Levels of Harvesting (GLH);
4. Reduce the subsistence hunt to lower than GLH levels if there is a need to invoke the principle of conservation.

Possible means of reducing the sport-hunt mentioned in the management plan included:

- adjusting the bag limit per hunter;
- reducing the total number of licences available for sale;
- varying the length of hunting seasons;
- limiting the hunt to male caribou only;
- closing some hunting zones.

In terms of controlling sport-hunting in general, the requirement for sport-hunters to use outfitting facilities where such facilities exist is another option mentioned in the JBNQA.

With reference to harvesting in the context of development projects, the JBNQA also contains provisions allowing the HFTCC to recommend the creation of special zones with more stringent rules applying to sport-hunting where temporary workers are present in significant numbers. One such zone is already in existence: the Weh-Sees Indohoun special sector. It was created as a framework to control the hunting and fishing activities of the workers at the Eastmain 1, Eastmain 1-A, and Rupert River Diversion hydroelectric project in the Cree area of interest. Other such special management zones will surely be created in the future in connection with the Québec

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[3] *Culminating in the signing of Complementary Agreement #12 to the JBNQA and Complementary Agreement #1 to the NEQA.*

Government's *Plan Nord*, a wide-ranging initiative placing renewed emphasis on natural resource–based industrial development projects.

The joint 2004–2010 management plan terminated on March 31, 2010. A new plan will need to be developed by Québec in collaboration with the HFTCC for 2010–2015 and will include the GRH, LRH, and Torngat Mountains herd. Work on the management plan will begin as soon as the results of the GRH census are available. Preliminary indications are that there is a marked decline in that herd's numbers.

Until a new management plan is developed and introduced, the following interim management measures apply:

- No allocation of commercial quotas (already the case in Québec for the past few years);
- No changes considered by Québec to its sport-hunting rules for 2010–2011;
- Opening of sport-hunt postponed in Labrador.

Knowledge used and knowledge gaps

The JBNQA calls for the parties to the Agreement to share all pertinent information. The HFTCC has no research capacities of its own as a committee and must therefore rely solely on the information it can gain access to. It makes use of all types of information, from western science (coming from governments and universities) to the field observations of non-Native hunters and outfitters, and the observations and traditional knowledge of the Committee's Inuit, Naskapi, and Cree members. In January 2010, the HFTCC organised a Caribou Workshop in Montreal that was designed to share knowledge and thereby assist the HFTCC in developing a joint management plan in coordination with Québec. The workshop was attended by well over 100 persons from Québec and Newfoundland and Labrador, including Native people, wildlife managers from Native and non-Native governments, and representatives of the tourism, research, and industry sectors.

The number of caribou harvested for subsistence in Québec and in Newfoundland and Labrador is, for all intents and purposes, unknown. There is no formal mechanism in place in Québec to obtain this information (the drawback for management in the absence of this information was pointed out during the January 2010 Caribou Workshop) (Guimond *et al.*, 2010). As the JBNQA does not require the beneficiaries to report their subsistence kills, the possibility of doing so has not to date been formally discussed between Québec and the Native parties at the level of the HFTCC. It is not known whether or not the Native parties would be willing to provide this information.

Management objectives and challenges

Given the HFTCC's mandate under the JBNQA, its contribution to the joint management plan for caribou must be to ensure, aside from the conservation of the resource, firstly, the Inuit's, Naskapis' and Crees' priority access to caribou for subsistence and secondarily, that the needs of the other users (such as the outfitting and caribou-meat–procurement industries) are met to the extent possible. The HFTCC is intent on convincing the governments of Québec and Newfoundland and Labrador to harmonise their management measures for the transboundary herds, especially the GRH.

In the current context, the HFTCC can at best hope to diminish the severity of the anticipated population crash by working to identify appropriate management measures for the herds and to elicit all user groups' support for, and compliance with, these measures. Committee members will be pursuing this goal despite occasional doubts as to the feasibility of actually modifying the course of a population trend. There are questions, for some, about the cultural appropriateness of even trying to do so, in light of native elders warning that what is needed for the caribou to return is, first and foremost, for it to be shown respect by human beings (HFTCC 2010 Caribou Workshop).

Governance issues

Since the creation of the HFTCC as the "*preferential and exclusive forum for Native people and governments jointly to formulate regulations and supervise the administration and management of the Hunting, Fishing and Trapping Regime*", many non-Native interest groups have sprung up in the Territory. It is now standard practice for governments to consult all stakeholders before arriving at decisions. While the legal status of the HFTCC and the constitutionally guaranteed rights of the beneficiaries are no doubt secure, the question arises of a potential dilution of the Committtee's influence over responsible governments now that, as a forum, it has lost some of its exclusivity.

The HFTCC's power is limited by several features of its structure and funding. The provisions of the JBNQA only call for Québec to maintain and fund a secretariat whose mandate is to receive and distribute data and to report results of meetings and decisions of the Committee, without any funding for knowledge acquisition. The HFTCC's decisional powers are limited to setting the upper limit of kill for caribou (and moose), given that under the Agreements, the responsible minister retains the ultimate responsibility for the wildlife's well-being. Such limited powers stand in stark contrast with those of co-management boards that have been more recently created. For instance, the Nunavik Marine Region Wildlife Board (created under the Nunavik Inuit Land Claims Agreement) (Anon. 2008) is established as an institution of public government with the responsibility to manage and regulate wildlife.

According to the member-parties' current policies, the members of the HFTCC are not free to act as independent experts but must promote the positions of the parties by whom they are appointed. The Chairperson is appointed from among the parties for a one-year term. The little independence and time afforded the members and Chairperson to discharge their duties to the HFTCC limit the scope and timeliness of what the Committee can hope to accomplish.

Committee strengths

The HFTCC can draw on a number of strengths to meet the challenges that the known or suspected status of the GRH and LRH will present. Many of its members and advisors have been on the committee for decades—a degree of understanding and respect exists among them and they have developed a good working relationship. They also maintain links with other scientists, managers, and Native and non-Native users. With the provisions of the JBNQA in mind, it is hoped that the members of the HFTCC will achieve a timely consensus on management measures that will benefit these herds.

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The responsibility for any inaccuracy or discrepancy in this paper rests solely with its author.

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Using dual knowledge systems to inform management decisions: a Wek'èezhìı Renewable Resources Board example

Joseph Judas & Jody Snortland

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The Wek'èezhìı Renewable Resources Board (WRRB) was established to perform the functions of wildlife management set out in the Tłı̨chǫ Agreement in the Wek'èezhìı Management Area and has shared responsibility for the monitoring and management of the Bathurst Caribou Herd. In late 2006, the Government of the Northwest Territories (GNWT) notified co-management authorities, including the WRRB, and caribou users across the Northwest Territories (NWT) that in their view significant declines had occurred in all barren-ground caribou herds in the NWT, including the Bathurst herd, and that management action was urgently required. In November 2009, the GNWT and Tłı̨chǫ Government submitted the "Joint Proposal on Caribou Management Actions in Wek'èezhìı" with nine proposed management actions, including the establishment of a total allowable harvest. As a result, the WRRB initiated its current Proceeding, including a public hearing held in March 2010. During the hearing, the Tłı̨chǫ Government made an application for adjournment to allow for further negotiations on management actions with the GNWT. This resulted in a revised joint management proposal being submitted at the end of May 2010 and a follow-up hearing in August 2010. Currently, the WRRB is preparing its final report for submission to the GNWT and Tłı̨chǫ Government in early October 2010.

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Tłı̨chǫ stories for Ekwǫ̀ management[1]

Joseph Judas

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Introduction

Masì, thank you. My name is Joseph Judas. I come from the Tłı̨chǫ Nation, from the community of Wekweètì on Snare Lake, north of Yellowknife, Northwest Territories. I'm Chair of the Wek'èezhìı Renewable Resources Board. I'm a hunter, I'm still trapping. I still like to go out on the land, make campfire, and cook meat and fish. I still do that. I'm proud of it. I'm most comfortable speaking in my language, but I'm sharing this with you in the English language.

Our community was established somewhere after 1974. Before that, we used to come back and forth to Rae, Behchokǫ̀, for the spring hunt. Then in the fall we would go back to Wekweètì. Every year in the falltime we used to see the Bathurst herd travelling across Snare Lake. It's a narrow lake that we're on, but it's more than fifty kilometres long. From 1962 to 1990, the herd used to cross Snare Lake near Wekweètì before freezeup. In those days, even with dogteams and dogs eating meat, we still had lots of ekwǫ̀.

Eventually the elders talked about it and decided that we can't keep going back and forth. Stuart Hodgson used to be a government leader at that time. One time when he came to the community, our people asked for a school. So we got a school first, and then the store and the freezer. That's three things that came in first. After that, we got a few more things.

We've been hearing about the decline in caribou populations over the last number of years. We're just talking about only one caribou. The caribou, ekwǫ̀, are all the same, the way I look at the picture. Ekwǫ̀ are all one, just one animal. I can go back to 1962, and I've observed that since 1990, the population has really been going down.

Within the last number of years I have not seen ekwǫ̀ close by Snare Lake. Last year in spring, somewhere around March, that's the last time we saw ekwǫ̀ when they're going back to the barrenground. Since then we haven't seen that migration. They must be going somewhere else. I didn't see this happen in the last number of years, so it must be decline, that's how I see it.

Our survival depends on the survival of ekwǫ̀. We've tried to work on a solution together with all our elders and our people back home. The elders have got long vision, they can see for the future generations, and they're talking for the younger people.

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[1] *This paper is adapted from contributions to the NACW Aboriginal Talking Circles, as well as the author's contributions to two co-authored presentations: "Using dual knowledge systems to inform management decisions: a Wek'èezhìı Renewable Resources Board example," with Jody Snortland; and "Monitoring Caribou and People," with Allice Legat and John B. Zoe.*

They've got lots of stories, lots of history to talk to us about. We are the ones that are supposed to be listening. We should be really listening and using our language. Right now where I'm from there are no elder men anymore. We had three elder men who are now gone. Just elder women left in our community of just over a hundred people.

We're trying to work on science and traditional knowledge together. Science has a lot of tools to work with. But we're not going to give away the knowledge, we're not selling it. We keep it and pass it on to all the generations of the future. That's my traditional knowledge. That's how strongly I feel about the knowledge that I have.

During the three cold months, January, February, March, ekwǫ̀ are heading back to the barren-grounds. Some of the bulls stop halfway, and others follow the females to protect them as they travel to the calving grounds. In falltime, August, September, that's when they come back this way and meet the other bulls halfway. That's how I've been taught traditional knowledge by elders. Science and our history and our knowledge are going to meet. We are trying to work together and try to make a better solution for us.

Raven hides Ekwǫ̀

I want to tell you a story about ekwǫ̀ that my father told me. In those days fox and wolf used to be people. There were wolf and fox and raven, and all these animals. The raven was always asking the elders for stories, because he was flying. The other animals travelled on the land.

One cold winter month, the younger wolves that hunt tried to find ekwǫ̀, and they couldn't find anything. Nothing. I don't know how many days they searched. All the women and men and kids were starving. The kids couldn't play outside anymore because they were starving. No meat, nothing. Just little animals, like grouse (what we call chickens) and hare (what we call rabbit). The people started hunting every day, but they didn't get any ekwǫ̀.

So one time the raven was coming back and forth and saying he was so happy just flying around. This old wolf said to him, "Raven, you know, you're so happy flying around. I see you almost every day. Our people are starving. The kids are starving. Everywhere it's all the same. There's nothing to eat. How can you be so happy?"

Then the wolf elder thought to himself, "Maybe we should just follow him some day. But how?" They had medicine power in those days, so they had to use that power. Raven took off that evening and they followed him, led by the old wolf. It was cold that day, but they kept following him. The old wolf couldn't keep up with the raven because it was too far for his medicine. So he asked for the ashes from the fire to be strewn right around that tipi. In those days, they used tipis made of branches, not the canvas tents that we use now. Then he put the ashes right on their eyebrows so they could see further, and they kept following this raven. But still he couldn't keep up with it.

So he asked for help. Another elder had come along, and he helped the old wolf with medicine power. Finally when that raven went back, he got into a foggy cloud. Raven's vision must have been getting old from the medicine power. So the wolves were able to catch up with raven.

Eventually they came upon a fence. The old wolf circled around the fence and discovered a whole bunch of ekwǫ̀ trapped inside. That raven had been hiding all ekwǫ̀ in a corral. Raven went inside his little tipi made of branches. The people peeked in the doorway and saw a big stash of ekwǫ̀ eyeballs. Then they saw that raven was smoking meat. He had a lot of meat. Raven was the only one who was happy, because he was hiding ekwǫ̀.

After they saw this, the people went back to their camp. That night the younger wolves that hunt couldn't sleep from the excitement of having found ekwǫ̀. So the next day everybody went to where the raven was hiding ekwǫ̀. "Now who's going to do something to set these ekwǫ̀ free?" they asked.

Then the fox said, "I can probably do it. I'll try. I'll do it. But how?" The old wolf said, "Put your tail in the fire and run around ekwǫ̀, and then ekwǫ̀ might stampede out of the fence." That's what the fox did. So that's how ekwǫ̀ stampeded out.

Now all these wolves and other animals that had been starving got ekwǫ̀ back. And the raven was squashed in his tipi, because ekwǫ̀ ran over it when they escaped from that corral. When they saw that, the elders said, "I guess we can't just leave him like that. Maybe we should make him human again." So they collected the feathers of the raven and they made him a raven again. That's the story I wanted to share with you.

I think that the raven tried to manage ekwǫ̀ within the fence. He was trying to keep the wolves and all the other animals from killing the ekwǫ̀.

It's good to listen to elders, the way that the animals used to listen to their elders. They said, go follow the raven. That's why the younger people followed the raven, and they found ekwǫ̀ again. It's no good to be greedy. It's not good that raven wanted to keep everything for himself. He should be sharing with the wolf and fox. But wolf and fox got together and went after raven, and that's how they got their meat, finally.

A law for Ekwǫ̀

Our Tłı̨chǫ people have a law for ekwǫ̀. Older people still observe the rules that people used and lived by on a daily basis. Even though life may be tough, especially in winter when it's super-cold, they still continue to observe how you treat ekwǫ̀ after it's killed. Even to the point where other types of leather, especially from beef, even buffalo and woodland ekwǫ̀ are not allowed to be carried to the barrenlands, because it's considered something that makes ekwǫ̀ go away.

In those times the elders were really protecting the animals, they really watched everything. For each animal from the hoofs to the antlers, they would use everything. They made tools from it, they ate the meat, and they made clothes from the hides. They made dry meat. They would even make lard from the bone marrow. Ekwǫ̀ brain is like ice cream, I cook it and I eat it. They used the whole thing. That's why they were really lucky with the animals in those times.

Forty-five years ago, I was using a dog team, hauling and hunting ekwǫ̀ for my family. I would walk in front of the dogs. I would chase ekwǫ̀ with snowshoes too. They weren't using the fast equipment. In those days, even though we would travel slow with the dogteam, we still had a lot of ekwǫ̀ with us.

Nowadays we're using skidoos and all those fast motors. But sometimes we're not lucky because the machine is loud and ekwǫ̀ won't go near. When we used to travel with dogs, there was no noise. The dogs were like our radio-collar for finding ekwǫ̀. When the dogs would start sniffing, we would know that there was something there, maybe animals like ekwǫ̀. That's how we would know where ekwǫ̀ were. But right now, we've got radio-collars and we know where all ekwǫ̀ are migrating, so if we want to hunt we can just go in front of them and then wait for them until they get there.

It was really tough work sometimes in those days, but it was worth it because the people got so much from each animal they harvested. And they managed their wildlife well. They wouldn't shoot lots. They would just shoot enough for themselves, enough for their living.

Ekwǫ̀ in the moon[2]

There is a story told by the elders about an elder woman who had no husband or children. She did her best to keep up with everyone, but they didn't help her and left her behind. She discovered a child sitting between the hoof prints of ekwǫ̀. So she picked it up and raised it until the child could be a good hunter. And he became a gifted hunter, because he came from the ekwǫ̀ hoofprint. He provided well for the mother that raised him.

But the people he lived with became complacent. One of the rules was that you're not supposed to step over the blood of ekwǫ̀. Once people started stepping over the blood of ekwǫ̀, he became frustrated and went away to the moon with a bucket of ekwǫ̀ blood. Even until today, on a good day you can see him up there with his bucket of ekwǫ̀ blood.

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[2] *This story, told during the session on Traditional Knowledge and Science, was interpreted by John B. Zoe.*

The 13th North American Caribou Workshop
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Caribou management in times of uncertainty

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The *Porcupine Caribou Management Agreement* (PCMA) was agreed to in 1985 by the five First Nation and three public governments. That agreement established the Porcupine Caribou Management Board whose mandate is managing the health of the Porcupine caribou and its habitat, making sure the caribou are there for future generations.

In 1989, the Porcupine Caribou Herd peaked at approximately 178 000 animals and then declined to a low of 123 000 in 2001. Currently, best estimates show the herd to be at approximately 90 000 animals. There are a number of factors believed to contribute to the decline, such as high calf mortality, climate change and harvesting pressures. In 2004, the Porcupine Caribou Management Board undertook the challenge of putting together a Harvest Management Strategy or Plan (HMP), while respecting the jurisdiction of various governments and five claimant groups' comprehensive land claim agreements within the range of the Porcupine caribou herd. The HMP was signed off by all Parties to the PCMA in July this year and an Implementation Plan is currently being developed.

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Assessing management needs and priorities for caribou management in an era of decline and uncertainty: challenges of the Beverly and Qamanirjuaq Caribou Management Board

Albert Thorassie

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The Beverly and Qamanirjuaq Caribou Management Board (BQCMB) is a co-management advisory board whose main purpose is to safeguard the Beverly and Qamanirjuaq caribou herds in the interest of aboriginal peoples from four different cultures which have traditionally relied on harvest of these two herds. The Board was established in 1982 during a period of apparent serious decline in both herds, and has since witnessed the highest population estimates ever recorded based on surveys in the mid 1990s, followed by more recent reports of declines in both herds. A lack of clarity concerning the status of the Beverly and Qamanirjuaq caribou herds has created difficulties for co-management in an era in which most barren-ground caribou herds across North America have declined. Identifying appropriate management actions is complicated by divergent views, both about underlying causes of population declines and short and long-term solutions. Management actions underway and proposed for many declining herds in the Northwest Territories and Yukon, as well as political aspects such as the aboriginal right to harvest, have further complicated the situation. What is clear is that the BQCMB and its partners are faced with a management challenge that will be a true test of contemporary co-management.

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Co-management – traditional knowledge and governance

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Dene traditional knowledge about caribou cycles in the Northwest Territories[1]

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Introduction

My name is Danny Beaulieu. I am a descendent of François Beaulieu, who came to Fort Resolution, Northwest Territories in 1752 from what is now the Manitoba area. There he married a Denesųłıné woman, my seventh-generation grandmother, and remained there until he died.

I was born on the trapline. I hunted and trapped and raised a family in the bush for twenty-five years. Ten years ago the trapping industry really bottomed out. People were making $100 000 to $120 000 a year trapping, and then all of a sudden with the anti-fur movement group, that went away. I was one of those people who lost that livelihood. So I became a wildlife officer. After working in Yellowknife for a number of years, I recently moved to Fort Providence.

This paper is about what I have learned about the caribou cycle over the past one hundred and ten years or so, talking to Denesųłıné elders in Fort Resolution, Łutselk'e, and Yellowknife. Mostly I've learned from my grandmother, my grandparents, and my parents.

I'd like to start with a story that my grandmother told me many, many times. It never had any meaning to me, it was just a story. But I heard it so many times, I can hear her voice when I tell it. I just thought it was one of those fairy tales that old people tell. But the more I hear it, the more meaningful it becomes. It takes a little while. I guess that's why elders tell stories over and over until they think you've got it. That's why I told this story twice at the North American Caribou Workshop (Fig. 1).

Fig. 1. My grandmother Judith Giroux, Fort Resolution, circa 1970. Danny Beaulieu collection.

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[1] *This paper is compiled from the NACW presentation of the same name, as well as contributions to the NACW Aboriginal Talking Circles.*

My Grandmother's story

A long time ago people and animals spoke the same language. They could communicate easily. One day long ago in the fall time, a bull caribou came down from the tundra heading for the tree line. When it got there, the caribou noticed there was a tent pitched along the tree line. He could hear a woman crying in the tent.

As most caribou hunters know, the caribou is a very curious animal. He wanted to really know what was going on. So he turned himself into a man and walked into the tent. There was a woman in there with two daughters. He asked the woman what was wrong. And she said, "Well, there was no caribou for a long time and all my people died. There's just me and my daughters left. Once we're gone, the people will be gone."

So the caribou thought, "Well, I've got to help her out." So he asked her if she would want him to live with her and to help build a nation again. He said, "The only condition would be that I'll have to leave some day." So he moved into the tent and lived with her for years and years and years until the people were strong again. He taught people to respect animals. He taught people how to hunt caribou. He taught people the ways of the land.

Finally, the day came that he felt the people didn't need him anymore, so he told the woman that he had to go. That was the agreement she had made, she knew he had to go, so she agreed.

So he left. They said goodbye, and he walked out and left. A few moments after he left, the woman decided, "Well, I don't want him to go." So she chased him. She followed him. She followed the moccasin tracks down the hill onto the ice. A little ways onto the ice, she noticed that his tracks turned into caribou tracks and headed north.

That's the end of the story. I always wondered what it meant. Today when we're in a period when caribou are declining, I think a lot about this story, about caribou. That's one story that keeps coming back to me because I think it's our turn to help the caribou. In reading this paper, maybe you'll figure out what it means.

A history of caribou cycles

The knowledge about the caribou cycle that I'm going to share with you comes from the people of Rocher River and Fort Resolution, Délı̨nę, Łutselk'e, Yellowknife, a lot of people I've talked with over the years who know most of the southern areas where the caribou winter. Caribou are important to us. The barren-ground caribou are what people lived with. You hear many, many stories about how people had really rough times when caribou numbers were low. Caribou populations go up and down. Scientists have spent thirty years trying to figure out why caribou go up and down. They can pound their head on the cement block as they'll never figure it out. It's a thirty-year cycle, up and down.

Fig. 2. I believe this is a photo of my great great grandfather Paul Beaulieu driving a dogteam in Fort Resolution. Date unknown. Danny Beaulieu collection

Paul Beaulieu was my great-grandfather (Fig. 2). He said when he was around twenty years old there were lots of caribou around Fort Resolution. That must have been in the 1890s. The elders don't tell you what year, but I was able to figure out the year because he said he was about twenty years old and that would have been in 1892. When elders tell me stories they think of events. Like somebody's birthday or an important event that people don't forget. So that's how the cycle is put together.

At that time there was so much caribou in Fort Resolution in the bay, all they had to do was hook up a couple of dogs and go out on the bay and shoot a caribou and bring it home. There are many stories about how many caribou were around in those years. If I have to tell all the stories we wouldn't have enough time in the day.

My grandfather said that there was no caribou during the First World War. That would have been around 1915. As you know the war lasted until 1919. He said that in those days, people had a hard time.

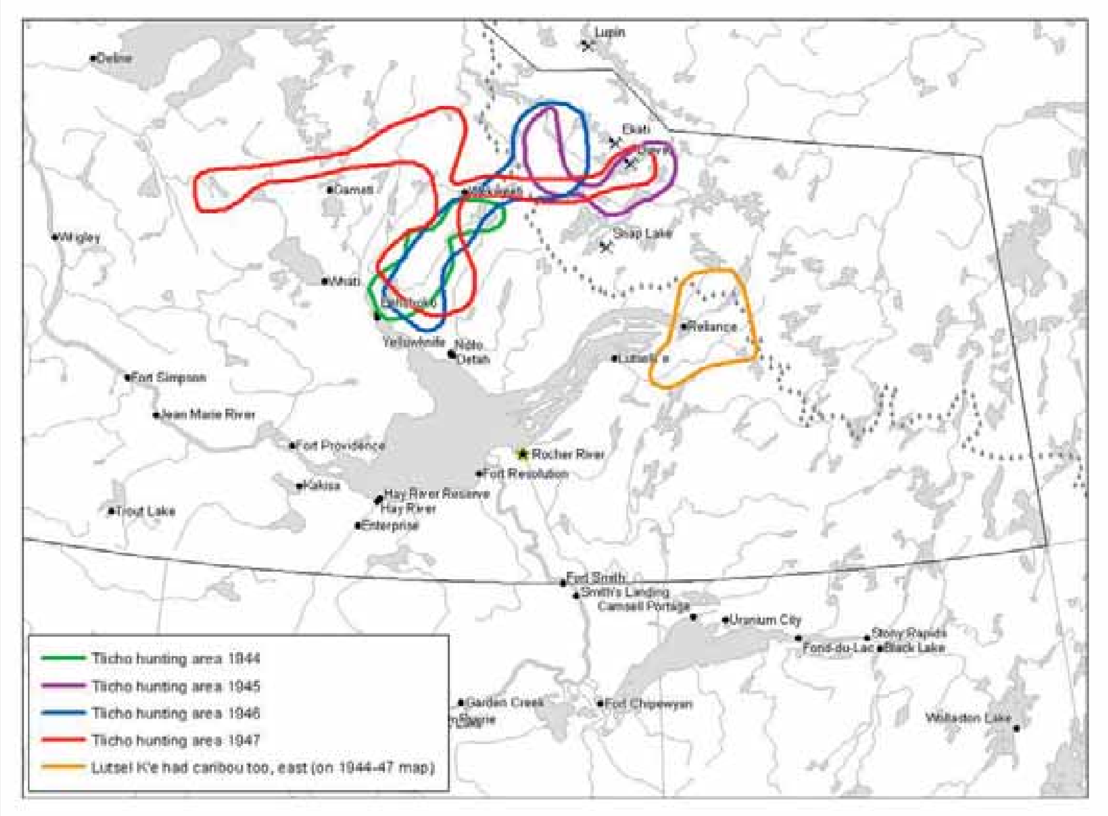

Fig. 3. Winter hunting areas 1944-1947. Tłı̨chǫ hunting areas adapted from Whaèhdǫǫ̀ Nàowoò Kǫ̀ (2001). Łutselk'e hunting area from information gathered by Danny Beaulieu through conversations with elders. Caribou were likely lowest in population in 1945, when the hunting area was smallest and furthest away from the communities, past the treeline into the barrenlands.

They all used dog team to travel, snowshoes, and there were many stories of hard times. Like stories of a father who would leave the family to go hunting on the barrenlands and not come back.

My grandmother told me that when she was about nine years old, when my great-uncle John was born, one morning in the winter time she heard thunder; by great-uncle's birthdate, this was in 1924. She also heard something that sounded like rattling dog chains. She said she went to the window and there were so many caribou moving through the community, the ground shook. In the former community of Rocher River where I was born, there were about a hundred people. There was an island on the river, and they said it was full of caribou migrating south. The migration went all day through the communities. Again there was a lot of caribou for the people.

My father was an Aboriginal trapper and hunter. I didn't come out of the bush until I was nine years old. My father said after the Second World War, that would have been in 1945 probably until 1950, there were no caribou around Rocher River where we lived (Fig. 3). People had to travel almost to the tree line by dog team to find caribou. Again there were hard times. To survive, people hunted moose, buffalo, fish and traded fur for dry goods.

There were airplanes. I think Punch Dickens came around one time with a little airplane and busted his propeller. My great-grandfather had to make him another prop so he could leave again. That's all we had for an airplane, so people couldn't really look for caribou. They just used dog teams. There were no skidoos either. That was after the Second World War.

In 1953, the year I was born, my father told me that there were a lot of caribou again at Rocher River. There are a lot of stories of that time. I'd like to tell you one about my uncle and my father:

My father told me they were trapping and they had to chase caribou off the lake to get the dog teams to the other shore where they have to set traps. So my uncle had these big fur mitts. They have these strings, we call them idiot strings, that go around

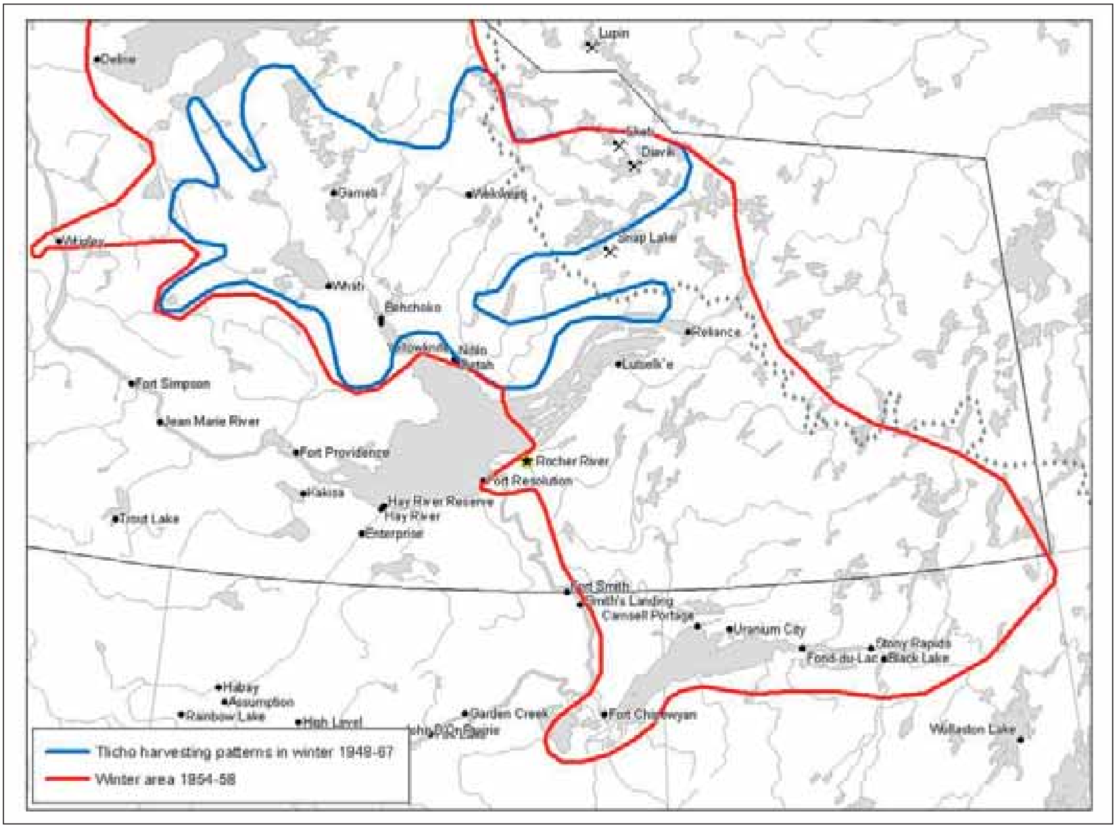

Fig. 4. Winter hunting areas 1948-1967. Tłı̨chǫ harvesting areas 1948-1967 adapted from Whaèhdǫǫ̀ Nàowoò Kǫ̀ (2001). Winter area boundary 1954-1958 gathered by Danny Beaulieu through conversations with elders. The population is high, and the caribou are spread out. Everybody had easy access to caribou in these years.

your neck and have a little pom-pom on the end. So he was using that to chase the caribou off.

He had a hold of the pom-pom and was twirling it and getting the caribou off the ice and walking his dog team across the lake. The pom-pom broke. The mitts landed around the antlers of a big cow caribou and the animal took off. So he ran back to the sled and he was trying to shoot that particular caribou. My dad said he was just jumping all over the ice trying to get a shot and this caribou was running with the mitts like a cowboy kicking a horse. It disappeared in the bush. He never did get his mitts back.

Those years there were a lot of caribou. My aunt and uncle Dorothy and Angus Beaulieu told me that there were caribou on the prairies east of Fort Resolution and on the ice on Fort Resolution Bay for seven years, until about 1958. There are buffalo there now. A lot of elders believe the caribou don't use that area now because of the buffalo.

During those years, the Tłı̨chǫ hunted at the end of Great Slave Lake, where Reliance is, down to Yellowknife and up to the barrenlands. The mapping of this history was done by Tłı̨chǫ researchers.

In Délı̨nę, they had lots of caribou between 1954 and 1958. I talked to an elder from the Fort Simpson area, his name is Jonas Antoine, and he said that in 1954 the caribou crossed the Mackenzie River into the mountains and stayed there for about seven weeks. When they returned, the caribou travelled single-file across the river, which is about a mile and a half wide. All day they were coming in a line that stretched all the way across that river. Thousands of them.

In those years there were a lot of caribou. There were caribou in Yellowknife and across the lake at Fort Resolution, and in Fort Smith. Caribou used to graze in Fort Chipewyan, Alberta, at the delta of the Athabasca River. I haven't talked to people in Black Lake, Saskatchewan but that area would have been the wintering grounds of the caribou in those years (Fig. 4).

The Tłı̨chǫ mapping project with elders for the 1970-1975 period shows that caribou didn't migrate

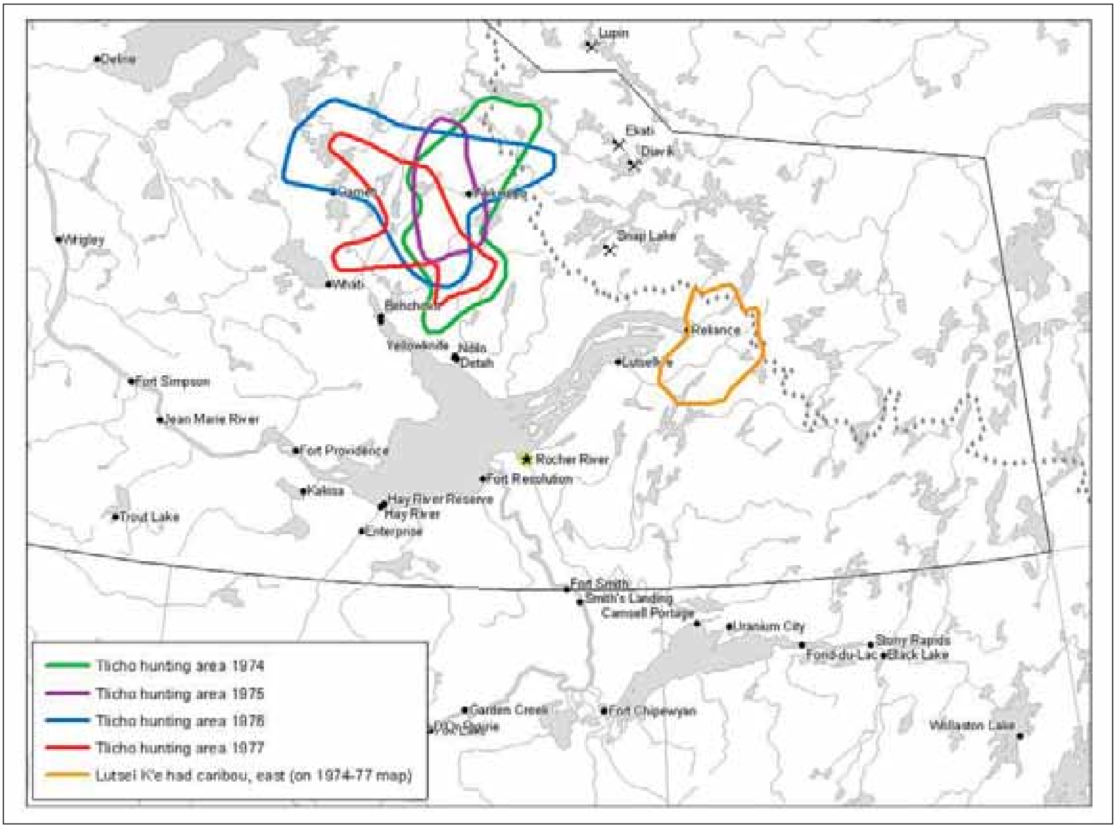

Fig. 5. Winter hunting areas 1975-1977. Adapted from Whaèhdǫǫ̀ Nàowoò Kǫ̀ 2001. The lowest caribou population was in 1975. The expanded range in 1976 may show that the population has begun to rise again.

very far when the numbers were low, but for some reason the caribou liked the area around Indin Lake, between Gamètì and Wekweètì. What we call the Eastern caribou (known by scientists as the Beverly and Ahiak) hang out between Artillery Lake and Łutselk'e when they're in low numbers. We still had to travel many miles to hunt from where I was living at Fort Resolution.

In 1975, I was working in a community called Pine Point where there was a lead-zinc mine. My father was in Fort Smith. From being a trapper, my father became a wildlife officer. I followed in his footsteps. I gave him a call one day and asked him if he wanted to go hunting. He told me there were very few caribou and the Commissioner of the Northwest Territories allowed only five tags to any people that hunted in the southern NWT. But I was told that this only lasted two or three years (Fig. 5).

In the 1970s, skidoos were new. There was a snowmobile they called a snow cruiser. It weighed about seven hundred pounds. You never want to get it stuck, so you just drive it around on the lake. Most people really couldn't afford to go hunting with airplanes. There weren't that many jobs. There was no mining, and there were no winter roads. There were very few non-aboriginal hunters. There was no outfitting. So there wasn't much impact on the caribou in the 1970s. The animals returned fairly quickly (Fig. 6).

Fig. 6. My father Jim Beaulieu, training young trappers with his 1967 Snow Cruiser.

In 1984 there were a lot of caribou again in Rocher River, the community that was located at the mouth of the Taltson River. I was trapping at Little Rat River in those days, and I hunted caribou at Taltson

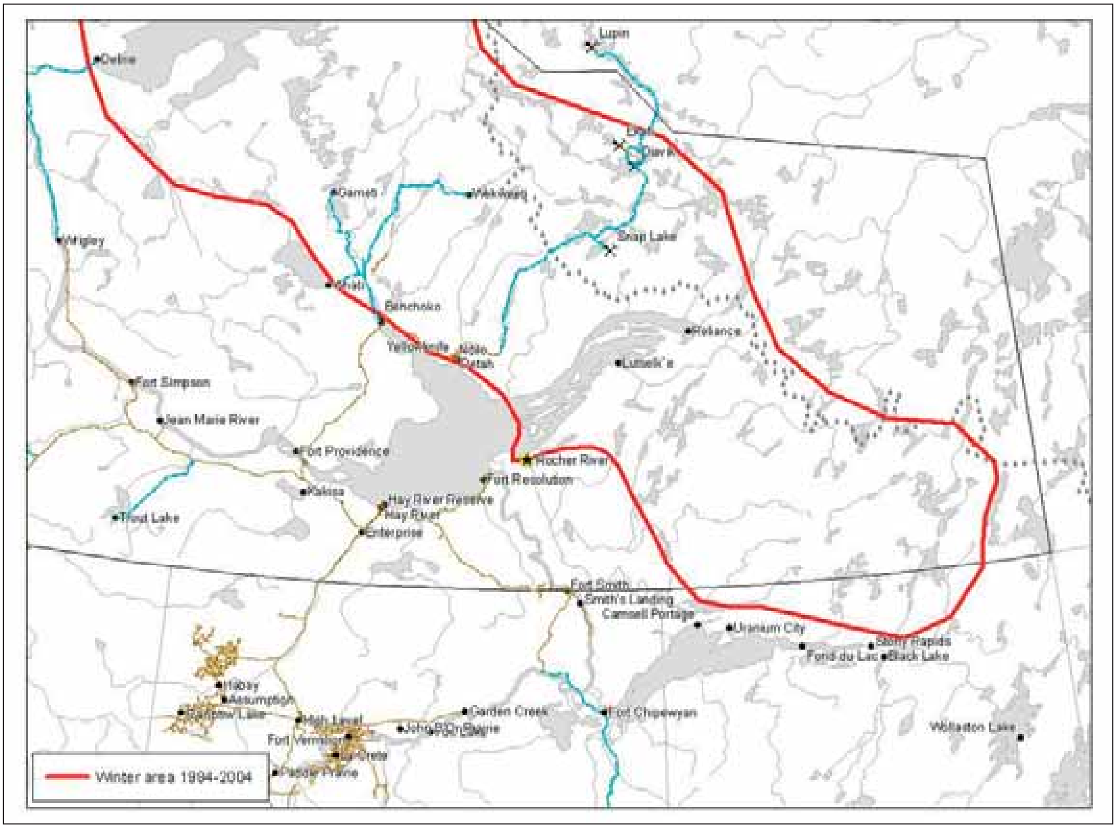

Fig. 7. Winter hunting areas 1984-2004. Adapted from NWT Environment and Natural Resources radio collaring data.

Bay. I think that's the first time that I killed a caribou. I usually hunt buffalo and moose. My uncle was down at Rocher River and it was only about a half hour drive from where my cabin was by skidoo. So I went down and I got to the Taltson Bay. The bay was just covered with caribou. I shot one and it was real easy to skin because it was so small. I put it in the sled and I got back to my cabin. Again there were a lot of caribou in the area. Since 1984, the caribou have moved to the northeast, further away from the community every year. By the 1990s, we had to go all the way to Łutselk'e to hunt caribou.

From 1984 to 2004, the wintering grounds were around Délı̨nę, Yellowknife, Rocher River, down to Stony Rapids (Fig. 7). I know this partly from traditional knowledge, partly from radio-collaring. The caribou didn't go as far south as they did in the 1950s. I don't know the reason for it, because we didn't fly around and count. I think when the numbers are lower they just don't go as far. Some people say it's because of forest fires. Whatever the case, the range extended that far south (into southern Saskatchewan) the last time the population size was high.

From 2002 to 2008, I did a lot of patrols travelling on the land, just talking with hunters and travelling with hunters where the caribou wintered when they were in the low numbers. Again they were on Tłı̨chǫ land around Indin Lake (Fig. 8). In 2005, the caribou were just east of Yellowknife, but that was it. They moved out and around north of Łutselk'e in those years.

Cumulative impacts

In 2005, we started talking about low numbers again, especially with respect to one particular herd, the herd that we call the Northern herd. Most biologists know them as the Bathurst herd. In 1984, this herd apparently numbered about half a million. Today they're about 30 000. The cumulative impact on them is unreal. There are about ten outfitter lodges that concentrate on the range of the Bathurst herd, three diamond mines, and about one thousand kilometres of ice road. I've been on that ice road between late January and mid March and every five minutes a big truck are going by you, where caribou migrate. The mine sites are very noisy.

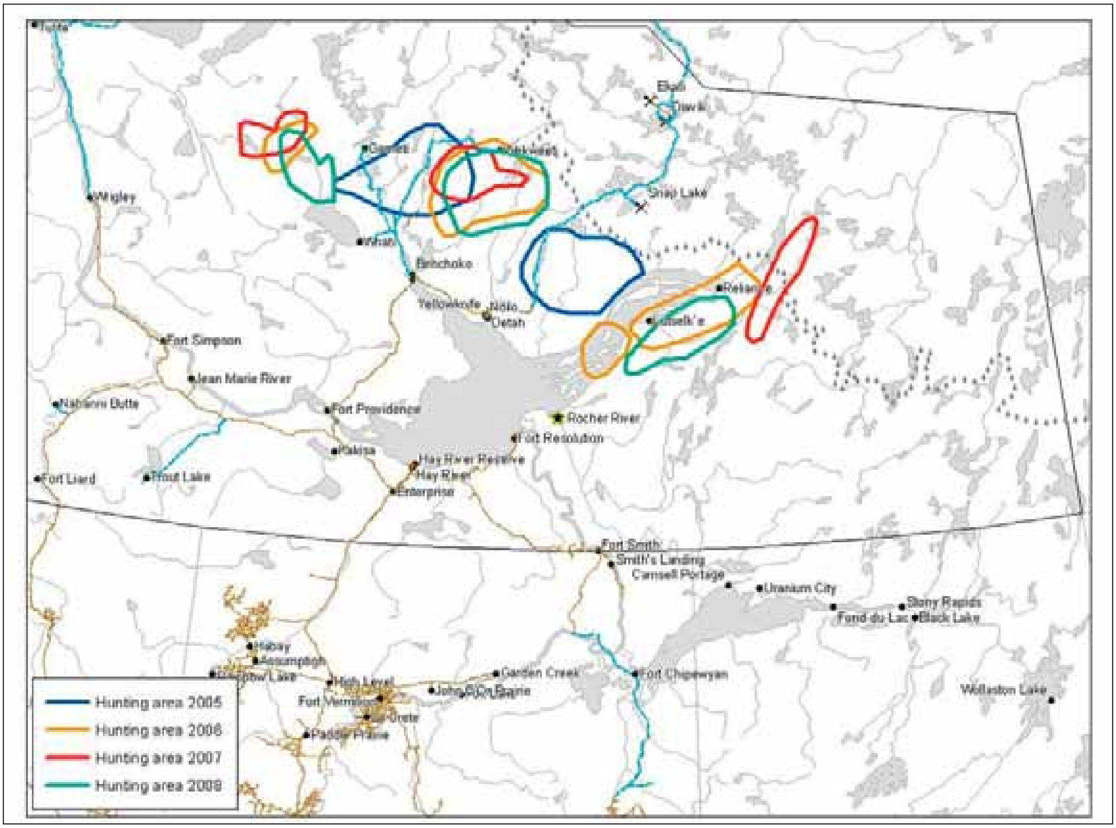

Fig. 8. Winter hunting areas 2005-2008. Adapted from NWT Environment and Natural Resources radio collaring data, and incorporating information gathered by Danny Beaulieu through conversations with hunters. The population was low during the entire period. Note the winter roads to Gamètì, Wekweètì and the Snap Lake, Diavik and Ekati diamond mines now influencing where people hunt.

The caribou are easy to find, they can no longer hide from us. We've got skidoos. I bought a skidoo two years ago, and I've never even run it wide open yet because I'm too scared, that's how fast they travel. We have lots of people nowadays. We have good jobs. We're working at the diamond mines. We get a couple of weeks off and we can rent airplanes and go find them. We have two ice roads that go into the heart of the wintering ground of the Bathurst herd. Since 1996, we have satellite collars on caribou in the herd, so if someone wanted to go hunting, they could just look on the computer to know where they are. After 2007, when numbers were getting low, the maps were no longer published on the website to help conserve caribou.

There's been a lot of hunting. There are ten outfitter lodges that concentrate on the Bathurst herd. We have more than 20 000 people in Yellowknife. Half of them are non-aboriginal people. There were up to a thousand non-aboriginal hunters that hunt the Bathurst herd. Both aboriginal and non-aboriginal hunters use the ice roads that go to the diamond mines. There are a lot of things that impact this one particular herd. There are other herds that don't experience as much impact because there are no roads cutting across their ranges.

There was a Denesųłiné prophet from Łutselk'e who said, "One day we're going to walk on the caribou trails with tears in our eyes." Sometimes you hope he's wrong, but the way that development is happening and the way our hunting practices are going, I just don't think he's wrong.

When I use traditional knowledge to predict the future of caribou, it doesn't look good for our grandchildren, our children. The future for the caribou is not good. Only we can help them. I think the big thing is to control development across our land, across Canada and the Northwest Territories. I hope that my son's children and his children's children will see caribou herds migrating through our land. But this will take the kind of help that biologist Jan Adamczewski shows in his painting of a human hand, holding a female caribou and her calf. If you think about the meaning of that story I just told you, maybe it's our turn to help.

Predicting the future

Traditional knowledge tells us that caribou herds increase quickly and decline more slowly. Where I lived is at the edge of the range used by the caribou. Elders tell me that when there are lots of caribou, they use all of their land. That is why we saw them in Rocher River when numbers were high, every thirty years. In the 1920s and 1950s, elders told me that caribou wintered as far south as Fort Chip and Fort Smith. During the peak in 1984, elders say there were not as many caribou as before because they only went as far as Rocher River.

So the way I see it, using traditional knowledge from the 1890s, 1924, 1954 and 1984, the caribou were in high numbers. Thirty years apart roughly. Someone told me one time I was wrong. They said it was twenty-seven years. And then somebody else told me ite was thirty-three years. So you take an average. The same thing happened to the buffalo in this area.

In 1915 and 1945 (during the two world wars), and then 1975 and 2005, caribou were in low numbers. Now, there are all kinds of reasons why numbers decline. My explanation is that decline is a natural phenomenon. And in the future, they are going to be in high numbers in the Bathurst herd and most caribou herds across our country.

The next time there will be a large population size will be four or five years from now. And the next low will be in 2035. So using traditional knowledge, my prediction is that they'll peak in 2014. When I look at the cycle that is from the 1970s when they started doing scientific counts, and in the 1980s when they really got the counts right, if you put their line on a graph it's pretty well identical with what I'm saying.

I think the caribou do move. But from a traditional knowledge perspective, the herd divisions don't really matter. The caribou on the east side, the Beverley, the Ahiak, to us they're one herd. We have a Northern herd that they call the Bathurst. Then there's the herd from the west, the Bluenose East and Bluenose West. But we don't split them up. People know where the calving grounds are. People know the caribou. When the caribou want to give the calving ground a rest from all the trampling and that the nutrients grow back, they will move. It's been proven with the Bathurst herd.

I'm confident in traditional knowledge and I love working with scientists. When traditional knowledge holders sit together, we come with different opinions. But if we talk about it long enough, we can work it out. It's no different for the biologists when they sit together. But beyond all these arguments, we have to work together to make plans for the future.

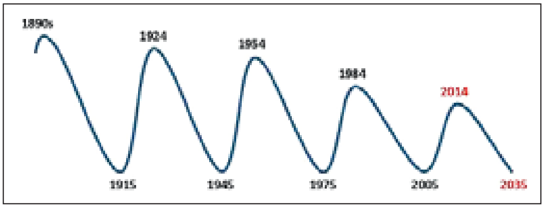

Fig. 9. Caribou cycle over 110 years. Graph by Danny Beaulieu. Caribou populations tend to increase quickly and decline more gradually. The peak population was significantly lower in 1984, likely because of cumulative impacts. Counts and studies by biologists have documented roughly the same cycle since 1975.

Helping the caribou

If we want the caribou to be strong, we have to reduce the hunting. We need to take a look at development, and maybe do some other things to help them along. For example, in 2010 the Bathurst herd, the Northern herd, came down very slowly. They didn't get to the fall hunting area at all that year. They stopped at the north side of the diamond mines. So they were about a hundred kilometres north of where they should have been in the fall. I find that in the last few years when the caribou numbers are low, they move slowly. I think they're not as brave when they're numbering in the thousands, and they move fast. But the calves are born on the calving ground where it's nice and quiet. When their mother takes them away from the calving ground and just goes a few miles on their migration in the fall, they start hearing these rock trucks and dynamite and other noises. It really slows them down. They stop. Looking at the satellite collars, they were at a standstill for about three or four weeks this year. They never moved until last week when they started going. They had to shut down the road to let them go over.

We need a management plan for the decline that's going to happen in 2035. We have twenty years to come up with a good plan so that caribou can increase again. We could work with developers like BHP and Diavik. Last year, for example, Diavik closed the mine down for six weeks at Christmas and had planned another six weeks during the summer, to save money. The diamond prices were down a bit. They had a workshop a couple of weeks ago and I suggested that they should shut down from the beginning of September until the middle of October instead, if they're going to do it again.

In 2035, when the caribou are going to be low again – and I hope I don't have to sit here and say, well, I told you so – we should be able to get together and figure out a plan. The caribou are on the increase. They're going to go up. They're going to start going up for the next four or five years. They'll level off. How quickly, how many is a mystery. I think the caribou in the east and the caribou in the west have a better chance than the Bathurst herd. They're very impacted and I know there are going to be more diamond mines going in there. I know our children need to work there, but I think we should really limit how many diamond mines we have running at once. We should talk to the companies that start these diamond mines and ask them to shut down the mine for a few years from 2037 to 2042. Because if they do that, if they put it in the plan and commit to it, then they'll help the caribou.

According to the stories that come from my seventh-generation grandfather François Beaulieu and my great-great-grandparents, there were hard times when the caribou populations declined, but they always came back. In my language they call the caribou "ʔetthën", which also means "star." When the caribou come back, they come back so quickly, our people say "ʔetthën-nedele," and it means "the caribou will land."

I'm so confident about the caribou cycle that I've learned about from my elders that I made a bet with a biologist. His model predicts that if there's no hunting, no pressure the Bathurst herd, it will go up to about forty or fifty thousand by 2014. I told him it's going to be over a hundred thousand. So I bet him a thousand bucks, but I told him to make it easy on himself, to give me $250 a year over the next four years.

But just one more thing I want to say to everybody. You know, sometimes your body gets tired. You need to lay down and rest. Without anybody bothering you, just rest. When you wake up you feel good. We need to do this for the Earth, let it rest for a little while. For example, they study the dust that comes out from the trucks at the diamond mines, as far as thirty kilometres from the mine. They tell us there's more dust every year. If they don't shut that mine down and let it sit for a few years, or they get a hell of a good vacuum cleaner, that's not going to clean up. You have to stop the activities so the Earth can rest.

Fig. 10. "Our Turn to Help." Painting by Jan Adamczewski. Reproduced by permission of the artist.

My grandfather had a really good story. He said if you take a perfectly balanced log and put the insects on one end of it and human beings on the other end they'd balance. If you kill all the insects, the earth will end in three years. But if you kill all the human beings, the earth will recover in fifteen years.

For the sake of my grandson and your children, think about cumulative impacts on the caribou, so we can make wise choices now. And remember the caribou helped us a long time ago, when we needed help. Now it's our turn to help.

Marsi cho, thank you.

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Ekwǫ̀ and Tłı̨chǫ Nàowo / Caribou and Tłı̨chǫ language, culture and way of life: An evolving relationship and shared history[1]

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Introduction

My name is John B. Zoe. I'm a member of the Tłı̨chǫ Nation in the Northwest Territories. Up until recently, I was the chief negotiator that worked on the Tłı̨chǫ agreement that was given effect in 2005. I've been involved in the talks about decline of ekwǫ̀ (caribou), in the Northwest Territories, and an interim plan has been put together over the past two or three years towards gaining a better understanding of herds status and recovery.

We are now going to go back in time to long before co-management was even contemplated and before the Government of the Northwest Territories existed, back to the pre-colonial relationship between Tłı̨chǫ and ekwǫ̀. We will consider how this has changed over time, with our people being influenced by the fur traders and the global market economy.

When ekwǫ̀ declined, it really became an emotional issue for a lot of people, especially the elders, because ekwǫ̀ is what defines our language, culture and way of life. Since the time of Yamozha, the Tłı̨chǫ have lived in co-existence with ekwǫ̀, with rules and laws of respect and appreciation defining their relationship with ekwǫ̀. Even where we live, and where the communities are situated is because of ekwǫ̀. All the trails that we have, the portages, all lead towards ekwǫ̀ grounds. And all our original pre-contact clothing, our blankets, our moccasins, our tents, all come from ekwǫ̀. The carry-alls on our dogsleds, the harnesses, the ropes, the babiche, the snowshoes, everything is derived from ekwǫ̀, including a lot of the ancient medicines and tools.

Many of the placenames on the landscape relate to activities that happened while travelling to the barrenlands and back, following ekwǫ̀ migration. We now call them trails of our ancestors. On those trails, there are very many placenames that talk about the fisheries along the way, areas where the moose live, and the different types and methods of harvesting that are embedded in the landscape. So we know that the placenames are built in layers from pre-contact times. The placenames have a lot to do with harvesting, and the movement of people, and habitat areas for different animals. It was very important for people to minimize their impact in these areas when they were passing through, so that those habitats would continue to exist.

Our relationship with ekwǫ̀ defines who we are. It's a foundation for our nàowo – a Tłı̨chǫ concept that encompasses our language, culture, way of life, as well as our knowledge and laws. So it wasn't surprising that people would get emotionally involved when they learned of declining ekwǫ̀ populations, and wanted to know what was happening. When there was talk of reduced harvest, it became a very difficult issue. And it will continue to be difficult. Our revered former Chief Mǫfwi, who was a signatory to

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[1] *This paper is adapted from the author's contribution to the NACW presentation co-authored with Kerri Garner and Jan Adamczewski, "Tłı̨chǫ People and Ekwǫ̀ (Caribou): An Evolving Relationship And Shared History," as well as contributions to the NACW Aboriginal Talking Circles.*

Photo 1. Forty tents at Gots'okati (Mesa Lake), August 1988. (Photo: John B. Zoe)

the treaty of 1921, said that he and his people would not be restricted from carrying on their nàowo, and that includes hunting. So when people hear about targets on total allowable harvest and restrictions, it is perceived as an attack on who we are as a traditional hunting society.

Old and new pressures on ekwǫ̀

A lot has happened in our traditional territory since the pre-contact period when we lived intimately with ekwǫ̀, with the outside influences of the global market economy and trade leading to commodification of this sacred animal. As early as 1700, the European fancy for beaver pelt hats brought trappers and traders to the North, increasing the need for ekwǫ̀ as a trade item. This caused people to begin hunting on a competitive market basis, and thereby altered the relationship between man and animal.

The original trading posts were set up in our area not for the fur trade, but as provisional posts. The Tłı̨chǫ would sell their ekwǫ̀ to the post, only to end up purchasing it back later at times. Ekwǫ̀ had now truly become a product to be bought and sold. The trading posts wanted to buy and trade for as much ekwǫ̀ as they could. They would trade for tongues, drymeat, pemmican, anything they could get their hands on, so that could be distributed along the Mackenzie River to the other posts. That way, people working at those trading posts wouldn't end up eating all the trading goods. So the trade in ekwǫ̀ actually started over a hundred years ago in the 1850s, and that pressure continued until the early 1970s when ekwǫ̀ trade was stopped (though they were still trading for fish and other resources).

After the treaty when the lands were now open for development, new exploration started to happen. The first wave of exploration was the prospectors. It was small time activity, but even those people had to eat. When the early exploration camps were being set up, a lot of trade happened with the cook shacks. Ekwǫ̀ meat, ekwǫ̀ clothing and firewood were traded for flour and other groceries. You can still see the remnants of the wood piles out in the bush, especially at the old mining camps. Then the first cat trains (Caterpillar tractors attached to freight laden sleighs) came into the area to replenish the exploration camps, and those people needed to eat too, especially ekwǫ̀ meat.

In the 1970s, the communities were becoming more permanent and children had to go to school, and so all the hunters, the women and their families had to stay in the community. Since it was no longer possible to make the long trip to hunt ekwǫ̀ by land, hunters began using aircraft to fly to the barrens and bring back ekwǫ̀ meat. That became the norm in hunting, even till today, almost thirty-five years later.

Now we have a lot of exploration in our territory. We have three diamond mines, and there are at least two major ice roads going right into the barrenlands on the migratory path. The pressures are great because these roads are still public, so anybody can go up there and do a lot more hunting than was possible before. And there are other pressures, like motorized vehicles that can go where dogteams couldn't go before. There are a lot more ordinary citizens going up with private vehicles, like skidoos and four-wheel-drives. With gas powered machines you can go where nobody's foot has touched in the history of the world. More and more, people are using high-powered rifles. Successful hunting no longer requires that you get as close as possible to the animal, which required a lot of experience and patience in the days of limited firepower. With so much access nowadays, there's no sanctuary left anywhere for ekwǫ̀.

I'm not trying to say that we have been the only culprits. There are other pressures that have developed, especially with the emerging territorial government that established itself in the north in 1967 to promote tourism and economic activity in a suppressed small market. There was a lot of support for big game outfitting, including more access to non-resident hunters, and an allotment of tags to the aboriginal groups for commercial purposes. In addition, access to the mineral resources became possible. So, since the late 1960s, there has been a lot more activity, a lot more pressure on the landscape.

New management actions

I think everybody's learning a lesson from the current ekwǫ̀ decline. But how can we act on what we've learned? That is the big question. It's no longer possible to do things the same old way, the way it was under the old colonial systems and policies. We need to raise our voices in the aboriginal world. The *Revised Joint Proposal on Ekwǫ̀ Management Actions in Wek'èezhìı* that was submitted to the Wek'èezhìı Renewable Resources Board by the Tłı̨chǫ Government and Government of the Northwest Territories (GNWT, 2010) is a good example.

The first version of the proposal was done exclusively by the GNWT – and here we are in the 21st century! We raised enough noise to force them to pull it back. The board realized that they needed our nàowo and the involvement of aboriginal groups to make it work. It's a two year recovery plan (2010-2012). That will give us enough time to put our heads together and move beyond what we've done so far. We'll need to learn from how we've come up with this joint proposal, and apply it to a longer term plan with provisions for adjusting to the changing times.

The overall intent of the Revised Joint Proposal is to help Tłı̨chǫ relearn their traditional ways, their nàowo, and respect and relationship with ekwǫ̀. If these traditions are renewed, ekwǫ̀ will come back, like the elders have always said.

Our legends talk about ekwǫ̀ disappearing long ago. There have been times of scarcity and times of abundance. The elders have always believed that when ekwǫ̀ became scarce they would go away to be left alone – to recover and replenish themselves. They would then come back to offer themselves to the Tłı̨chǫ. When hard times came upon the Tłı̨chǫ and other aboriginal people, they turned to other sources of food – moose, beaver, muskrat or fish. The elders knew to always leave "seed on the land" in order to ensure that the species they were hunting or trapping would be able to recover. There was a mutual respect between man and animal.

The most recent memory of a time of scarcity was in the 1960s. At this time, the community of Wekweètì had to be evacuated to Behchokǫ̀ (Rae-Edzo) and Gamètì (Rae Lakes). This move led to significant changes in the political and social fabric of Tłı̨chǫ society. Due to an influx of people and lack of infrastructure in Rae, the community of Edzo was developed by the GNWT. During this period, the Tłı̨chǫ endured the greatest exodus of their children, who were taken residential schools in exchange for relief from the government. The Tłı̨chǫ culture and way of life changed as a new day school system and amenities such as a hospital further influenced the Tłı̨chǫ to live in communities and leave their bush life behind.

We know that scarcity is a reality that repeats itself over time. The big difference today is that there are a lot more pressures on ekwǫ̀ than existed in the era before industrial development, before the fur trade, when aboriginal peoples led a natural way of life on the land. Now we have a lot of development, we have a lot more people, we have new methods of harvesting. These modern pressures caused by humans are something that must be dealt with.

And so new management actions are being taken. But the harvesting targets that are allotted for our territory also provide a good opportunity to return to the traditional style of hunting, where we're actually reviving knowledge of the placenames. The placenames describe the state of ekwǫ̀ back at the beginning of time, so that by comparison with the present, it's possible to understand changes that have

Photo 2. Tłı̨chǫ elders and youth at Edzo's Rock, Gots'okati (Mesa Lake), August 1988. (Photo: John B. Zoe)

occurred. That traditional view needs to be shared, so that the scientific community can take those things into consideration. But that's like pulling teeth because the laws don't necessarily recognize the traditional view of rights and titles.

The only way to get our perspective recognized is through negotiations. Management regimes rooted in the laws and processes and imported from England just don't work. We need to ensure that our nàowo and the information that exists on the landscape is brought forth in a meaningful way. The practice of those laws that existed in pre-contact times have always been what ekwǫ̀ were comfortable with in their recovery.

Traditions for the future

The young people are going to inherit the decisions that we make. We need to ensure that there's something left for them to inherit. But the survival of future generations as Tłı̨chǫ in this environment requires that they remain rooted in their language, culture, and way of life.

Way back before the communities were established in the NWT, people would fish and hunt small game to get their food, wherever they were for the summer. But in the fall they would head out towards the barrenlands, following the ancient canoe routes, the waterways and portages. They would take their dry fish and the things they needed to get to where they were going, to where ekwǫ̀ were. They went only as far as they could carry food and supplies to survive on the barrenlands. Tłı̨chǫ did not control the land; the land controlled the people and their actions.

I remember that in my youth as a small kid, the whole community would rush to the shoreline, and the people would get in their boats and we would watch them leave. They would be gone for weeks. While they were gone, people were always talking about where the travellers might be and what they might have seen. A lot of stories would be told in the community by the old people who were remembering their own journeys on the land. So it was a really good time to listen to them. The community was waiting and filling time by telling stories about their own experiences.

Some of the young people who were brought to those trails were picking up a lot of information, especially around the camp fires. The elders say that the more camp fires you have, the more you know.

Among them they have thousands of camp fires. It's an information network. When they came back to the community, there was a big celebration with guns going off and people rushing to the shore to unload big bundles of dry meat. The meat was limited to what could be carried on the backs of the hunters over the portages on that two hundred kilometre journey, so it didn't last more than a week for a community that big. But the meat was less important than the coming together of a community, the coming together of new stories, and the knowledge and experiences gained by the young people. Those youth were always changed when they came back.

That stopped in 1972 when the aircraft was introduced in order to keep children in the schools, and allow people to continue hunting even though they no longer could take the full month needed for travelling by land. Between 1972 and 1988, all the hunters flew right to the barrenlands and brought their meat back to the community. Though the fall chartered hunts are not the truly traditional way of doing things, they did allow people to go to the barrenlands in a communal way, harvesting and practicing their traditional activities and ways of respecting the land.

Community freezers were installed. The availability of ekwǫ̀ was no longer limited to certain seasons of the year. It became available all year round, whether or not ekwǫ̀ close to the communities. The need to depend on other species at periods of time throughout the year now became a choice, not a necessity.

But all those stories of experiences travelling along the trails, the memories that were embedded on the land, were starting to fade from the community. Although the community still had good shooters, good hunters, they had no longer had the stories.

So in 1988, our community came together with the elders to have a discussion about culture, language, and way of life. One of the first things that the elders were saying was, "Take us to the barrenlands. We can't go by land now. But if we fly there, you younger people can go by boat and meet us there." So they flew, and we took the boat. We did that the first year. The second year and the third year, we made a side trip. But this initiative died in 1991.

So I hooked up with sub-arctic archaeologist Tom Andrews of the Prince of Wales Northern Heritage Centre. Tom wanted to do an archaeological survey, but he wanted to do it differently. He wanted to do what you call ethno-archaeology, which is about asking people about their history first, before doing the surveys. We needed someone to come with us. I had heard about the elder Harry Simpson from the community of Gamètì. He used to tell a lot of stories. I was very intrigued by this man. I asked him if he could come along with us, and he was just ready to jump in a boat.

We visited a lot of sites over the following three years. The elder showed us where they had the winter hunting camps. All the places that we visited were based on the stories of the old people. We plotted it out on a map and spent a lot of time visiting. Every site was an archaeological site, still used today. On the last year, we were sharing the same tent, spending twenty-four hours a day together.

One day the elder said, "You know, we've been travelling for three summers now and we've seen geologists, we've seen teachers on holidays, we've seen Americans, we've seen Europeans travelling all over, but we haven't seen any of our people. There's something totally wrong here. We have to get the young people out there, because otherwise our nàowo is all going to end up in a museum. That's the last place we need it. We need to get the information out to the young people. We should make an effort to get them out."

That was in 1994. Harry and I worked on it all winter, and managed to get five boats. So in the summer of 1995 we started taking out youth. We took out thirty youths the first time. We travelled ekwǫ̀ Trail, or the trail going to the barrens. We went all the way, almost to the barrens, and we followed the trail to the barrens from the next community. From there, we came back to where we started. It took almost a month.

Ever since 1995, we've been doing these canoe trips with the students and community members and elders every summer. Last summer we took out over two hundred and sixty people by canoe. In the last fifteen years we've taken out over a thousand people. But teaching language, culture, and way of life is not an easy task. It takes years. We've been doing it for fifteen years, taking people out over a week at a time.

If we say we're going to have to prepare our young people for the future, in order to protect our language, culture, and way of life, the important word is "protect." The only way to protect what you really believe in as your way of life is to build an army to protect it. But it takes a lot of training for those new recruits. Years and years of training for them to have as many camp fires as they can, so that they can have nàowo that they can pass on to the new recruits.

It all goes back to the beginning of time when the animals and people came together in a big meeting. They would feast, and they would dance. They all had to come together, but very many of them were far way and they could not wait until those ones arrived. They started the festivities and were dancing. By the time Notaa arrived people were petered out, animals were petered out. So Notaa started to sing a song. Then the dance started again and it really became strong. And Notaa was so tired that he just fell back, and they danced over his feet. That's why today he still has flat feet.

The gathering was closed off with a dance. It's a tradition. When there was a dispute resolved between tribes, it was closed off with a tea dance. When the early traders came into the area and we traded with them, it ended with a tea dance. When the treaty parties came in and the people accepted treaty, they ended with a tea dance. Those are what you call traditions. Tradition is an activity to remember your own history, and pass it on to the future. It's to strengthen the young people. It's very important for them to be involved. But it's not an easy thing. You have to do it over and over and over again.

Yes, in the old days when people were living in the bush, the old people had everybody with them. They were living the life and talking to the youth every day. Now we not only have to do the activities on the land, we have to push it in the schools as much as we can to bridge that gap and recover what we have lost. Our children have a right to enjoy ekwǫ̀ as we once did. It is our responsibility to begin to change our thinking and expectations, to give the herd an opportunity to recover. The future really belongs to the youth.

Masìcho, thank you.

Ekwǫ̀ Trail: A Childhood Memory

On the way back from the barrens, we always stopped on a certain island. Harry remembered this place. "We were here a long time ago," he said. He could see these old tent rings over here, old camp fires. All of a sudden somebody found something. It looked like an eagle feather, but it was made out of wood. Nobody knew what it was, so I gave it to Harry. He said, "Oh, that's dechı̨ tsetłu. I remember that as a kid. I remember the person who made this thing. We were here."

And here is the story that Harry told: "Late that spring after living among ekwǫ̀, we were now going north to Hottah Lake. So the elder left in the morning and we followed by dog team, but it was slushy. The dogs couldn't pull very fast, so everybody walked across Faber Lake. They walked and walked and walked. Finally they got to where the old hunters were. The hunters were laying on a rock resting, because they had just shot over ten ekwǫ̀. So they made camp and they did all the preparation of the meat and the hides. It took them a couple of days to make dry meat and hang it up and get it all ready to move. But the sun was so hot that not even the sled could be pulled with all the weight of that meat.

"So the elders all got together and one of them carved out what looks like an eagle feather. They attached a piece of babiche to a short stick. Then they got young people, because they have lots of energy and power, and made them stand on a little rock. I was one of them, as a kid. They made us stand there and take this stick, and swing it around our heads. And it's called dechı̨ tsetłu. It was notched in such a way that it made a whirring sound. What they were doing was calling the north wind. Sure enough, the wind started to pick up. It blew from the north all night long, and in the morning everything was frozen. They were able to load their sleds with the meat and started heading north towards Hottah Lake, towards what they call the noeʔe, which is the place where ekwǫ̀ would swim across. Ekwǫ̀ crossing before they head back to the calving grounds. The idea was to get there to do the last harvest of the season. And they made it there."

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Renewing our traditional laws through joint ekwǫ (caribou) management[1]

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Introduction

Fred Sangris is my English name. When I was born, my grandfathers gave me my Dene name, which is Nogache or Wolverine Tail. To my community I'm a hunter and trapper, and the last of the Yellowknives Dene who have trapped on the barrenlands north of Yellowknife. Over a period of about twenty years, I used to spend up to five months of the year in the barrenlands trapping white fox just south of Lac de Gras where the diamond mines are placed today. My life has always been on the land, with the wildlife, with ekwǫ̀ (caribou). I was very happy to be born into a family with a unique culture and way of life. Our ability to live on the land with the wildlife is something that I'm very proud of, to this day.

I'm a former Chief, and former Grand Chief. In 2010 I negotiated a harvesting agreement with the Government of the Northwest Territories (NWT) for the Yellowknives Dene First Nation, so the Aboriginal people can harvest their traditional foods.

I'm going to talk about how we can co-exist and still walk side by side with ekwǫ̀. We need to really work on that.

I'm going to share a story with you. My grandfather David Sangris was born on the Coppermine River around 1865. He was born there, living on the land in nomadic times. Nothing came from stores or from the European trade. They lived mostly by themselves in the traditional way on the Coppermine River, surviving on muskox and ekwǫ̀. Clothing, everything came from there. My grandfather and his family didn't own a rifle. They were still using bow and arrows, spears, snares, traps.

When I was born in 1957, my father was still driving sled dogs. My grandfather lived with us at that time. I remember in my early years travelling by dog sled across many, many lakes in the NWT, just north of the city of Yellowknife. Then I was introduced to ekwǫ̀. I had never seen this animal before. When I first saw them, I asked, "Grandfather, why are there so many sled dogs on the lake? Big sled dogs. And they're all wandering free!"

He said, "Those are ekwǫ̀. They are our traditional food, given to us by the Creator. Ekwǫ̀ is there to take care of us until the end of time."

I truly believe that ekwǫ̀ did come to live with the Aboriginal peoples of the North, and ekwǫ̀ has always sustained them. To this day we still harvest ekwǫ̀ as we have done for many, many generations.

Understanding traditional law

In my youth, my father would take me to the barrenlands every year just after I got out of school. He said, "I'm going to teach you, so that you will be knowledgeable. Before you harvest animals, you have to learn to understand them. The way they think, their habitat, the way they live, what they eat. Before you harvest ekwǫ̀ you must understand them first. You must understand the names of ekwǫ̀ and the reason they're doing what they do, migrating, going to the forest from the arctic barrenlands and back again. And there are traditional laws that come with ekwǫ̀. Every Aboriginal child has to understand the laws pertaining to ekwǫ̀."

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[1] *This paper is adapted from contributions by Fred Sangris at the NACW Aboriginal Talking Circle.*

Because I was taught those skills, today I take care of my game in a manner that is respectful to the Creator. My father explained to me the traditional names of the parts of ekwǫ̀ – the antlers, head, hide, hind quarters, intestines, hearts, kidneys, livers. In our language we have names for all the parts of ekwǫ̀, similar to the names that scientists have given all those parts.

Our knowledge goes back thousands and thousands of years. Some of the stories are so old that they have spread out among the communities. Many communities share these stories. The stories are still there.

There are laws with ekwǫ̀, traditional laws that go back hundreds of years. These laws apply not only to my people, but to many of the Aboriginal people throughout this whole country who depend on moose, ekwǫ̀, muskox and buffalo. We all come from different communities, different languages, but all our minds are the same. Our hearts are with ekwǫ̀ and we have great respect for this sacred animal that we all depend on.

In my younger days I learned about the Aboriginal biology of ekwǫ̀ from my grandfather and my father and many of the older hunters who I travelled with. Over many campfires, they explained to me the importance of ekwǫ̀ and the laws that go with them. One of the first things I was taught as a child is to respect and honour ekwǫ̀, because without this herd many of my ancestors would have perished and would be gone. Ekwǫ̀ give us life, so in return we have to do our best to guard and protect them.

My grandfather told me many years ago that ekwǫ̀ had a great concern one time. He wanted to talk about his concern. So he called upon the man and said, "I want you to gather as many animals as you can and people from all this land. I want to talk about laws and how I should be used in the future, because right now I don't like what's happening with me. When the wolf takes me down they do all sorts of things to me and I'm not happy with it. I want to talk about making laws."[2]

So a big gathering was called where all animals came together. Ekwǫ̀ talked about how he was being handled and how he was being abused and how there were laws that weren't followed. He blamed a lot of the things on the wolf and fox, and told them that there has to be a law for how he would be respected and used in the future.

And ekwǫ̀ said, "From now on, if the wolf takes me down, he shall not break my bones or chew my bones. That I don't want. I would like a law put in place so the wolf and fox will respect me and use me wisely and not scatter me all over." After a long discussion the wolf agreed, the fox agreed. Then they talked about the laws for other animals, including the ravens, birds, mink, marten, everyone that came. They agreed there should be laws put in place that they should all respect each other.

The meeting was over and they were ready to leave, there was a voice calling, "What about me? What about me?" They looked all around and they didn't see anybody, but they heard a voice. They looked down on the ground and saw a small little ant. He said, "Me too, I live on this earth. I don't like how the moose is kicking my house and animals are digging my house. When it rains I have a hard time with my family. When my house is broken I can't survive in the winter. There should be a law in place that when you see my house you don't break my house, but walk around it."

And a man was invited to witness this great gathering. The man was told to take all that he heard and pass it on, make laws and pass it on to not only animals, but all the people as well. They should have respect for the animals, and treat them with great care.

Today in my village we still live by these old traditional laws. When I came back from hunting, my old man used to ask me, "When you took ekwǫ̀ down, did you give honour to ekwǫ̀?" I would say, "Yes, I took his right hand, I put it on my forehead, and I shook it and I said, 'Welcome. You've come back to me again, and I'm happy to use you and I give great thanks to you. But I hope that in the future you will come back to me again in great numbers.'" So we still practice those traditional laws on the land.

One time I was hunting with an elder and we were cooking ekwǫ̀ kidneys. He said, "Young man, you can't eat that. That's not for you. You're not an elder. You should leave that alone." So I learned very quickly about the traditional laws of ekwǫ̀.

One must not hit or abuse ekwǫ̀ or wildlife in any way. When you shoot ekwǫ̀, you perform a small ceremony. You thank the Creator for this animal who has given up his life so that others can live. Once that animal is honoured, then you take care of it and bring it back to your families, to your villages, to share among the elders and people. Those are old ways that are still practiced today in some communities.

My father didn't put me on the barrenlands to punish me. He put me there to learn. I didn't go to an institution to learn, to sit behind the four walls and try to understand ekwǫ̀. The best way to understand those species is right there on the land. You have to interact with them. You have to watch them daily.

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[2] *A Sahtúot'įnę/Délįnę First Nation version of this story is discussed in Walter Bayha's contribution to this volume.*

Watch what they eat. Watch what they do. Aboriginal people learn by watching the behaviour of ekwǫ̀. We don't learn about wildlife behind four walls. We learn by being in the field, by being with ekwǫ̀ all the time.

An ancient management system

Aboriginal people are very careful. We have been managing our resources for generations, way before the arrival of the Europeans. If we didn't manage them, there would be no ekwǫ̀, there would be no buffalo, there would be no animals on earth. The same thing goes with the fish. We don't fish out the whole lake. When one lake is fished out we move on to the next one. So we're very careful. We have to manage the animals because this is our food source. We still make sure that our stock are not thinned out. We make sure that the food source is going to be there for many generations after we're gone.

For example, one time my grandfather said, "Go hunting in this area. Get some moose, get some ekwǫ̀. But once you've hunted there, don't go there again for a while. Go to another place, and harvest other animals too as well. Because if you stay in one area too long you continue to harvest the same animals, eventually they're going to thin out and disappear." So as Aboriginal people we've learned to manage our wildlife. We've learned to take care of our food source. We've depended on these animals for thousands of years, and we still continue to depend on them today.

What's happening today in my community is that the young people, my young generations are not following those protocols. They're not being taught. So I'm trying to push a hunter education program in my community to bring back the old traditional ways and the cultural ways, and teach the young people about respect and only taking what you need. I see young people bringing in many ekwǫ̀ come down, fifty or sixty. I see no reason why such great numbers are taken.

I'm not a leader in my community, but as a hunter I take responsibility. I step forward and I'm going to try to do my best to work with young people to bring back education in our culture, hunting skills and the traditional laws of the people and wildlife. We need to go back to these laws because ekwǫ̀ said, "If you don't keep the laws I will go away, and I might not come back." This is what we've got to think about: respect, and bringing the laws back, and trying to protect the sacred animal.

Working together

Other peoples have come to this country. They want to manage and control the animals and to have authority over them. For example, nowadays biologists are flying out on ekwǫ̀ surveys mostly on their own, with no participation from Aboriginal communities. This leads to conflict. The only way to avoid those conflicts is to have collaboration. If you put Aboriginal knowledge and the scientific knowledge to work together, it will be possible and find a way for ekwǫ̀ to be managed well for the future. One group cannot go and study animals and make decisions by themselves.

I've always believed that science is a good thing. But it's still young. Aboriginal people were the first scientists in North America, and that information is still there today. The scientific community needs to get involved in our communities. They need to work out arrangements with the Aboriginal peoples, ways of collaborating and bringing science and Aboriginal knowledge together. The scientific community has to engage with Aboriginal people and strike up cooperation. You have to do it that way, because the elders, the people, the hunters, the harvesters have knowledge of what the scientists are trying to understand, thousands of years of information.

Today we live in a very different world. It used to be I was travelling with sled dogs and living my traditional, cultural life as a Dene, as my grandfathers and my fathers did before me. Now I live in two different worlds. I'm educated, and I also live in a very traditional world. I've been working with scientists for about ten years now, and I've seen how scientists collect their data through surveys. This is good too. But I really believe that science and traditional knowledge can go hand in hand.

Changes on the land

A lot of changes are happening in ekwǫ̀ nowadays, whether it be climate change or activities on the land. Where I come from north of Yellowknife there is a lot of exploration going on, winter roads being built. When they find minerals, industry will pressure governments until they get what they want. But when they don't do proper planning at the beginning, the results can be really devastating.

There are two mines in the city of Yellowknife near where I grew up, Con Mine and Giant Mine. Both mines have really devastated the whole area. It will take a thousand years for those mines to clean up themselves. And the people who got rich off the mines walked away. But my community has to live with that mess. We're facing the consequences today through illness, bad water, many problems. Governments must do their best to get a grip on industry. Industry has to be managed.

The rules in some areas are too flexible and some rules are not really good. For example, I know a non-Aboriginal person who went and got a moose and he didn't have a licence. He knew he was going to pay a fine. What he told me was, "I know I'm going to pay a fine and it's going to be $200 or $300. That's nothing. I'll pay that up and I'll still keep my moose." These are the kinds of things that are happening up North. People are taking advantage because the penalty is too low.

Ekwǫ̀ are thinning out where I come from north of Yellowknife because of many things: mining activities, overhunting. I never see Aboriginal people overhunting. They always take home what they can provide for their families. But access to winter roads is a big problem. It brings in poachers from all over. The wildlife officers in the community go home at 5:00 pm and the poachers are out at 6:00 pm.

When the Crown came into this country, Aboriginal people had a treaty agreement that our way of life would not change, that we would continue to hunt, harvest, and provide for our families. In the North where ekwǫ̀ are thinning out, we have to take action. We must protect those calving grounds, the home of ekwǫ̀. There are people who are exploring for gold at the calving grounds. If we don't put some kind of protection on the calving grounds, those ekwǫ̀ are going to have problems. It's like disturbing a bird nest. If you disturb a bird nest, the birds don't come back. Same thing with ekwǫ̀. If you disturb the calving ground, they'll go elsewhere. They may decide to disappear.

Ekwǫ relationships

Ekwǫ̀ are part of this world. They're part of the ecosystem. They were brought here by the Creator to live alongside us. After many thousands of years, they remain wild animals, free and roaming. People are still trying to understand why ekwǫ̀ migrate back and forth. Maybe that a question that the scientists should take on: Why do they migrate? There must be a good reason for it.

In northern Canada we have ekwǫ̀ all over northern parts of the Arctic Ocean, all the way from Alaska, Yukon, NWT, and then Quebec, Innu, Labrador, even as far as Newfoundland. There's ekwǫ̀ all over the place. I've talked with many elders, and the elders always say that all ekwǫ̀ are the same, whether they're barrenland, woodland, or mountain ekwǫ̀. They know each other. Sometimes they migrate. When they migrate they migrate together. No one has done a DNA study of all the herds from Newfoundland to Alaska, including the NWT and the coast to determine if ekwǫ̀ are all related, or if they're different herds. That's something we should find out.

One time I went to Colville Lake, a very small community in the NWT of about a hundred people. That's the population. One of the elders was sharing a story with me about ekwǫ̀. He said in 1946 the whole migration of ekwǫ̀ went through Colville Lake and to Mackenzie River at Fort Good Hope. The elders thought ekwǫ̀ was going to stop at the river and go down the river to the rest of the communities. Strangely, ekwǫ̀ did something they had never done before. They crossed the Mackenzie River and disappeared into the mountains in the Yukon. The hunters tried to follow them by dogsled. But it was impossible for them to follow ekwǫ̀ into those rugged mountains. For about ten years after that they never had any ekwǫ̀. Then one day ekwǫ̀ returned and not just a few hundred of them. They came back in the thousands. It was very unusual.

Nobody knew where they went or what they did, but they were gone for years. The elder that I talked to thinks that they might have gone to migrate with the other herds. I asked him, "Why do you think they would have migrated together with the other herds?" He said, the way nature works is that ekwǫ̀ could be in big numbers, but in some years the breeding bulls are not there. When the breeding bulls are not there, immature bulls will take over. There is more inbreeding, and the herds become weak. The calves are not strong; many don't survive. He said the cows sense that something is wrong, so they leave, and migrate with other herds. Then years later they come back, when they're strong again.

I have been monitoring the Bathurst herd north of Yellowknife for many years. The scientists say that the herd was 350 000 in 1996, and more than 128 000 in 2006. Then in 2009, just a few years later, it went down to about 32 000. A big drop. We were trying to find out where the 100 000 ekwǫ̀ went. We asked the pilots, we asked the exploration companies, we asked the mines to keep an eye out. If they found 100 000 carcasses on the land somewhere, that could be the answer to the disappearance of all the ekwǫ̀. But no one to this day has found anything like that.

The elders suspect that ekwǫ̀ have probably gone east because there's been too much exploration or drilling going on in the calving grounds. And at the same time, the calves are not strong. And heavy sports hunting is going on for big game, so for years and years the mature bulls have been taken out. The elders believe the cows might have sensed something is wrong and gone to join other herds.

The older people who are former hunters suspect something is going on. Now we have climate change, we have a warmer climate. Ekwǫ̀ are acting very strangely. They're going west, east, and in the last couple of years ekwǫ̀ that my community and the Tłı̨chǫ community depend on wintered over in Contwoyto Lake, which is up north near the calving grounds. By November, many of them haven't migrated down yet. I talked to an elder and he said, well, there are no leaders. There are no mature bulls to take the lead and guide them to the tree line and into the forests. So the younger ones are kind of lost and out there trying to find their way.

The scientists have been doing studies on one herd at a time. So if a herd moves over to another neighbouring herds, they may be count the same herds again the next year. So I believe there needs to be a counting of all the herds all at once, in one season. This way we can determine the numbers.

Taking responsibility

Last winter was very hard for our people because of the ekwǫ̀ decline. The elders in the community, some of them who were diabetic, wanted to get the hunters to go on the land and bring some lean meat back because the diabetic people can't eat meat from the store with all the fat on it. Ekwǫ̀ is very lean and it's really good diet for diabetic people. So the hunters went out, and ekwǫ̀ were taken away from them. I could see that in the future things were not going to be good. I don't want these crises to continue.

There was a chance to get people together, to make people understand that this is not the way. Working together, we could find another way to work with ekwǫ̀ and protect ekwǫ̀.

In 2010 I was appointed by the Chief of the Yellowknives Dene to lead the negotiations with the NWT Department of Environment and Natural Resources (ENR) to come up with an agreement. The Chief instructed me to find a way to make it possible for my people to still continue to hunt, while at the same time addressing the ekwǫ̀ crisis by taking only what we need, so that we do our part in conservation.

It was very hard for my elders to talk about coming to an agreement. I sat down with them, and I talked to them in my language. I told them that if we don't do this there will be more crisis. If we don't make an agreement, soon there might not be any ekwǫ̀ left at all. The time has come where we have to take responsibility, and do something to protect ekwǫ̀ like we always have. I told them that yes, we do have treaty rights to hunt, but with that right comes our responsibility as stewards. Then they agreed. They said, "You're right. We have a right, but responsibility is another thing. It's a bigger thing. We have to work on that."

So with that they gave us a mandate and their blessings, and we went to negotiate an interim agreement with ENR that was signed by Yellowknives Dene Chiefs Edward Sangris (Dettah) and Ted Tsetta (Ndilo) on October 7, 2010[3]. It's only for twenty-four months, two years, until ekwǫ̀ comes back. In a year we're going to review it and then determine what we should do. This is the first step in taking measures that are important to our community.

We want to do our part. We want to make sure there are ekwǫ̀ for future generations. I would like to go on the land one day with our young children and tell them, "Look, there's ekwǫ̀ there. They're still surviving because years ago we did something right. We took measures to protect them and they're here." We can still use and harvest ekwǫ̀. But because they are sacred and they look after our communities, we have to go back to our traditional laws and ways, and respect ekwǫ̀ and try to protect them as much as we can.

The Yellowknives Dene of Dettah and Ndilo are very cultural people, though we live right next to the big city of Yellowknife. We have little to do with the city that grew up beside us. Our villages are older than the city. Every fall, many of my people fish for their winter stock. We hunt not only ekwǫ̀, but also moose, and even the buffalo that have moved into our area over the past few years. My elders are afraid of buffalo, they think we shouldn't eat them. Never before have we had buffalo on our land. Now we're trying to understand how we can get along with this new species, and how we can use that and take less ekwǫ̀. We also have other animals, like birds, ptarmigan, rabbits, many other kinds of food that we can depend on.

I believe the interim agreement that we made is a really good one. I think it will work for us and I think the Yellowknives Dene are going to go out and work jointly with ENR to ensure that ekwǫ̀ are monitored and taken good care of, and that our hunters are taking only what they need. We have to try to take responsibility and I think the Yellowknives Dene have done that. Many years from now, ekwǫ̀

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[3] *Barren-ground Caribou Harvesting Interim Agreement Between Yellowknives Dene First Nation And the Government of the Northwest Territories. A press release and backgrounder on this agreement is available online at http://www.enr.gov.nt.ca/_live/documents/content/Yellowknives_Dene_and_GNWT_Sign%20Agreement.pdf. Accessed December 18, 2011.*

will continue to be the topic of many of our meetings. The issue will not go away; the discussion will go on for a long time.

That’s all I want to share with you. Hunter education is really important. As Aboriginal peoples of this land, we all have culture. We all have language. But behind our language are our laws. They may be invisible, but we can put them in writing and start using them and pass them on to our young people, so that in the future they will also take responsibility to protect ekwǫ̀.

Masì, thank you.

The 13th North American Caribou Workshop
Winnipeg, Manitoba, Canada
25–28 October, 2010

"They're going to come back"[1]

Gabriel Nirlungayuk

Rangifer, Special Issue No. 20: 81–82

Introduction

I come from Rankin Inlet. I was born in a place called Pelly Bay (Fig. 1), but the real name is Arviligjuaq, which means "place with lots of bowhead whales." I belong to the Netsilingmiut, People of the Seal. Seal is very important to us. But it gets cold up there, so tuktu (caribou) was very important for clothing for my people. Without the tuktu, people would not have survived in the very harsh climate where I come from.

I come from a matriarchal society. My great-grandmother was very strong woman. She made sure that all of her kids and grandkids respected the skills of the woman and the knowledge of the woman. My great-grandfather had a sense of humour. When he was asked if he was going to do something, he always said, "I've got to check with the boss first." That's how strong my great-grandmother was. She stood up to Stuart Hodgson. At that time Stuart Hodgson was Commissioner of the Northwest Territories (which included what is now Nunavut Territory), telling the people up in Pelly Bay to move to somewhere else where it's cheaper. My great-grandmother stood up to the government, and now that community has thrived.

Our people kept their traditional ways alive for a long time. It wasn't until about a hundred years ago that Netsilingmiut had contact with outsiders. A hundred years is not a long time. Knut Rasmussen was one of the first outsiders that they met, in the 1920s.

I want to share just one story about the tuktu. I come from a large family and I was the oldest. My mom was the oldest in her family. My grandmother was the oldest in her family. I barely missed my great-grandmother making kids, but I remember quite clearly when my grandmother was making kids. I have uncles that are younger than me. So every month it seemed like there was a little baby coming out from somebody.

I guess it was because I was the eldest, I became the gopher for my great-grandfather. My uncles knew that this kid could be told what to do. So I was told what to do a lot. But I didn't mind, because I was learning a lot from my grandfather and my uncles. One time in the early 1970s, being young and naive and not knowing any better, we were seal hunting in the spring time by canoe. We went up to the top of a little island, about maybe two hundred feet up. He wanted to go check out where he could safely travel, because there was still broken ice around there. We came out on top of this hill, and there was an old cache.

When I saw the cache I started laughing, thinking somebody must have been very stupid. My grandfather said, "What's wrong?" I told him, "Somebody's stupid. They dragged a seal all the way up here, two hundred feet up, and buried this seal." I was still laughing. But he said, "No, that's not for seal. Many generations ago there were lots of tuktu here." I thought to myself, "Yeah, right, Grandfather. We have to go hundreds of miles to catch tuktu." At that time I would go hunting with my grandfather and my dad towards Baker Lake for days on end, and we were lucky to get tuktu. We were lucky to get two.

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[1] *This paper was adapted from contributions by Gabriel Nirlungayuk, the Nunavut Tunngavik Inc. delegate to the NACW Aboriginal Talking Circle.*

We were really lucky if we got five. So we had to go far to catch tuktu.

Then my grandfather said, "They're going to come back." In my mind I was thinking, "That crazy old man doesn't know what he's thinking. He's getting too old." But sure enough a few years later, before my grandfather died, it was October and we were fishing, and I saw smoke or fog up there. All the men were busy fishing. I looked again, and there was smoke or fog. The river was freezing up, so there was supposed to be no river up there. So I said, "Grandfather, there's smoke up there." When I said that, the men started looking up and took out their binoculars. I noticed they were getting excited. They shared the few binoculars that they had. "Tuktu, tuktu!" they said. "Lots of tuktu!" I saw it first, so my grandfather told me, "You're a man now, you saw it first." So I was a big man. I was just a kid, but he made me a man, he was so proud of me seeing that tuktu first. That day we caught many tuktu, at least five per person, and there were twenty of us.

Fig. 1. The author's son and caribou herd outside of Rankin Inlet. Credit: Gabriel Nirlungayuk.

At first I struggled cutting up tuktu. I didn't know how, but I tried. Then my grandfather said, "You'll learn soon enough. It will just take you some time." That's my little story about tuktu.

Up in Nunavut we're going through a lot of changes. It disheartens me to hear what people are going through with the impacts on tuktu and on the land from my southern First Nation friends. We're very lucky up in Nunavut. We're not too concerned about the tuktu. But there are a lot of pressures from the mining companies. We have very large uranium deposits right in the calving grounds of the Beverly-Qamanirjuaq herd near Baker Lake. The Bathurst and Bluenose East herds go right up on the west side of our territory, and we hunt them. And up in the High Arctic is the Peary herd. So like my First Nation friends, tuktu is very important to us.

We have an agreement between our Government of Nunavut that we have to go towards *Aajiiqatigiingniq*, consensus decision-making. We have to discuss what we're planning to do. The government cannot do it on their own. They know it, and we know it. We cannot do it on our own either, so we have to collaborate between the hunters and the government. Some of the concerns are exploration camps, helicopters going back and forth. As we've heard from other speakers in the Aboriginal Talking Circle, there are lots of fast machines now that affect our impact on the herds.

The elders tell us that when tuktu start coming from the tree line, don't hunt the first ones. Let the leaders go past, so that the herd will reach other people further north. Then hunt the late ones. We're starting to hear that from our elders. The elders also tell us to use everything. Don't leave carcasses. If you're going to leave some of the food, you have to cache it so you can go back to it. There's a big push up in Nunavut now to make the clothing. It is very inexpensive, but it takes skill. So there's a push now for young women to learn the skills. We both need each other, women and men.

Quyanami, thank you.

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Surviving with tuktu (caribou)[1]

Devalynn Pokiak

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Rangifer, Special Issue No. 20: 83–84

Introduction

I'm Devalynn Pokiak, from Tuktoyaktuk, Northwest Territories. The name of my hometown means "it looks like a caribou" in our Inuvialuktun language.

I'm going to high school. My dad took me out of school to come to this conference for an experience, to see what he does in these places. It's my first time in a big meeting like this. It's pretty cool.

I'm an Inuvialuit hunter and trapper. In this Talking Circle we are Aboriginal, so far apart and yet we all have the same respect and relationship with the land. Without our tuktu (caribou) thousands of years ago, we wouldn't have been able to survive. I was also taught to use every part of tuktu that we kill. Tuktu gave us food, clothes, and even shelter.

Biologists want to try to help tuktu, but they aren't really helping them by moving their equipment right into tuktu territory, making tuktu move away. Studying them and then doing nothing to help them when they're done, just leaving their mark. And my generation will have to clean up all the mess that the government left behind.

Traditional knowledge for survival

I believe what the elders say about wolves. Wolves need tuktu, and tuktu need the wolves. Wolves use tuktu for food. Tuktu need the wolves because wolves kill the unhealthy and weak that can't survive. They leave the strong tuktu. If wolves weren't there, the weak and unhealthy tuktu would have calves that are weak and unhealthy too.

Without the traditional knowledge that our elders taught us, we wouldn't be able to survive. My dad always took me out hunting, ever since I was a little kid. I know our land around us. I know what kind of animals we hunt and what we need. I notice that most of my friends don't ever go out hunting, and their parents don't know how to hunt. So my friends don't have a chance to learn what I know about the land. I always try and talk to them and tell them stories, what I hear from elders.

Learning from others

I really find this conference interesting to come to, and know more about what's happening. I know about my side of the territory, and now I am trying to learn what people from other places are talking

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[1] *This paper is adapted from Devalynn Pokiak's contributions to the NACW Aboriginal Talking Circle.*

about. Even though we're all different, and we talk different languages and have different cultures, we all do have the same respect and the same relationships with the land. I find it really interesting that we're all somehow connected, all of us. We're all the same.

Quyanainni, thank you.

How Tuk got its name

Although *Tuktuyaktumiut* live in the modern world, we try to hold onto our stories, like this one about how Tuk got its name.

As the story goes, there were some caribou that were about to cross to a point of land near where Tuk is today. A young woman was sick, so the people told her, "Don't look out at the caribou, you're sick. Something might happen to the caribou." She agreed, but when the caribou started swimming across to the point she peeked, and the caribou turned into rocks. To this day, you can see the stone caribou when the water is low. That is how Tuktoyaktuk or, "something that looks like a caribou," got its name.

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New caribou crisis – then and now

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Abstract: The reported decline of the Bathurst herd has caused considerable concern and has raised rumours of a "crisis" in which there is a possibility of extinction. This paper reflects on relevant lessons learned from the officially declared "crisis" of population decline in 1955/56 and a second crisis of overpopulation identified by the author a decade later.

Key words: Barren ground caribou; Bathurst caribou herd; Canada; crisis, management history; population decline; resource management; traditional knowledge.

Rangifer, Special Issue No. 20: 85–102

Introduction

The recently estimated declines in the Bathurst herd and other migratory caribou has become a matter of grave concern to the governments of the Northwest Territories (NWT) and its neighbouring jurisdictions. With Bathurst herd estimates of more than 100 000 in 2006 descending to about 32 000 in 2009 (NWT Environment and Natural Resources, 2009), concerns have escalated to a point where the Bathurst herd at least is said to be threatened with extinction[1]. In my preliminary review of information pertaining to the current condition of the Bathurst herd, I found a disturbing similarity between the conditions associated with the alleged Bathurst herd decline today and that of the mainland herds some 60 years ago. Wisely, the term "crisis" has been avoided in official documents; however the sense of anxiety that has pervaded meetings, press releases and documents has brought about proposals for measures to stop the decline and/or bring about a recovery of the herd that, as in the 1950s, were ill-informed, premature and inappropriate and could be harmful to caribou in the future.

My objective in this paper is to explain how the lessons I learned during the 1950s and 1960s might be relevant to the management of the Bathurst herd. Then as now, knowledge of the status and condition of caribou herds was a quagmire of conflicting reports, differing perspectives and great lacunae in the management data available. I want to offer a cautionary tale about the earlier conceptions of crisis, and discuss lessons that might be used to avoid inappropriate crisis management actions in future caribou resource decisions.

This paper reflects on methods in understanding caribou population dynamics and harvesting as two critical aspects of caribou management. I begin by providing a brief description of my own scientific and experiential formation in order to properly situate my perspective. Subsequent sections reflect on two contrasting management scenarios that emerged from distinct census approaches in the 1950s and 1960s: the officially declared crisis of declining caribou populations in the 1950s, and my own argument put forward in the 1960s that there was an impending crisis of caribou overpopulation, and that contrary to the prevailing view, harvesting could play a positive role in caribou conservation.

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[1] *"The proposal concludes that if hunting continued at the 2008/09 levels, that the herd may be eliminated in 4 years" (Gunn, 2010).*

The first so-called caribou crisis was defined by leading biologists in the 1940s and early 1950s, coming to a head, so to speak, in 1955/56. This was based on the assumption, ill-founded in evidence, that the migratory caribou populations of the mainland NWT were in serious decline brought about primarily by indigenous hunters engaged in "wanton slaughter" of caribou and by wolves. It was argued that this situation would inevitably lead to the extinction of those caribou, if not controlled immediately. This author hypothesized a contrary kind of crisis ten years later (Ruttan, 1966), arguing that burgeoning populations (especially of the Bathurst herd and augmented by the Beverly herd) would soon exceed the carrying capacity of their range and "crash" if not quickly reduced by systematic hunting of 100 000 or more animals for several years.

I argue that the prevailing conception of crisis during the 1950s and 1960s focused on maximizing populations and minimizing hunting without adequate regard to the complex factors affecting population dynamics. This situation, in my opinion, is still operative with regard to the Bathurst herd..

I have not been directly involved in caribou research or management in the NWT since 1969, but was an observer of the so-called crisis of the 1950s and an active participant in the crisis of the 1960s. Unfortunately, my extensive personal files pertaining to that period were lost, although at the time I submitted full reports of my findings to the Canadian Wildlife Service (CWS). I have to rely on my vivid memories of the period in these reflections, leaving archival and scientific verification to a younger generation of researchers. Moreover, my own training and experience during the 1950s and 1960s is the window through which I view caribou ecology. It is not within the scope of this paper to compare my perspective with recent theoretical and applied developments in caribou population and conservation science.

I bring a unique historical perspective to the complex topic as a result of my dual grounding in wildlife management and ecology, and traditional indigenous knowledge as it was practiced by people still living on the land 60 years ago. It is my experience that the two areas of knowledge enrich each other and together they provide a clearer picture of the interaction of land, people and animals that we are seeking to learn about. As there are few living today who have these memories, it is my modest hope that my experiences from an earlier era might shed light on management approaches in addressing current concerns about declining caribou populations.

From classroom to field experience

Since my perspective concerning the cause of the alleged decline of the Bathurst herd and the response of governments to it may differ noticeably from that of the government biologists, I believe that I should describe the two key aspects of my training and experience that have shaped my point of view, including formal science-based management training and field experience.

I received my academic training and a Bachelor of Arts and Sciences degree at the University of Saskatchewan in 1950, where development of my credentials for caribou management included informal training in wildlife management with D. S. Rawson. I was one of his research assistants in a regional study of the suitability of impoundments for the introduction of pond fish (Rawson & Ruttan, 1952)[2]. Rawson was a specialist in limnology; moreover, his knowledge of ecology and of the management of renewable resources was of the highest order. While his knowledge and insights were wide-ranging, several key principles he espoused have remained with me and guided my approach to wildlife management throughout my professional life: *Get the data* before *you come to a final conclusion; it is all right to speculate, if you do not confuse speculation with fact; and, do not overlook an anomaly in the data simply because it is not statistically significant – it may be of great importance.*

Most of my training in caribou ecology, however, was through hands-on experience as a hunter and observer of caribou and of indigenous hunters that began with my first observation of barren ground caribou near the Churchill River at Buffalo Narrows in the winter of 1951/52. Subsequently, I served six years as a fur and game management biologist for the province of Saskatchewan and participated in frequent reconnaissance flights followed by systematic aerial censuses of moose and deer upon which management recommendations were made. I also participated in the 1955 re-survey of caribou (Kelsall & Loughery, 1955)[3] and became one of its severest critics.

As a fur management biologist, my work often put me in close contact with Cree, Métis and Chipewyan trappers who were also hunters of barren ground caribou. I often camped and hunted with Saskatchewan Dene in such locations as Scott Lake, Wollaston Lake

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[2] *I had the privilege of co- authoring this work with Dr. Rawson while an undergraduate, doing all the field work during this two year study and sharing the lab analysis (Rawson & Ruttan, 1952).*

[3] *T.A. Harper and I conducted the Saskatchewan portion of the aerial resurvey while J.P. Kelsall and Saskatchewan Game officer F.W. Terry conducted the Northwest Territories portion.*

and Stony Rapids, Black Lake and Cree Lake, and through their tolerant and patient teaching, gained an understanding of traditional ecological knowledge (TEK) that few academic students have access to. Subsequently I spent more than four years as an outfitter (and part-time logger and trapper) whose hired guides were Cree trappers from Canoe Lake. These guides also introduced me to woodland (boreal) caribou and boreal caribou ecology, sharing knowledge that I drew upon in 1960 in a three month study of winter ecology (Ruttan, 1961).

Between 1962 and 1969 I also spent time with Inuit hunters who had survived the relocation programs of the 1950s and was able to observe their hunting practices and use of caribou. I found their relationships with caribou differed little from those of Dene, except in their often greater dependence on them as their primary source of nutritious winter food and beautiful winter clothing.

I continued with intermittent field studies of woodland caribou, moose and furbearers in Saskatchewan until 1962 when I was selected by the Administrative Committee for Caribou Preservation (a Federal/Provincial organization with a strongly political orientation) to be the only officially designated barren-ground caribou management biologist for the mainland Northwest Territories and northern prairie provinces. The position was to be administered by the CWS. My mandate was to study the status and condition of caribou populations and how they were being utilized by indigenous people. Prior to my appointment as Caribou Management Biologist for the CWS, I had developed a reputation as a critic of the department's operations. During an interview I mentioned this to Dr. David Munro, director of the Service, and he hastened to reassure me by saying that "The Service could use new blood." I was pleased with this response and went ahead with my work on June 1, 1962, believing that my findings would be accepted, even welcomed by the service. As a management biologist I understood that a primary determination of the status and distribution of the caribou herds should be done. To this end I conducted many reconnaissance flights, several systematic aerial surveys and ear tagging programs that together identified four major herds, and their basic migration patterns.

In preparation for field work, I spent several days at CWS headquarters in Ottawa where I studied many files and reports, particularly those by W.A.F. Banfield and J.P. Kelsall, that might provide me with guidelines and allow me to proceed with field work without duplication of their efforts. Upon arriving in the field, I was startled at the variance between what the literature led me to expect and the actual conditions I found.

Until I went north, Banfield's 1954 report caused me to believe that the migratory barren-ground caribou existed as 19 distinct herds (to which he gave names). It was soon apparent to me that several of those herds were only segments of large herds, sighted at different times and in different places, during the first caribou surveys that Banfield conducted in 1949 and 1950. In addition, Kelsall's description of unusual movement and change of range by a large herd between the summer of 1956 and winter 1957/58 turned out to be a series of consecutive sightings of three large herds, the Beverly, Bathurst and Bluenose (once called the Coppermine herd). The first sighting was of the Beverly herd in the summer of 1956, followed by the Bathurst and ending with the Bluenose in the winter of 1957/58[4]. I often wonder if this was the origin of the frequently suggested concept of migration between herds since it was cited several times by Kelsall in his 1968 monograph, a document of considerable influence among students of caribou ecology.

I have explained my eclectic background in unusual detail because it provided me with a foundation for developing a perspective on caribou research and management that often diverged from that put forward by more conventionally trained caribou biologists. Certainly it was not always a comfortable path, but the reward was to gain important insights and understanding of caribou and their interaction with indigenous people. I feel there is still merit in the approach I was taught, which emphasized the need for, hands-on collection of information; avoidance of forming unsupported conclusions; awareness that errors are an omnipresent possibility, being willing to correct them and, finally, the dangers of oversimplification.

The logistics required to fulfill the obligations inherent in my mandate, however, were complicated by the immensity of the study area that included the mainland Northwest Territories and the Prairie Provinces, the divisions of migratory caribou populations and their seasonal ranges, and the concurrent spring and fall migrations, which at that time were not fully documented. In addition, there were limits and uncertainties to the availability of and funds for experienced pilots and survey aircraft, so it was both difficult and arduous to describe and record seasonal distribution and other behaviour patterns, much less

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[4] *I often wonder if this was the origin of the frequently suggested concept of migration between herds since it was cited several times by Kelsall in his 1968 monograph, a document of considerable influence among students of caribou ecology.*

conduct estimated herd size, composition and productivity, which are prerequisites for management. Aside from aerial observation, I spent a great deal of time and energy tracking caribou movements on the ground and personally identifying range conditions, behaviour patterns and calving ground locations. Many of the problems inherent in caribou study remain difficult and costly to this day, modern technology notwithstanding.

The first caribou "Crisis": A new conservation strategy

Crisis: *a state of affairs in which a decisive change for better or worse is imminent; now applied esp. to times of difficulty, insecurity, and suspense in politics or commerce. (Oxford English Dictionary Online)*

The term "crisis" refers to a balance point in which the fate of a population such as the caribou is determined; to survive or not to survive. Since the response to a "crisis" is frequently a heroic effort to shift the balance point in a positive direction, the declaration of a "crisis" is a call to arms to mobilize all resources in support of this effort. It can also create a sense of urgency which can give rise to inappropriate reactions. In my experience the coupling of the term "crisis" with any game management issue, and particularly the barren ground caribou, sets off alarm bells that may detract from effective caribou management. Moreover, my experience in the 1950s and 1960s shows that management measures hastily developed in the context of crisis may persist without adequate review of their effectiveness long after the crisis is over.

The crisis of the 1950s has been thoroughly researched and described by Sandlos (2007), Usher (2004), Tester & Kulchyski (1994), and Kulchyski & Tester (2007). I will make no attempt to add anything to their excellent work. Instead, I will only extract and highlight certain facts concerning the development and outcomes of the crisis that was announced in 1955 and published in 1956 by Banfield, and my own involvement in it.

Although an impending crisis was not clearly identified prior to the 1940s, concern for the future of caribou populations and their use by indigenous people in the north were manifested in regulations governing seasons, bag limits and the uses of caribou, and from contradictory reports of "wasteful slaughter" of caribou at Fort Fitzgerald (Sandlos, 2007), by the "caribou eaters" (Usher, 2004), by Inuit of the eastern arctic mainland (ibid), and by other Dene of the Northwest Territories (which then included Nunavut) and the prairie provinces.[5]

The perception of a crisis in the caribou population began to develop in 1949 and 1950 from an extensive aerial survey by W. A. F. Banfield of the mainland caribou populations (between Hudson's Bay and the Mackenzie River) wherein the total population of the migratory barren ground caribou was estimated at about 680 000 (Banfield, 1954, as cited in Kelsall, 1968 and Sandlos, 2007). Previous estimates, based mainly on an assortment of anecdotal reports and yarns from explorers, white trappers, missionaries and even the RCMP, ranged up to 30 million, as suggested by naturalist and author Ernest Thompson Seton (1911; 1929) who visited Contwoyto Lake in 1907 during the annual August migration[6].

Although Seton's estimate was not accepted by everyone, Banfield's estimate of 680 000 was, and so the alarm bells began to ring. However, this perceived decline was not declared a crisis until 1955 following a "range wide resurvey" (Kelsall & Loughery, 1955)[7], in which I was involved[8], that estimated a total population of 278 900 animals, less than half of Banfield's previous estimate some 5 years earlier. The re-survey estimate was seriously flawed, however, having been

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[5] *Usher contends that this concern "arose in the 1920s with expansion of the fur-trade and the influx of white trappers." White trappers dominated trapping areas of northern Canada throughout the 1930s and 1940s, often to the exclusion of indigenous trappers who were wholly dependent on the wildlife for their survival. Many of those white trappers occupied the winter ranges of caribou especially the barren lands (tundra) and tree line regions east of Great Slave Lake until the 1950s where they killed many caribou for themselves, their dog teams, and bait for arctic fox, wolves and other fur bearers. One of the last of those trappers was Mr. Fred Riddle who continued as predator (wolf) control officer and trapper until the mid-1960s. During the tagging programs on the Thelon River in 1963, 1964 and 1965, Fred Riddle was employed as our camp cook and tagging helper.*

[6] *I can understand Seton's reaction on seeing the Bathurst herd in its August migration past Contwoyto and Pellatt Lakes. I witnessed this migration in 1963, 1964 and 1965 and again in 1969 when a dense and seemingly endless column of caribou marched by the Pellatt Lake camp for hours on end and then spread out to pasture on a huge tundra area that extended to tree line at the headwaters of the Coppermine River. To Mr. Seton the world must have seemed filled with caribou.*

Note: Kelsall states that Seton's estimate of 30 000 000 was a "clear impossibility" (1968, 144). That figure, however, appeared on the cover of Tuktu, *a CWS authorized and edited publication (Symington, 1965) linked to an article by Fraser Symington. Symington was a writer not a wildlife biologist and the information in* Tuktu *was supplied by CWS in support of the caribou conservation program.*

[7] *The resurvey was not "range wide." Large portions of the winter range, particularly in Manitoba, Alberta, and the NWT were not included in the re-survey. Kelsall lists the resurvey in his literature cited, but does not describe it in his 1968 monograph.*

[8] *T.A. Harper and R.A. Ruttan conducted the Saskatchewan portion of the aerial re-survey.*

obtained by an early spring survey when caribou were beginning to migrate north and when many were hidden while feeding under the forest cover. Although transects approximately 20 miles apart revealed widespread distribution on the winter ranges in Saskatchewan, they did not provide sufficient coverage for census purposes. Also, our estimate of the Saskatchewan portion of the herd was reduced and a large correction factor developed by Harper, Kelsall and myself[9] was omitted from the final report by its authors (Kelsall & Loughery, 1955)[10]. Had the correct Saskatchewan estimate and the correction factor been included in the re-survey results, the total population estimate would have been much higher and the crisis management measures might not have been justified.

When the incorrect estimate came to our attention, both T. Harper and I protested through the Saskatchewan Game Branch. Our protest may have found its way to the Administrative Committee for Preservation of the Barren Ground Caribou by way of the Saskatchewan Game Branch Commissioner, who was a member of the committee. However, no change in the estimate occurred. As far as wildlife agencies and officials were concerned, the caribou decline was real and the reports of excessive and wasteful hunting by indigenous people and predation by wolves were factual causes. When combined with an estimated total kill of 86 000 to 100 000 caribou per year attributed to indigenous hunters and a great deal of adverse publicity concerning indigenous hunting practices (Sandlos, 2007), the official reaction was a demand for immediate action—any action to prevent extinction of the caribou. Although other natural mortality factors were identified, they paled in the eyes of the wildlife officials when compared with predation by humans and wolves.

Nevertheless the false estimate from the re-survey and the caribou crisis reported by Banfield in *Beaver* magazine were accepted immediately by administrations involved with caribou, and the response was swift.[11] This was all the excuse that was needed for rapid expansion of a conservation program that ranged from conservation education (Kulchyski & Tester, 2007)[12] to the enforced relocation of the Sayisi Dene of Duck Lake in Manitoba (Code, 1993)[13] and their Inuit neighbours in the Kivalliq Region (formerly referred to as Keewatin) in 1956 (Tester & Kulchyski, 1994)[14]. The wolf poisoning program was also intensified as were other conservation measures designed to reduce hunting pressure.

Even though the Saskatchewan government did not willingly accept the false estimate, they went along with much of the conservation program.[15] For example they allowed wolf poisoning, continued to ban sport hunting and feeding caribou to dogs while encouraging fishing for dogs. Along with Indian agents they tried (unsuccessfully) to persuade indigenous hunters, who were protected by Treaty Rights, to accept hunting licenses and a small quota of caribou per hunter. I didn't witness the reaction of indigenous trappers in the NWT until after 1962, but saw little difference in attitude or action on the part of Dene or Inuit. The production of fish in many tundra lakes and streams is not enough to support a dog team for very long, even in summer ice-free periods. Even in the western arctic the number of productive fishing lakes is limited by their depth and by 6 to 8 feet of ice. Trappers who fed fish were often forced to haul them long distances to their camps.[16]

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[9] *The correction factor was designed to obtain a measure of the error in transect counts of caribou on forest range, when numbers of caribou remain hidden under the forest cover until the census plane has disappeared. Only those caribou that are resting on lakes and open muskegs are counted. The extent of error was obtained by having two planes with their observers fly one behind the other a mile or more apart along the same transect. Both crews only counted those caribou that were in the open but the following crew counted significantly more than the lead plane.*

[10] *The deliberately reduced and false estimate was only published in Banfield (1956).*

[11] *Kelsall provided no details of the resurvey but stated, "The results of the 1955 resurvey stimulated immediate administrative and enforcement action .... for the first time many native hunters had enforcement and conservation officers watching their field activities" In the Fort Rae, Fort Reliance and Yellowknife areas "almost every major hunt was accompanied by an officer of one agency or another, and many hunts were strictly supervised." (1968, 202)*

[12] *Kulchyski & Tester (2007) cite the caribou conservation education pamphlet published by the Canadian Wildlife Service entitled* How To Save the Caribou, *published in the 1960s. This was incredibly paternalistic, bordering on insulting.*

[13] *Directed by Alan and Mary Code. Mary was a child in 1956 and became a survivor of this relocation. The film depicts traditional life and the consequences of the disruption of the lives of the people.*

[14] *Tester & Kulchyski (1994) describe the relocation of the Kivalliq inland (Keewatin) Inuit. In August 1962 Tommy Duck, a Sayisi Dene now a resident of Tadoule Lake Manitoba, told me that all of his people were moved on very short notice to the Hudson's Bay coast during August 1956. He said he had been away working to get money to buy a canoe and/or "kicker" but when he returned he found "everyone was crying" as they waited for the airplane. This relocation of the Dene in August was designed to prevent another "slaughter" and must have caused them to miss most if not all of an important harvest of caribou, thus adding to their suffering through loss of this customary winter food supply for the winter of 1956.*

[15] *There are several possible reasons for "going along with" the conservation program, but I expect that if the Saskatchewan commissioner did protest it was too late, or he was outvoted by the majority of the members of the Administrative Committee or it was not considered to be politically expedient given the financial support provided by Federal Government through Federal/Provincial Agreements such as the fur program.*

[16] *This problem was offset in the 1960s by the use of snowmobiles, which were expensive to own and operate. When I asked one Dene trapper what he thought*

After 1956, the publicized estimate of the total herd was only 200 000, despite reported increases in increments, calf crops and in the size of some herds in the late 1950s. In fact I found that the frequently reported estimate of the total mainland population remained at about 200 000 until 1964 or 1965, despite increased estimates by Kelsall and my findings during my sojourn as caribou management biologist. The publicly reported total harvest also remained at 100 000 caribou per year, although estimates of total kill were much reduced in some areas. One might excuse such errors or omissions by the fact that the results of Kelsall's studies after 1955 did not become public knowledge until 1968 and publication of his monograph.

Indigenous hunting continued to be regarded as the principal cause of caribou decline while other mortality factors such as predation, low conception rates and poor survival of calves were noted (Kelsall, 1968)[17], but not considered as seriously as hunting. I suspect that management agencies had lost interest in data collection related to populations, conditions and other factors, or did not recognize the complexity of environmental conditions that affect the production and survival of caribou calves.

Barren ground caribou occupy a staggeringly large range in the course of their annual and seasonal migration during which they access many discrete environments, numerous ecological regions and countless plant communities in their daily search for nutritious food. Throughout their lives they experience the widest range of temperatures and other weather extremes that typify the arctic, and traverse the dangerous rivers, lakes and diverse land forms. They also endure the afflictions of insects, disease, parasites and predation from several sources, and are affected by fires and human activities on the landscape. Drowning is also a common hazard to migrating herds, especially in early winter when caribou attempt to cross thin ice which is hidden and insulated by a layer of snow[18].

The specific impacts of indigenous harvesting and associated co-factors prior to and following the introduction of guns are not well understood. Throughout all phases of the first crisis, hunting with firearms was a recurring theme. For many of the earlier non-Dene observers, the use of guns became the catalyst for the "wanton slaughter" concept [19] and its supposed effect on the caribou numbers.

Over time I have also come to believe that "mass slaughters" with modern rifles that have been reported were rarely if ever perpetrated by subsistence hunters, at least in the first half of the 20th century. Until the 1960s few Dene and Inuit hunters could afford high calibre guns and ammunition, even when they were available. This is not to deny that large numbers of caribou were killed, dried and turned over to trading posts along the Mackenzie River and probably other areas as well at the behest of the Hudson's Bay Company. There are several possible scenarios: they could have been the result of widespread harvests; accumulated gradually by individual hunters or groups and then traded; or collected by "trading captains" who had been given guns and other presents as inducement to collect furs and dried meat from the hunters. In 1965 when I first visited the Bathurst Inlet Post where CWS believed a very large number of caribou were 'slaughtered' each year, I found that most of the local Inuit hunters were equipped with only old 303 army rifles that Father Lou Menez O.M.I., the resident missionary priest said were "more dangerous to the hunter than to the caribou"[20]. It appeared that the only good rifle belonged to Father Menez who used it to finish off caribou that were wounded or crippled as a result of using inaccurate rifles.

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about skidoos he replied, "They {are} okay for hauling, but are like hunting with a bell around your neck" (John Carmichael, pers. com., 1967). John Carmichael was a resident of Inuvik and a highly successful trapper of the Anderson River region, who used snowmobiles and charter aircraft for hauling freight. His son Freddie, who I hired from time to time for reindeer census in 1967 and other wildlife surveys, was the owner and chief pilot of Reindeer Air Services.

[17] *In 1955-56 and 1956-57 the percentage of calves (short yearlings) that Kelsall observed was 6.9% and 8.0% respectively. His estimates of increment data before and after the two year period were significantly higher but in all cases were based on small and widespread samples.*

[18] *In the mid-1950s I witnessed such an event, after the fact, on Cree Lake Saskatchewan. A band of caribou had fallen through the ice and perished. The floating carcasses had frozen into the ice which thickened to several feet. Wolves, foxes and wolverines had found the site and the feast had lasted most of the winter. When I visited the site, the bodies had been consumed except for lower legs, hooves, hair and antlers. Another drowning occurred at the east end of Lake Athabasca, where caribou of the Beverly herd customarily crossed the ice in southward migration soon after the rut. In this case a period of unusual warm weather and water from the tributary river at the east end of the lake had opened a channel at the crossing, leaving shelves of hanging ice along each shore. The opening was many metres wide and required a long swim in icy water between the shelves of shore ice. Dene witnesses said that most of the victims were calves and "big bulls" that perished from fatigue and chill or were too weak to climb out on the south shore. Viewed from the air, it appeared that hundreds died there.*

[19] *From my association with "professional" white trappers and their negative attitudes toward indigenous trappers, I suspect that they contributed to the "wanton" slaughter notion. At the same time, the effect of white trappers who dominated northern Canada from the 1920s through the 1950s was not seriously considered. By the time of the caribou "crisis" of the 1950s, many had either retired, passed away, or quit trapping because of changes in the fur market.*

[20] *Fr. Lou Menez O.M.I. Oblate Missionary served over 40 years in the north. He was posted to Bathurst Inlet from 1954 to 1964. He returned to Lyon, France for health reasons, and died in 2006. He shared his experiences with me in 1963.*

I am disgusted by the estimates of crippling losses of caribou that I believe are unfounded and grossly exaggerated, but which have nevertheless been published in "scientific" papers and reports such as Kelsall's 1968 monograph. Among traditional hunters it was an offence against the Creator and the caribou to allow a wounded animal to escape. In my experience with Dene and Inuit hunters loss of a wounded animal was rare, and if it did occur, was disapproved of. It was also common practice for many Dene and Inuit trappers to include one or more dogs in each team that could be turned loose to track and hold a wounded animal until the hunter was able to complete the kill.

My caribou studies in the 1960s

My first work in the NWT as a caribou management biologist involved a twofold mandate: first, to assess the status of migratory caribou, and second to monitor the utilization of caribou by indigenous people. On my arrival in NWT in June 1962, I worked with Don Thomas and Quinangnaq, an Inuit hunter, on the Thelon River between Beverly and Aberdeen Lakes, a traditional crossing point for barren ground caribou, recently called Box Crossing. We tagged several hundred caribou from the Beverly herd while it was crossing the river, in northern migration after the June calving period. This ear-tagging program was repeated under my direction in 1963, 1964, and 1965 with the able assistance of Inuit workers Quinangnaq, Qaqimat and Tuluqtuq[21] as well as Saskatchewan conservation officer Ted Jonasson and Ducks Unlimited biologist Tom Stirling[22] and an Indian Affairs officer, Bill Reis. I also assisted the Manitoba Government biologists and tagging crew during the Qamanirjuak herd's August migration across Nejanilini Lake which lies across the migration route to Little Duck Lake, the former home of the Sayisi Dene who were relocated on the shore of Hudson's Bay in 1956.

Although a total of some 6700 Beverly herd caribou were ear tagged over the four year period, the tag returns were disappointing. I believe it was less than 1% in any one year starting after 1962. However, the returns did identify the winter range of the Beverly herd in the Mackenzie District and in Saskatchewan and Manitoba. At least one tag was collected near Yellowknife and one in the Churchill Region, indicating overlap of the Bathurst on the west and Quamanirjuak herd's winter range on the east by the Beverly herd. Another tag from the Quamanirjuak herd was collected near Stony Rapids, Saskatchewan that was taken as evidence of overlap of the Beverly and Quamanirjuak herds on the Saskatchewan winter range. However, on at least one occasion I saw separation of these herds during the early stages of spring migration from winter range. At that time it was not unusual to see groups or columns of caribou moving in opposite directions on the same lake. The tag returns showed no overlaps of summer ranges or permanent migration between herds during the summer.

The tagging program on the Thelon River confirmed the existence of the Beverly herds' calving grounds somewhere south of the Thelon River, not north as reported in at least one unpublished report (Gunn, Fournier & Nishi, 2008)[23]. I cannot recall the exact location and size of the calving ground but I think it was around Mosquito Lake near tree line, west of Dubawnt Lake and covered a wide area. A few days after the June 1st to 21st calving period, a segment of the herd, complete with many cows with very young calves, began to cross the Thelon River which was now open but not always totally ice free. The calving segment of the herd (sometimes referred to as the "calving herd") also included a few adult and sub-adult males and all of the yearlings that had migrated to the calving grounds with their mothers.

A few days after the calving group had crossed the river, a very large contingent of adult and sub-adult males, barren females and their yearlings approached from the southwest and crossed over in small groups or dense columns of several hundred individuals. This segment of the herd, which I called the "non-breeders," had remained more or less stationary in a large area near the junction of the Clarke and Thelon Rivers throughout the calving period. In the summer of 1964 a few cows with calves crossed the Thelon River near Beverly Lake after the non-breeder

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[21] *I was given to understand that, Quinangnaq (English name Samson), was a Back River or Chantry Inlet man who was living at or near Schultz Lake, and later moved to Baker Lake. Thomas Qaqimat was a year round resident of Aberdeen Lake, who later moved to Baker Lake. Tuluqtuq was a younger man who had lived at one time in the area of Henik Lake, Ennadai Lake and Padlei until the relocation, but was now the adopted son of Kingilik who camped on an island in Aberdeen Lake near Qaqimat's winter camp.*

[22] *Tom Stirling who is retired and living in Victoria was the D. U. Biologist for Saskatchewan. He came several times to the Thelon River to band Canada Geese when they were moulting and flightless in July. While waiting for the moult to begin he assisted me and Ted Jonason and my Inuit crew tagging caribou. When that was over, my crew and I assisted in his goose banding program.*

[23] *This paper provides a composite map of calving ranges of the Beverly herd from 1957 to 1997, all of which are shown to be north of the Thelon river, including 1962 and 1965 the first and fourth of four consecutive years when calving took place south of the Thelon river.*

movement.[24] The phenomenon of separation of calving and non-breeder segments of the herds during the calving period also occurred with the Bathurst and Quamanirjuak herds. Although I was directed to the Beverly calving area by Don Thomas in 1962, I found and identified the non-breeder segment of the Quamanirjuak herd by following the spring migration trails from wintering areas in Saskatchewan and northwestern Manitoba to the tundra. There the non-breeders left the calving herd trails and went to the area around Ferguson Lake while the calving herd went to the east side of Quamanirjuak Lake. I did not find the calving and non-breeder areas of the Bathurst herd by following the migration trail from wintering areas, but only by searching both sides of Bathurst Inlet after the June calving season. The breeders of the year (and their new calves) were occupying a separate range than the non-breeding part of the herd. After completing the Thelon tagging program in early July of 1963, I found many non-breeders west of Bathurst Inlet and north to Arctic Sound, but hundreds of cows with calves east of the Inlet[25]. These segments of the herd joined in late July to become the August migration through the Contwoyto Lake/Pelatt Lake area.

During the Thelon portion of the tagging program, I conducted an aerial survey estimate of the Beverly herd at least twice. On one occasion it was only the calving herd and the second was both the calving and non-breeder segments. I remember the calving herd estimate on one occasion was about 139 000 based on transects that provided approximately 12% coverage. I can't recall the non-breeder estimate but it was at least as large as the calving herd estimate.

In 1963, 1964 and 1965, I also noted tracks and then later individuals and small groups of caribou that had crossed the Thelon River before breakup. These must have been part of the year around tundra dwelling caribou population identified by Ann Gunn as the "Ahiak" herd, which had wintered as far south as tree line. (Gunn, Adamczewski & Nishi, 2008). Near the end of July in 1963, 1964 and 1965 I extended the tagging program to Contwoyto Lake where three Inuit (Simon Kadlun, Henry Algona and Simon's son Joseph Niptinatiuk) assisted me in tagging a small number of caribou from the Bathurst herd during their August migration.[26]

My observations indicated that the status of the Beverly and other herds I worked on were not as catastrophic as widely feared. On the contrary, I warned of an impending crisis of overpopulation that might be addressed through increased harvesting. However, my results were greeted with extreme incredulity by some officials and generally had little impact on the accepted wisdom of the day that conservation measures imposed in the 1950s should be maintained.[27]

Indigenous utilization

The other aspect of my mandate allowed me to continue my association with Dene and develop new relationships with Inuit hunters. In the process I was able to deepen my understanding of Inuit cultures and the use of caribou by both eastern and western Inuit. I worked with them and found them to be friendly, co-operative peoples who maintained a deep respect for caribou. They were absolutely not wilful or mindless slaughterers of caribou or any other game. On the contrary I found that they, like their Dene counterparts, regarded caribou as gifts from the Creator, which offered themselves to people as long as the hunter obeyed a number of spiritual and practical laws, among which respectful hunting practices and sharing of the gift were paramount. Waste was disapproved of.

I have long been troubled by inadequately documented and self-referenced reports by Kelsall of wasteful hunting and selective consumption of embryos by the people of Stony Rapids in the Spring of 1957, and blatantly ethnocentric judgements he offered as objective data.[28] I believe such statements

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[24] *This is the terminology I customarily use to avoid confusing caribou groups. Portions of herds, or segments, have sometimes been designated as herds, leading to substantial errors. Banfield identified as many as 19 segments as herds, and gave them names. The confusion lasted for years. A migratory herd retains its membership over a yearly cycle, even if it separates into groups or segments for periods during yearly round, For example, segments such as the commonly named "calving herd" are composed of parturient females and their offspring, with few exceptions. Realizing this assists interpretation of census data. Caribou that normally live year around on the tundra year around do not migrate as an identifiable unit but shift southward in small groups as far as tree-line in winter. Those observed in the western part of Nunavut have been called the Ahiak herd.*

[25] *For many years prior to my visits in the 1960s the Bathurst herd was known to calve east of the Inlet, a condition that continued until at least 1967.Since then contemporary biologists have come to believe that the herd now calves west of the inlet, the primary evidence being radio-collared females being found west of the inlet during the calving season. Since the non-breeder segment of the herd commonly includes all or most of the barren females plus a few parturient females, is it not possible that the radio-collared female was barren? If there were sightings of females and new born calves on the west side is it not possible that they were latecomers to the inlet and did not cross to the east side before calving.*

[26] *One late summer I also provided Simon, Henry and Joseph with tags and tagging equipment, but I don't recall the results. Don Thomas had also tagged a few there in 1960, as mentioned by Kelsall (1968).*

[27] *For details of government response to my investigations, see Kulchyski & Tester (2008), who describe it at length some 45 years after the fact.*

[28] *Kelsall (1968:216). Kelsall cites himself (Kelsall, 1960), repeating unsubstantiated rumours, at best speculations.*

should be disregarded by contemporary researchers or students of caribou management because they make it impossible to view objectively the relationship between indigenous hunters and caribou populations at that time.

As a personal observer of and occasional participant in spring hunts of Saskatchewan caribou, I find such reports totally inaccurate and preposterous. In the hunts I observed and /or participated in at Stony Rapids and Cree lake, I found that unborn calves were collected and given, for the most part, to pregnant women and respected elders who did not participate in the hunt. At that time of the year the caribou were gathering and resting on lakes and open muskegs or feeding and moving under forest cover. Both the hunters and caribou tended to be scattered over a wide area, the exception being settlements such as Stony Rapids, Black Lake, Fond du Lac and Uranium City. The spring hunting Chipewyans in the Stony Rapids region were roughly divided into two groups; those who resided or trapped near the settlements and outlying areas, and those who had gone with members of their families to hunt and trap in the NWT as far north as tree line and who now were drifting back to their homes in Saskatchewan. There they met the vanguard of the spring migration that was composed primarily of pregnant cows with their calves (now short yearlings) and a smaller number of bulls, two years old and older. The harvest included pregnant females as well as those young bulls that were often in better condition than other members of the herd.

The numbers of caribou killed in the spring hunt varied widely among hunters but rarely exceeded the number required to feed the hunter, his family and dogs for more than a few days. By this time his ammunition supply was low and he was often anxious to get home before warm weather and break-up made travel difficult if not impossible. As spring approached both the migrant hunters and resident hunters began to encounter non-breeder (barren) caribou cows that had begun migration days or weeks after the pregnant females and if their wintering range had been productive, many would be suitable for eating, with quantities of subcutaneous and internal fat that was an essential part of the hunter's diet. A hunter who had killed a few caribou while travelling or near his home community would usually remove the tongues while they were easy to remove, but if his travelling camp or home was nearby he might load the carcass on his toboggan that he had left with his dogs in the forest. Then he would remove heart, lungs, liver, kidneys and any internal fat and portions of the viscera such as the rumen (which in the 1950s would most likely be fed to the dogs) and the reticulum, omasum and abomasums that even today are considered to be delicacies by elder Dene. While camped with Dene (Gwich'in) on Old Crow Flats one spring in the 1970s I was treated to fried small intestine and brain that had been lightly boiled. One of my hosts, Charley Thomas an elder who has since passed away, jokingly called the brain "Indian potato".

During the spring hunts most hides were discarded because of the many warble fly larva holes. They were not left carelessly about but were often fed to the dogs or buried in deep moss beneath the late snow. I often noted that skins were left on large portions (e.g. the "hams") of the butchered carcasses until they were cut up and cooked or made into partially dried and smoked meat (called wet dry meat in English), or totally dry meat that was often prepared and dried in tents wherever people camped. To state that only the tongues, embryos or lower leg bones were used and that the lean muscle meat was commonly fed to the dogs or left to rot (Kelsall, 1968) is ridiculous and untrue. In fact, when I examined reported kill sites only hours after a successful group hunt, I rarely found anything but blood spots and hair. As a rule, all edible meat was consumed along with the marrow from the long bones and only inedible portions were discarded.

The role of caribou as "staff of life" to past generations of indigenous people living on the land cannot be overstressed. All trappers, indigenous or not, and early settlers such as missionaries, RCMP and government employees relied on caribou as a vital source of protein that could not be found elsewhere. However, the reality is that until the 1960s there were few other adequate sources of food in caribou country, especially during the winter. Moose were often rare and small game such as ptarmigan, spruce grouse and hares were rarely taken in quantity sufficient to feed a family for any extended period. Trading posts in NWT, at least, contained very little food even in the 1950s and early 1960s, and some were only open for short periods during the winter months, even for other trade. On my earliest visits to Fort Good Hope and Bathurst Inlet I found that the stores often closed for long periods and contained very little food, especially in spring before the first barge arrived at Fort Good Hope (Joe Masuzumi, pers. comm., 1963)[29] or the ship came to Bathurst Inlet in mid-summer (John Stammers pers. comm., 1963)[30].

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[29] *Joe Masuzumi, an elder resident of Fort Good Hope, was a major informant during a traditional knowledge study conducted in that community (see Johnson & Ruttan, 1993).*

[30] *John Stammers was the last manager of the original H.B. Co. post at the south end of Bathurst Inlet which closed in 1964.*

From the beginning of my assignment in the NWT, I was aware that rumours and stories of excessive harvesting abounded, but the sources and whatever foundation there might have been was unknown to me. Many stories made their way to the CWS, and occasionally I was asked by contact officers to investigate them. Subsequently I personally followed up on several reported incidents of excessive harvests, thought by the CWS officials to be 5000 or more caribou for the Coppermine and Bathurst Inlet communities. But when I visited Bathurst Inlet during the spring hunt in 1963, I only saw verifiable evidence of approximately 50 harvested animals. Although there were doubtless more, the numbers were hardly the 5 000 reported years later (Kelsall, 1968). The Fond du Lac Saskatchewan Dene were also accused of killing 5000 or more caribou. However when I visited them at Scott Lake at the behest of Ward Stevens I found a band of 75 people and many dogs near starvation, as the fall migration of caribou had stalled some 60 miles north, and the fish in the lake had been heavily harvested by commercial fishermen during the previous summer. They had only 2700 rounds of ammunition in several calibers, as verified by the Indian Agent at Stony Rapids in Saskatchewan, but were very pleased because this was the largest amount that had ever been issued to them at one time. Clearly it would not have been possible to kill 5000 caribou with 2700 rounds.

Hunting and food handling practices by indigenous people varied widely among ethnic groups and were usually incompletely observed, inaccurately reported, and almost always misinterpreted by outside viewers. In the interest of bringing a clearer perspective to this subject and to correct some of the misinformation widely circulated at that time, I wish to relate some of my own experiences and observations. They were part of the information I gathered as I conducted my field studies and were an important part of my mandate. While the activities I was privileged to witness and to share are important in themselves, the underlying beliefs and cultural values are even more significant, as they are the foundation of the survival of indigenous communities for countless years in a challenging and rigorous landscape.

When large herds of caribou were located, which might be only once or twice each year, it was essential that enough be harvested to sustain life for an indeterminate time, especially in winter. Usually, they took as many as possible at the time, as there might not be a second chance for several months. On being asked how many caribou he cached in autumn, one Inuit elder said "enough". The number of caribou a hunter required for feeding himself and his family for several months was a matter of judgement that varied with the size and needs of each family, and the uncertain availability of alternate foods such as fish, ptarmigan, and the carcases of assorted fur-bearers. A mistake commonly made by non-indigenous people was to think that a large number of animals could not be processed, stored and used quickly enough to avoid spoilage, and therefore must be wasted. Observers would be astounded to see how quickly a group of indigenous hunters and their wives can skin, butcher and process a season's harvest of caribou that are accumulated on a lake or lake shore, and to understand that all of it will be consumed within a few months.

In northern Saskatchewan in the 1950s and when I went north in the 1960s, I found that the heads of a family were not the only hunters that took part in the hunt and different individuals killed different numbers, which might be shared with several families. I found that it was impossible for me to learn the actual numbers harvested by an individual, much less a group. However, this did not prevent some researchers from obtaining precise harvest information from interviews with the hunters. Hugh Ungungai, a Baker Lake resident and interpreter once described to me such an interview[31] which I have paraphrased as follows: When the informant did not respond to the researcher's request for harvest information with a number (because he could not count) the researcher asked "Was it 50?" The informant answered "imaa" (yes in the Kivalliq dialect). Then the researcher said "Maybe it was 100?" The hunter agreed "imaa". This form of questioning continued until the informant said "imaa, 125." And so it was that the estimated kill of "125 per head of family" became the accepted norm for Inuit and at least the northern Dënesųłiné (Chipewyan) who were the primary caribou hunters.

I also found that even experienced non-indigenous observers tended to over-estimate the number dead caribou or parts of caribou that they saw on one area. On one occasion I was directed by Ward Stevens to go to Brochette, Manitoba, to observe a reported slaughter of 500 caribou on Lac du Brochette. I arrived at the site, a few days after the reported kill, to find only blood spots where each animal had fallen. It was fortunate that the event occurred while there was snow on the ice or it would have been nearly impossible to gather any information on such a large lake. I spent at least an hour of flying time over the lake, in which

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[31] *Hugh Ungungi could not remember the researcher's name. It may have been either Kelsall or Banfield, who conducted studies of caribou numbers and utilization during the 1950s. See Banfield (1954) and Kelsall & Banfield (1956, cited in Kelsall, 1968).*

time I counted less than 200 blood spots. While this is not as precise as could be wished, it sufficed to demonstrate that 500 animals were not harvested or the additional blood spots would have been evident.

On another occasion I landed at Stony Rapids to find a patch of ice that was covered by parts of caribou that had been unloaded only minutes before we arrived. My pilot was disgusted by the sight and made some very uncomplimentary remarks about Dene hunters and how they killed so many caribou, needlessly. I asked him to tell me how many caribou were involved, and then I counted all the body parts and estimated 12 caribou, a number much smaller than my pilot had stated. Later I spoke to the pilot who had hauled the animals, who confirmed my count of 12. They were the result of an authorized community hunt. I became convinced that precise "counts" of the community harvest as reported in documents such as Kelsall's monograph (Kelsall, 1968) were either hear-say stories, products of the author's imagination or attempts to discredit indigenous hunters.

The storage of meat in stone caches during warm August weather for cold weather use also seemed unbelievable to researchers, hence the reports of wastage that pervade some documents. Cache meat is rather strong smelling but is a totally edible and nourishing winter food which I have shared, and been grateful for it and the generosity of my hosts. The practice of allowing whole caribou carcasses to become buried under snow, and retrieved and used months later also seemed unbelievable to non-Dene observers at Duck Lake, Manitoba. On the Thelon River I also saw skinned carcasses submerged in the cold water to avoid blow flies.

I also observed imaginative methods of handling meat for immediate use. For example, the hide, legs, and head would be removed from the caribou carcass, and the internal organs removed through a transverse cut across the abdomen just forward of the pelvis. The abdominal flap would be hooked over the *symphyses pubis* to seal the abdomen against blow flies, and to provide a place where valuable food items such as the tongue and internal organs might be stored temporarily. This was called the "drum" by some indigenous hunters. Blood or body fluids were not washed, but were wiped so that the surface of the flesh would dry quickly and form an impervious surface for preservation to occur. In cold weather the head might be removed, and the tongue cut out so the head (a valued delicacy) could be frozen indefinitely. Removing the tongue was only one step in conventional butchering, although it too was considered a treat. I sometimes laugh when I read that only the tongues were used, since I found, to my embarrassment, that consuming too much rich tongue in an otherwise empty stomach can have unwanted gastric consequences.

Other treats include the reticulum, omasum and abomasum (3 of the 4 parts of the stomach), even portions of the stomach contents, aged and fresh marrow bones, kidneys, the small intestines and other parts of the gut tract, and even the warble fly larvae; salty morsels. Most of these items that were unfamiliar to outside observers supplied essential vitamins and enzymes that were missing from store bought foods. Fat was always highly valued, as it was absolutely essential for digesting the lean meat when carbohydrates and other fats were not available.

Another subject that used to elicit unfavourable comment was the feeding of caribou meat to dogs. Dogs were the only beasts of burden, providers of transportation and hunting helpers for indigenous people, long before white men came to the Arctic, and trappers continued to use dog teams for many years. They were not pets and were not pampered, although some individuals took special care of their teams. On the other hand, in some parts of northern Saskatchewan, dogs were turned loose to survive as best they could in the summer months and then recaptured and reconditioned in the autumn. In other places some dogs ran free on islands during the summer, and were fed fish periodically. Others were tied to stakes or trees at the water's edge, so that they could submerge themselves for protection from heat and mosquitoes, between feedings, commonly of fish. The role of dogs in the survival of northern people and their cultures was critical, and remained so through the 1950s. In extreme circumstances they could even be eaten, a last ditch survival strategy that was not uncommon.

Of course, any domestic working animal must eat, and their owners must provide the food. No one begrudged a pack horse its forage, yet some observers were outraged when sled dogs were fed caribou meat. During my visits to both the Dene and Inuit camps I found that the people avoided the use of good caribou meat for dogs, if alternatives were available. More specifically, the paunch, entrails, bones and scraps and even skins were often fed. Old caribou bulls, unfit for human consumption for some time after the October breeding season, also fell to the dogs. Fish also were common dog feed in northern Saskatchewan and other forested areas in NWT. They also nourished the people who owned them. It is worth noting however that the food value of fish as a sole source of nutrition was considered inadequate for hard working dogs in eastern arctic winters. The

Northern Service Officer at Baker Lake, Tom Butters, noted that dogs that were not feed meat could not work well, and frequently did not survive the winter[32]. Whatever the people ate, so did the dogs. Were it not for the dogs and their extraordinary labours, far fewer humans could have survived.

Crisis of overpopulation

Most of the foregoing observations were derived from my activities during the 1950s and early 1960s and relate more to the circumstances of the officially declared crisis of 1955/56 than to the crisis of overpopulation that I warned of ten years later. However, I believe the latter crisis was one product of the so-called conservation measures that were developed to prevent extinction of the caribou.

But first, let me provide some background information leading up to the crisis that I believed was imminent in the 1960s. I was not involved directly with barren ground caribou research from 1955 until 1962 so for details, I must depend on materials from the secondary research of Sandlos and Usher, and the primary research of Kelsall, who was still active in that period, and who describes the results of his and other CWS research in a comprehensive monograph (Kelsall, 1968). However when reviewing his published information for this paper, I am troubled by inconsistencies and contradictions regarding the stated size of the total caribou population between 1955 and 1961, and uncertainties in the status and trends.

In exemplum: Although an increase in the estimated size of some herds, notably the Beverly herd was documented (Kelsall, 1968), the publicized estimate of the total population was still 200 000. In the words of J.P. Kelsall: "No range-wide census was taken after 1955, but several independent population estimates based on partial census and extrapolation indicated that the population in 1958-59 was approximately 200 000 animals. It is believed that the population increased, but only slightly, in 1961. It may have increased since that time" (Kelsall, 1968:282). His highly speculative and somewhat pessimistic comment also seemed to extend the perceived low status and net productivity until at least 1958/59 based on losses of calves due to severe winter conditions, which might have limited the annual increment. He provided no convincing data but credited the increase in the 1957/58 estimate of the study (Beverly) herd to an influx of caribou from the Quamanirjuak and Rae herds[33] when they may have overlapped the Beverly winter range. This assertion was not supported by direct observation or by tagging (a technique that was not used until the 1961–1965 period).

In 1962, I observed and reported substantially larger estimates of the Beverly herd than the 148 500 population reported for 1957/58[34]. This line of discussion is to show that before 1962 no one seemed to have any clear idea of how many caribou there were, how many were being harvested, and of course no one had any clear knowledge of the population trends at that time. However, I contend that in the late 1950s there were considerably more than 200 000 caribou on the land as my Saskatchewan colleague and I found during the 1955 resurvey. If the publicized estimate had been correct, we would have been fortunate if we observed *any* caribou in the vast range.

In his monograph (Kelsall, 1968) he cautiously noted that beginning in the late 1950s, the population trend appeared to be towards an increase in herd size, although he supplied very little supporting evidence. I believe the abrupt reduction in hunting pressure and predation of some herds, particularly the Bathurst and Beverly herds which may have been held at or even below the carrying capacity of their habitat until 1956 by professional white trappers and indigenous hunters, probably allowed a pronounced increase that would have continued upward until the carrying capacity was reached or exceeded. Kelsall (1968) describes the response of governments to the false estimate obtained in the re-survey, which advocated severe "people management" measures that included relocations (previously described), policing of hunting and hunting communities and movement of indigenous hunters from the land to the settlements. In addition, a series of milder winters after 1962 probably contributed to the enlargement of some herds since more calves survived to increase net productivity and annual increments in both the Beverly and Bathurst herds. I have no surviving survey notes to support this, however I remember that they were much higher than that of the Quamanirjuak herd which was about 10%, and probably high enough to stabilize the population near the 150 000 mark. The total mainland population east of the Mackenzie River also included an unknown number of Bluenose caribou as well as those that remained on

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[32] *Sandlos (2007) cites comments by Tom Butters, then the Northern Services Officer at Baker Lake, to the Regional Administration concerning the low value of fish for feeding dogs. Butters subsequently became editor of* The Drum, *an Inuvik newspaper that published several of my articles.*

[33] *The "Rae herd" were the caribou that were hunted by the people of the Fort Rae region and could have been part of either the (present) Bathurst or Bluenose herd.*

[34] *Kelsall's results are critiqued in Sandlos (2004). Kelsall found an increase from 79 354 in 1955 to 142 500 in 1957/58, but by tortuous logic he found an overall decline.*

the tundra the year around and came to be known as the Ahiak herd.

In the meantime, however, the total area of the accessible winter range continued to decline as a result of fire alone, without considering other factors such as mining development. George W. Scotter, a CWS lichen specialist, addressed the problem of annual losses of winter range due to fire and found them to be very significant (Scotter, 1964)[35]. The Saskatchewan government maintained a limited fire control program in the Uranium City region during the early 1960s, but I am unaware of any comparable fire control program in the Northwest Territories. In fact, I understand that a request to implement fire control in NWT made by South Slavey residents was rejected on the grounds that fire was a natural factor in forest development[36].

In addition to losses of habitat through wildfire I noted that the summer and early fall tundra ranges appeared to be drastically overgrazed, although I did not understand the implications of the overuse of tundra at that time. At some point, however, I noted the abundance of lichens and other vascular plants on islands where no grazing had recently occurred. That observation was in marked contrast to the remainder of the range being utilized during the summer.

Although I was concerned about shrinking winter habitat, there were no conclusive Bathurst population data until the late Archie Mandeville[37] and I completed a Bathurst census in August 1965. After searching for about nine days Archie and I, accompanied by Dr. Joseph Shoman, Director of the Nature Centres division of Audubon Society[38], found the herd when it was nearly stationary and spread over an area of about 16 square miles near Mara Lake between Bathurst Inlet and Contwoyto and Pellatt Lakes. Immediately after its discovery the herd moved toward Pellatt and Contwoyto Lakes, then spread out over a wide area and began foraging everything edible including mushrooms that appeared almost daily during early August. The mosquitoes and sand flies were very bad at the time although they did not appear to have lasting effects on the caribou[39]. However, when a cold wind began to blow from the northwest the herd coalesced into a long column and began to move rapidly upwind toward the end of Contwoyto Lake. This provided the first opportunity to make an estimate of the herd size so Archie and I immediately began our count (estimate) of the herd, which was then about 30 km long. We obtained our estimate by flying along the column at low level while counting and recounting segments of the herd. This method might have produced questionable results, but fortunately another biologist came by with a good camera and the presence of mind to photograph the whole herd. He confirmed our estimate of 250 000 which did not include calves of the year. Not long after the estimate was made, the caribou spread out over a wide area that extended southward as far as Little Marten Lake and the headwaters of the Coppermine River.

With the burgeoning caribou population and the shrinking winter habitat I feared that a catastrophic population crash was imminent. Therefore, in 1966 I published an article warning of a "New Caribou Crisis." The Bathurst herd had exceeded 250 000 in 1965, the Beverly herd was at least as large and probably still growing, and my estimate of the Quamanirjuak herd was 148 667. The Bluenose herds were part of the total, which I had estimated conservatively at 700 000 in 1965. In the article I also recommended that 100 000 caribou be harvested immediately to prevent severe overuse of the reduced habitat and prevent a crash decline and great loss of caribou. In my opinion such a harvest was not unreasonable, divided among three or four herds, and representing less than 15% of my total population estimate of 700 000.

However, given that the estimated annual mortality (mainly from hunting) of about 100 000 caribou in the years prior to 1956 had been touted as a major threat to the survival of the mainland population, my recommendation was not well received. The only

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[35] *Scotter concluded that "there is little doubt that forest fires have been one of the principle causes of {the decline} of barren-ground caribou." As noted by Kelsall (1968).*

[36] *Clayton Burke, pers.comm. 2010. Mr. Burke, a resident of Fort Smith NWT and a fire control officer in 1969 told me that in a meeting to discuss fire control in the South Slave region, respected forest ecologist Dr. Stan Rowe advised against fire control on the grounds that it was a natural factor in forest development and that fire control would not benefit caribou.*

[37] *Archie Mandeville, who passed away in 2010, just prior to his 99th birthday, was born in the NWT in 1911 where he resided until his retirement from government service, an Assistant Game Officer in the NWT. I met him in 1962, and during the next three years he often assisted me as co-observer on aerial surveys and ground studies.*

[38] *Dr. Joseph Shoman, Director of Nature Center Division of Audubon Society came to my camp on the Thelon River a day or two after all the caribou had finished crossing, so I invited him to come to Contwoyto Lake where he witnessed the spectacular August migration of the Bathurst herd. He later described the event in a memoir titled* Beyond the North Wind *(1974).*

[39] *I often observed caribou feeding calmly on a sedge meadow in the midst of a cloud of mosquitoes and black flies or sand flies, and even lying down after feeding. Then they might suddenly spring to their feet and race to the top of the nearest windy hilltop, where they would crowd together shaking their coats and kicking and stamping for hours at a time. But it is a fact the caribou are under constant attack by mosquitoes and biting flies throughout the "fly season" that lasts from mid to late June, until mid-August but the cumulative effect on the growth and health of the animals is unknown.*

positive response to my article was from the NWT Commissioner Stuart Hodgson, who invited me to Yellowknife to discuss my article and my unsolicited proposal to develop a management program for the mainland caribou population. The only noticeable outcome of that proposal that I perceived was some relaxation of hunting regulations and the introduction (or resumption) of licensed commercial hunting. The latter was a low priority, but was intended to utilize those caribou that exceeded the needs of indigenous hunters and licensed residents.

In fact my article was dismissed by at least one member of the Administrative Committee for Caribou Preservation as "being full of dangerous information" (Administrative Committee on Caribou Preservation, 1965, cited in Sandlos, 2007)[40]. It is interesting to note that while I had estimated the total population at about 700 000, a subsequent survey with timing (late winter and early spring), scope and methodology similar to the 1955 re-survey was conducted by CWS Biologist Don Thomas who estimated the total mainland population at 387 000 despite the fact that the entire range was not covered in his census. He argued that an increase from 200 000 in 1958 (Kelsall's dubious figure) to 387 000 in 1967 would require either the "extremely high" recruitment rate of 17.6% or would indicate that "the 1958 population was larger than 200 000" (Thomas, 1967, cited in Kelsall, 1968)[41]. Thomas has made my point exactly. Certainly there were more caribou in 1958, and just as certainly the 1967 survey result was very limited, predetermined by study design.

My recommendation to harvest 100 000 caribou was derived from my management experience in Saskatchewan and my understanding of the role of harvesting as a management tool. Although many interested observers will insist that hunting with rifles is the root cause of population decline, one can argue to the contrary (as I did in the 1960s) that population control by hunting is the most common management technique and is beneficial where it reduces competition for food and space, and prevents the overuse and depletion of the habitat. Furthermore, if the population does not exceed the carrying capacity of the habitat, harvesting can maximize herd productivity. In Saskatchewan, these concepts were demonstrated with other species, notably muskrat and moose.

It was common knowledge among wildlife managers that an uncontrolled (i.e. unharvested) population of herbivores will increase until it exceeds the ability of its habitat to support it. Then it will either crash dramatically (as happens with the varying hare) or decline more slowly until it reaches the carrying capacity of the habitat, or descends below it. The concept of overpopulation of habitat followed by decline was first applied to caribou by Biologist C.H.D. Clarke in 1939[42] although it was probably common knowledge among indigenous hunters long before Europeans arrived (Johnson & Ruttan, 1994). At the time I wrote the article, however, I was not aware of Clarke's research. The slower decline as a result of overuse of habitat is more common with large herbivores such as deer, moose or caribou that are mobile and are able to utilize a greater variety of habitats and habitat conditions.

Although I left the CWS in 1965 to teach Wildlife Technology and Management at the Saskatchewan Institute of Applied Arts and Sciences (S.I.A.A.S.), I returned to the NWT during the summers of 1967 and 1969 under contract and spent a few days in early August collecting herd composition data from the Bathurst herd while it was moving past Pellatt Lake. With the assistance of Joseph Niptanatiak and his sister Mimilena I recorded the sex and age composition of a large sample of the herd[43] which revealed high percentages of both long yearlings (at 14 months of age) and young calves. I was informed by the Wildlife Division that the yearly increment had also been high in 1966. Thus the herd must have increased considerably beyond my 1965 estimate, which had been the basis for my 1966 recommendations to harvest 100 000 from the total caribou population, not just the Bathurst herd. By this point the total population might conceivably have been one million or more.

In the years following the great increase in the Bathurst herd that I had estimated in 1965, I can find no record of an assessment of the degree to which the range was damaged by years of grazing and trampling or loss to wildfire, nor of the scope and effect of the development of human communities and the mining industry upon it. In retrospect, there may have been parts of the range I did not see that were not overused, and that might have reduced the pres-

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[40] *Until I read about this in Sandlos, I was unaware of the extent of the paranoia induced by my activities and writings. Actually I am not displeased, but I have yet to search out the reference for myself.*

[41] *This study is significant because with all its flaws, it points to the validity of the 1965 Bathurst survey figures.*

[42] *Clarke's results were published in 1940.*

[43] *In order to randomize the sample that included four sex and age categories (bulls, cows, long yearlings, and calves of the year) in the massed moving column of caribou, only those that passed through the field of a fixed spotting scope were identified by Joseph, who had been taught the English designations. They were recorded by Mimelina. The sampling continued until the column of caribou had passed our observation point.*

sure and prevented the more precipitous decline that I had feared. Hunting pressure and other mortality factors may also have acted as brake as well. It is also possible that over the centuries the caribou have developed resistance to the stresses brought about by overpopulation. Such speculation is tempting, but unproductive. Apparently the Bathurst herd gradually became smaller over the next three decades.

A slow decline from serious overpopulation, nonetheless, is every bit as catastrophic in the long run as a crash decline. If the population is in decline for a long time, the range will be even more heavily damaged by prolonged over-use, and probably take longer to recover. Keeping this in mind it is not surprising that there has been no noticeable recovery of the caribou populations to the numbers that I observed in the 1960s. When I predicted a crash decline, I thought the use of the phrase evoking crisis would get the attention of the wildlife administrators most effectively and that positive action would follow. A tactical error, no doubt, for I got the attention but not the action.

Although I had received a positive response from Commissioner Hodgson, I was disturbed by the failure of other administrators to respond positively to the overpopulation that I found so alarming. I was not the first to have made such an argument. As early as 1939 C.H.D. Clarke, then a respected biologist, warned that too many caribou were just as bad as too few and an increase in caribou over the carrying capacity could result in a disaster. Clarke had been conducting studies in and around the Thelon Game Sanctuary while herds of caribou were present and identified the importance of hunting and predation in maintaining the caribou at or below the carrying capacity of the habitat. However, in the mid-1960s the CWS clearly did not agree that overpopulation was a problem, and were not interested in considering evidence that contradicted their strongly advocated program of conservation that emphasized a reduction in hunting, and continued wolf control. From the point of view of management, this was a recipe for disaster.

The Bathurst problem: Is this another crisis?

There has been a drastic decline in the estimates of the Bathurst herd during the past decade or more and with it, as with the alleged crisis of the 1950s, there seems to have been a sense of panic and corresponding management actions have been undertaken. It is perhaps useful to consider the current situation in light of the two perspectives on crisis that emerged in the 1950s and 1960s.

Having no access to the truth and panicked by the publicized crisis, government agencies in the 1950s rushed to implement conservation policies and programs that in hindsight were cruel, self-serving and damaging to indigenous cultures and of questionable value to the barren ground caribou that could now increase beyond the carrying capacity of their habitat. The crisis of the 1960s that I hypothesized was based on empirical data concerning the increases in the Bathurst and Beverly herds and reductions in the winter range, which I believed could bring about a crash decline and the loss of many caribou. But the data I was drawing on was inadequate. An inventory and evaluation of the existing range and its carrying capacity would have been more convincing to government managers. My message in the 1960s was and still is that too many caribou are just as big a problem as too few, as Clarke warned back in 1939. The deliberate reduction that I suggested could have spared the habitat some of the damage incurred by continued overpopulation. However the Bathurst herd, at least, appears to have gradually deflated like a slow leak in a balloon, rather than a sudden bang, while the range possibly suffered substantial damage as a result of prolonged overpopulation.

Is the current condition and status of the Bathurst herd the result of over-population of habitat that has also been reduced by expanding industrial and community development, in addition to natural factors such as fire? Is it also possible that the herd has finally become adjusted to changing conditions and has ceased to decline?

In 1955 it was assumed that the alleged decline was caused by over-hunting, although no incontrovertible data were provided to support that assumption. In 1966, I recommended that a large harvest might prevent a population crash, with no published precedent to support the recommendation. The common feature of both scenarios was lack of data that would support assumptions concerning the status and trend in the herds and the impact on them of hunting, predation or range conditions. Are the mistakes of the 1950s and 1960s being repeated in decision-making based on unverified assumptions concerning the causes and extent of decline with very little supporting data?

In my assessment of census figures to date I see no evidence that the Bathurst herd is in immediate danger of extinction, although the herd is threatened by annual losses of habitat and by industrial development and increases in human population. But now I think there are reasons to believe the history of the 1950s is starting to replay. Now as then the numerical status and composition and productivity of the herd are unclear and I have seen no conclusive data concerning the condition of the range or impacts of industrial or human development upon it or to the population that it supports. Yet recommendations to ”help the caribou” to increase have been developed and are being tested for validity (Joint Proposal, 2011). They feature a reduction in the hunting of cows and an increase in the hunting of bulls, measures which are intended to increase calf production and recruitment rate. These recommendations have been promoted for the neighbouring Bluenose herds as well without data to support their value.

Some Dene harvesters have made it known that they are concerned about such an approach. Their objection may be based on the fact that more cows than bulls have been harvested in winter for many generations without seriously affecting the herd size or productivity, and an increased harvest of bulls could remove prime breeding bulls that would otherwise maintain a high conception rate.

Notwithstanding the caribou research that has doubtless been made since the 1960s, I suspect many would agree that there remain great risks and uncertainties in assessing the status of caribou herds and identifying factors driving population dynamics. For example, a focus on the numbers of parturient cows on the calving grounds errs in not including those barren cows, their calves of the previous year (now yearlings) and most of the adult and sub-adult males that are some distance from the calving grounds during the calving period and the census. Inclusion of this group which I call non-breeders may have been a factor in the sudden “increases” in the 2010 estimates of Bluenose East and Porcupine herds as it did with the Quamanirjuak herd back in the 1960s[44]. Will such an “increase” be found in the next census of the Bathurst herd? And, if so, what will the response of governments be to it? It is also possible that the recorded or estimated total kill could have included caribou from both the Bluenose East and Beverly herds because of their mixing with the Bathurst herd on its the winter range. Moreover, the calf- (short yearling) to-cow ratio that has commonly been used as a basis of the increment does not provide a correct calculation of the annual increment. The more accurate annual increment is calculated on the ratio of yearlings: adults of both sexes.

Another common assumption that may lead to error is that a reduced number of parturient females observed on the calving grounds are the consequence of too many females, especially pregnant females, being harvested. From my personal experience and knowledge acquired from Dene hunters, the number of parturient females on the calving ground is more dependent on conception rate than on mortality of females during the winter. Experienced Dene and Inuit hunters know that not *all* females return every year to the calving area where they were born. Most barren females do not (Kendrick, 2003). The conception rate is subject to many variables one of which is the range of circumstances under which females in oestrus and prime breeding males contact each other during the short breeding season. One autumn, I observed the “rut” of the Beverly herd when it occurred at treeline near Damant Lake, the site of a traditional Chipewyan hunting camp. A severe snow storm interrupted the breeding season on the tundra and drove the Beverly herd past tree line and deep into the forest where they dispersed over a large area making it difficult for prime bulls to find all cows that were in oestrus.

The window of opportunity for mating is about three weeks, and thus timing is critical. If snow storms should occur in that time that would drive the animals beyond tree line, or for some indeterminate reason the males and females were too widely dispersed or separated during the breeding season, conception would not be optimal in that year. This separation of the sexes was observed by Kelsall (1968).

It is also common knowledge among mammalogists that good condition of the female is essential for conception and the survival of embryos until birth and weaning time. It follows that the condition of the females depends on the food supply prior to breeding. For a very long time I equated the health and reproductive success of caribou with the condition of the winter range, but recently I came to realize that the summer range is probably as important for the following reasons. During July, August and September the breeding bulls put on body fat that they lost during the previous breeding season and did not fully regain during the ensuing winter and spring, while the cows recover and retain much of the health and vigour required for conception and survival of the embryo through birth and the first year of life.

I reported my concerns about winter range conditions and their role in the dynamics of the Bathurst herd in 1966 (Ruttan, 1966), however no studies to inventory and/or evaluate range conditions, or determine carrying capacity, were ever implemented. I have found no definitive study of the Bathurst herd range or of its carrying capacity in the literature since they were briefly discussed in Kelsall’s 1968 monograph, but I often wonder if the underlying

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[44] *See Sandlos (2007) which refers to a survey that Art Look and I conducted in 1965 that increased the herd estimate to 148 677 from a much lower estimate based only on the calving herd. During our survey the non-breeders were found and estimated while they were in the Ferguson Lake area more than 80 km west of the calving grounds.*

cause of the decline was over-population of a reduced and degraded range. Is it not also possible that the gradual decline, rather than a population crash, is the Bathurst herd's natural response to deteriorating range conditions through a reduction in productivity?

Required action

Although certain components of the data are readily available, the creation of a complete picture of the dynamics of the herd and factors affecting them is a daunting project that requires a great deal of painstaking investigation. Given the enormity of the task, those scientists and indigenous harvesters who attempt to assess the herds now merit great respect. The herd is a moving target as many of the components are frequently changing.

The herd is almost constantly on the move while feeding, growing, reproducing, being harvested and dying of other causes. The vegetation communities encountered in their travels and on which they depend are broadly divided into forest and tundra, where plant communities that typify them are growing, being eaten, trampled, burned, frozen or fragmented by seismic lines and transportation corridors such as the ice road from Contwoyto Lake to Yellowknife and other roads between communities and mining developments. Both the caribou and their habitat are subject to often extreme climate and weather variations. However, with patience, persistence and attention to detail, it will be possible to find certain consistencies, constants of you like, that extend beyond those of the timing of migration, breeding or calving. Herd behaviour during spring and fall migration, or, before, during and after calving are good examples.

Such constants are features of the traditional knowledge that served the indigenous hunter so well. Variations will occasionally be observed in such normally consistent activities as migration, such as when the herd fails to pass through or near a traditional hunting camp or area. In the past such unforeseen situations have caused starvations, but did not necessarily mean the herd size had decreased. Such events cannot be avoided but if the herd is kept under surveillance or frequently observed or monitored via direct observation and radio telemetry, uncommon variation in movements by the herd (or portions of the herd) can be detected. Serious errors have been made in the past that would not have occurred if the caribou herd had been kept under observation.

A feature of the Bathurst herd's "picture" is the productivity of the herd that can be calculated each year from the herd composition and expressed as the ratio of yearlings to adults (of both sexes) just before or during the June calving period. When combined with reasonably accurate estimates of the total population, the allowable harvest can be calculated. Since the 1960s biologists have been most concerned with the ratio of calves to cows on the calving grounds, or of short yearlings on the winter range which are interesting but of little value when calculating productivity. That requires a clear knowledge of sex and age composition of the entire herd. An inventory and evaluation of both winter and summer range are also an important part of the "picture" required as a basis for effective management proposals.

Achieving a comprehensive view of the Bathurst herd and the factors that affect it will be complicated by the fact that the herd seasonally occupies portions of two large political jurisdictions: Nunavut in spring and summer and the Northwest Territories in winter and early spring. (As an additional complication, Bluenose and Beverly caribou frequently occupy portions of the Bathurst's traditional winter range). The Bathurst herd is also utilized by several Inuit and Dene communities as well as residents of the city of Yellowknife. Since the herd occupies and is shared by all these jurisdictions, a fully developed co-management system based on a clearer knowledge of the status and condition of the herd and its habitat combined with respectful dialogue that brings science together with the traditional and acquired knowledge of Dene and Inuit peoples will be best situated to bring about positive results in caribou stewardship.

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The Null Hypothesis: Co-management doesn't work

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Introduction

For the past 40 years I have been an active participant in all aspects of co-management from biologist and facilitator to executive director, member and chair of several organizations. Over this time I have become aware of a few patterns that are both disturbing and endlessly repeated. I thought that a different approach to the whole issue might challenge the norms and inspire some readers to be more courageous and adventurous in how they address co-management.

To be consistent with my goal I have purposefully not employed standard academic methods or modes of communication. The following is basically a summary of my personal experience in the Yukon and Northwest Territories, augmented by a number of in-depth interviews with people involved in co-management organizations across northwestern Canada.

In the all-embracing spirit of the 13th North American Caribou Workshop I am writing this primarily for for northerners who belong to co-management organizations and who want to make a difference.

1970 B.C. (Before Co-Management)

When I arrived in Yellowknife caribou co-management did not exist. Such matters were in the hands of federal biologists. As a young man I listened to these old guys talk about caribou and what they thought was going on. In all such discussions they never mentioned what aboriginal people thought because that was not 'scientific'. After their 'field trips' were over they went back down south and wrote reports for the Canadian government.

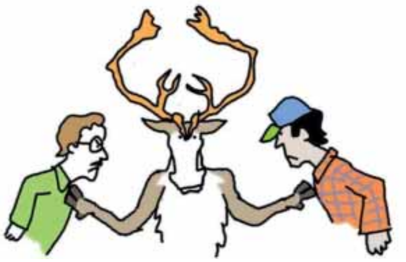
These biologists were following in the footsteps of 'arctic explorers' who also traveled on the land with local people and wrote adventure books.

Sometimes the adventurers would report to Ottawa and decisions would be made about the north. This is how reindeer were introduced to the Western and

Eastern arctic. Aboriginal people were not involved in such matters.

Eventually, aboriginal people stepped out of the background and began to demand their rightful place in decision-making about caribou and everything else on the land. This is when co-management arrived in the north

1976 The arrival of co-management



Co-management organizations often arise from conflicts between aboriginal communities and governments. The organization may consist of local members only, or include government representatives as well. Usually, all fish and wildlife are included in the mandate but there are a few that deal only with certain animals like moose or caribou. Regardless, the intent is always to incorporate traditional knowledge and science into recommendations to governments and the means of doing so are pretty similar.

If you begin with the Hunting, Fishing, and Trapping Coordinating Committee in the 1976 James Bay Agreement, then co-management has been around for 34 years. After so long, it is time to ask, “Is co-management really doing what it was intended for?”

I have focussed on caribou co-management alone which is handled either by regional boards that include local herds along with other wildlife, or specific boards that span political boundaries to cover the entire range of large barren-ground herds. In all cases, however, the intent is the same which is to:

1. Bring people together to talk about caribou
2. Improve caribou management
3. Benefit caribou on the land

Everyone agrees that co-management has been very successful at bringing people together.

And a great deal of time has been spent discussing caribou management – mainly research.

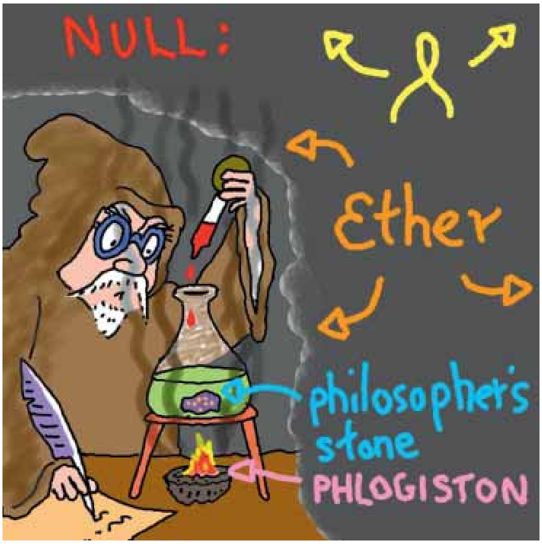
But what has co-management really achieved for caribou on the land?

This is what I chose to investigate. “What changes are happening to real caribou out there on the land as a result of co-management?” It’s a tricky question. I did not want to fall into the trap of looking for facts that support the success of co-management. Instead I wanted to make sure I was not deceiving myself just because I wanted co-management to look good. This is why I chose the “**Null Hypothesis**” approach.

The ‘Null Hyptothesis’

The ‘Null Hypothesis’ was invented long ago by scientists who realized they were often fooling themselves. They wanted so much to find the answer they believed in that they would bias their experiments to support their theories. This picture shows four big mistakes that scientists made in the past because they wanted certain answers.[1]

So, they invented the **‘Null Hypothesis’** which states that “Nothing (Null) is happening between the two things we are studying.” Then they designed experiments to prove nothing was going on. And only if their experiments failed – *only then* would they begin to think maybe there was something happening.



How the ‘Null Hyptothesis’ works

Shown above are ‘A’ and ‘B’. Is there a relationship between them? Is ‘A’ having an impact on ‘B’? The ‘Null Hypothesis’ says, “There is no relationship between ‘A’ and ‘B’”. Imagine measuring ‘A’ and ‘B’. Your observations show many changes in ‘A’ but no changes in ‘B’. Therefore the ‘Null’ Hypothesis is true. ‘A’ is having **no effect** on ‘B’.

This is what I did with co-management. My hypothesis says, “Co-management does not work. That is, co-management does not affect animals on the land.” Then I started looking for information to support that statement. I looked at ‘A’ (Co-management) and then I looked at ‘B’ (changes for caribou). If my observations showed ‘no impact’ (or only a tiny bit) I would say, “The Null Hypothesis is true.” If my observations did not support this then I would say, “I must be wrong. Co-management does work – it must actually be affecting animals on the land. The Null Hypothesis is false.”

Here is what I found from interviewing long time associates in co-management and also recalling my own experiences over the past 25 years.

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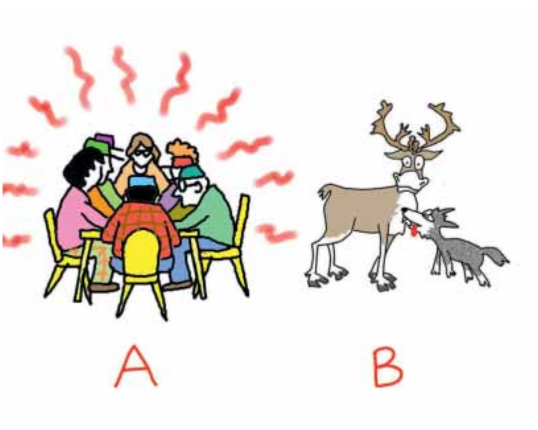
[1] *The top squiggle is Einstein “Cosmological Constant’. He believed that the universe was stable but his equations said that it was expanding. So, he invented this ‘constant’ to make his equations say it was stable. Later, when he found out the universe is always expanding, he said it was the biggest mistake of his life. ‘Ether’ was the fictitious medium that scientists invented to carry light waves. ‘Philosoper’s Stone’ was a hoped for element that would change base metals into gold. ‘Phlogiston’ was created to account for the loss of weight when anything was burned.*



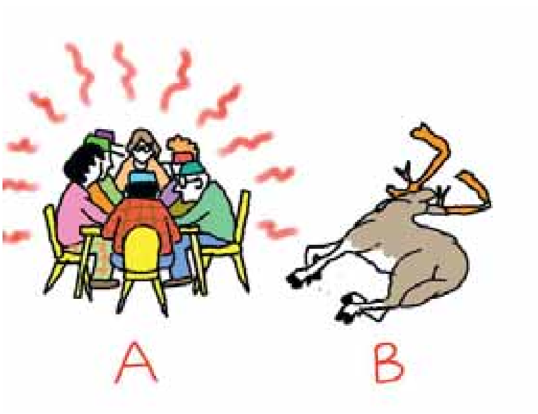
Wolves

Because every community in the north is concerned about wolves and caribou, every co-management organization has dealt with predation at some time or other. Often the discussions are very passionate and many solutions are considered.

But, from all I personally witnessed and all the people I interviewed, I could not find **one example** where co-management started something that truly reduced the number of wolves. Sometimes a group supported government wolf control, or called for other methods (Alaska style snaring) which had little effect.

Caribou are experiencing **no difference in wolf attacks** because of co-management.

The Null Hypothesis is true.



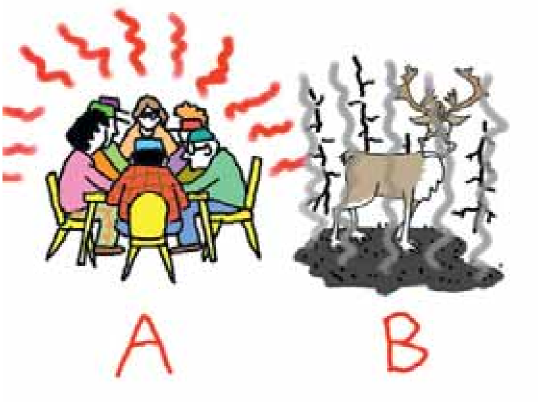
Wounding loss

For many years the Beverly and Qamanirjuaq Caribou Management Board (BQCMB) and the Porcupine Caribou Management Board (PCMB) worked very hard to improve marksmanship. At first they provided life-sized targets for people to practice on. Nowadays the targets are 11” x 17”. Sometimes communities stage shooting contests using the targets. The Boards have also written much about this and I think are still producing such material.

But I asked a number of people who had been involved for many years if they thought all their work had made any real difference – that is; significantly fewer caribou were being wounded. And they all felt there probably was **little or no improvement**.

Poor hunting practices are still discussed all the time at board meetings.

The Null Hypothesis is true.



Habitat loss

Going back to the early 1980s, the BQCMB tried very hard to protect winter ranges of the Beverly herd from forest fires. Much expensive research was done, many big reports were written, many meetings held, many strong letters sent to government.

But after more than 20 years, **most of the Beverly Caribou winter range has now been burnt.** This summer was the first time that fire fighters considered the needs of these caribou – but it’s too little too late.

The Null Hypothesis is true for fire and habitats.

Disturbance

Much work has also been done by the BQCMB and the PCMB on protecting caribou from hunters that chase them and from aircraft that buzz them to get pictures. We have tried posters and stickers and education programs. But, we could not afford to make this an annual campaign.

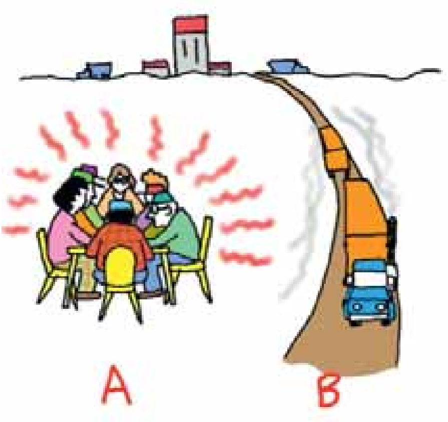
Once again, those whom I interviewed felt that little had been accomplished. When a hunter on a skidoo sees caribou he naturally tries to catch up with them. Every year new pilots are flying new tourists around and no one knows or cares about stressing caribou. And most - but not all, exploration and development companies go about their business without bothering to avoid caribou.

The Null Hypothesis is mainly true (see below).

Industrial development

Co-management organizations spend a lot of time reviewing development proposals to protect caribou habitats and minimize disturbance. The people I interviewed felt that their efforts were making a difference in where and how companies did business - also that their contributions were much appreciated by regulatory authorities and communities.

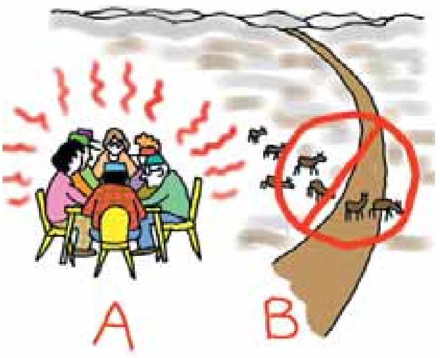
Caribou habitats are in **better shape and caribou are disturbed less** by development due to co-management.



My observations do not support the Null Hypothesis.

The Null Hypothesis is false.

Let the leaders pass

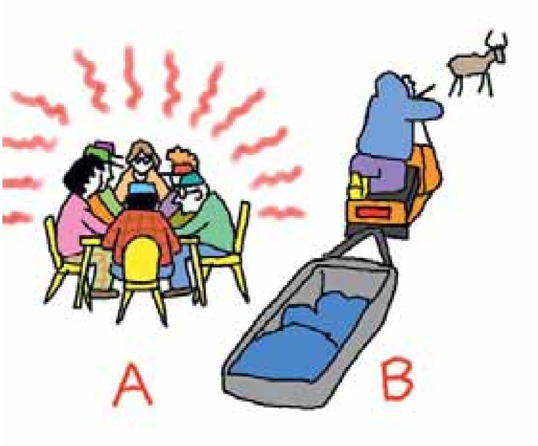


Traditional Knowledge on the Porcupine caribou range teaches that female caribou lead the migrations and maintain the collective knowledge of seasonal ranges for the herd. It is therefore traditional practice to let the first bands of caribou pass by on the fall migration in order to take the herd to its winter range. One winter range in the Blackstone Mountains of the Yukon cannot be reached except by crossing the Dempster Highway. The PCMB strongly recommended to all governments and communities that hunting near the Dempster Highway be prohibited for a week from the time the leaders first appeared in that region so they could take the herd to ranges east of the highway.

Many aboriginal hunters did not want to comply with this recommendation. The Yukon Government stopped its licensed hunters for a few years. But, when one First Nation challenged YTG's authority over aboriginal hunting on the highway, the government gave up the ban entirely and so did all the First Nations.

For the past three years there has been **no ban on hunting** when the leaders reach the highway.

The Null Hypothesis was false but now is true.



Harvesting

Since most hunters are aboriginal people, government restrictions on their harvest are rarely applied. Although there is much talk about hunting levels and bull hunting versus cow hunting, nobody pays much attention to co-management until there is a population crisis. As of fall 2010, there were reported to be at least 6 crises on the North American barren-ground ranges.

Co-management organizations were involved in the present harvest restrictions on the Bluenose West and Bluenose East herds, and their co-operation was vital to the success of the restrictions. The PCMB recently completed a harvest management plan for the Porcupine Caribou Herd and the Wek'eezhii Renewable Resources Board has approved a harvest plan for the Bathurst herd. Neither plans have been implemented yet.

Perhaps the 'Null' test is not fair for this issue. When there is a crisis the Null Hypothesis is false. But as to preventing a crisis so far, it's true.

Why is co-management so ineffective?

From the above you can see that, generally, caribou are receiving very little direct benefit from co-management. Not for lack of trying, that's for sure. Co-management organizations struggle mightily to benefit caribou on the land. But their best efforts frequently go nowhere.

Why is this so?

The bureaucratic jungle

It's a jungle out there. On one side of the jungle is co-management. On the other are the caribou. What's in the jungle that stops co-management from reaching the caribou?

1. **No authority**
   Co-management boards have it tough. Governments don't care much for advice. They like to do things their way. Governments like co-management when it supports their programs. But when they don't like what they hear they can just hang up the phone. In theory boards legislated through land claims have more clout, but they still labour hard to be heard.

2. **No money**
   Co-management is underfunded by governments. Getting everyone together for meetings uses up most of the money. Special projects about marksmanship, disturbance, education, etc. cannot be maintained at a high level. Often the money comes from time-limited private grants.

3. **No communication**
   After a meeting, the local representatives are supposed to go back and inform their community. But that's difficult – the issues are too complicated and too many. Besides, co-management is there not only to inform but also to listen. If this is not clearly demonstrated then the whole thing breaks down. And finally, means of getting the message out, such as newsletters, articles, and radio bulletins are costly.

4. **No follow through**
   We humans suffer from 'analysis paralysis'. We love to discuss things – forever. But nothing actually gets done. For instance: no government (territorial or aboriginal) will ever undertake another wolf control because they are too afraid of the international backlash. But this will not prevent endless meetings and reports about it in the future.

5. **No dialogue**
   Despite decades of dithering about the roles of western science and traditional knowledge, the gulf between them is still vast. There is very little common ground and almost no common language. Presently there are 203 employees in the Yukon Department of the Environment. Of these 8 are of Yukon First Nation Ancestry – less than 5%. Yet First Nations make up 25% of the Yukon population. I would expect that the figures are similar in other jurisdictions especially for positions of bureaucratic authority. Western Science, as it is practiced and presented, does not work for people from traditional backgrounds.

   And yet, Western Science still dominates most discussions. The big issues of 'Conservation' are mainly debated and decided by western science standards. The old joke is "I'll manage and you cooperate." When the other shoe drops, it's rarely a moccasin.

The future of co-management

Co-management is here to stay. It is a feature of every land claim settlement. And soon there will be aboriginal Self-Governments from Nunavut right across to the Yukon. Given the handicaps co-management is saddled with, what can be done to make it more effective?

More authority

Can quasi-judicial organizations be created that give more decision-making power to citizens? The Yukon Water Board (grandfathered into the Umbrella Final Agreement) and the Alaska Board of Game have such authorities.

Can existing co-management agreements be modified for aboriginal government representation rather than local membership? This would give much needed authority for opinions expressed at meetings as well as direct linkage to the recipients of the final recommendations. Another approach is to craft intergovernmental agreements that incorporate a decision-making mechanism. The Porcupine Caribou Harvest Management Plan has an Annual Harvest Meeting involving the Board and all the "Parties". The meeting determines the status of the herd and, based on that, the responsibilities of each government are already spelled out in the plan. There is less wiggle room that way.

More attention to aboriginal governments might be worthwhile. So far the focus of co-management has been the territorial and federal governments. In the Yukon there are 12 self-governing First Nations. But they rarely get recommendations from the Renewable Resources Councils or the Fish and Wildlife Management Board. Aboriginal governments may be better suited to some forms of management on the land, such as habitat protection, wolf control, and harvesting protocols. They should be expected to participate just like every other government.

Failing any of these measures, in the absence of real power the only alternative is to *lobby hard*. Arrange meetings with government officials – as highly placed as possible. Utilize the media and schools to get strong public support. Recommendations alone carry little weight. In the jungle you have to hustle to get anything done.

More money

Getting financial increases from government is always frustrating. Some budgets are frozen for decades. Existing funds barely cover the cost of meetings with nothing left to make things happen. Many co-management organizations turn to private foundations for support. It is also possible to partner with governments, industry and NGOs. A skilled proposal writer can find weird funds you never heard of.

Better communication

Meeting summaries should be sent to all appropriate governments and stakeholders. Expecting a local representative to go back home and explain everything is unrealistic. Where possible, employ all media to let people know what is going on: radio bulletins and interviews, newspaper articles, website, youtube, school presentations – blanket coverage wherever possible. All such material should show how community information and opinions were factored into the outcomes.

Be your own critic

It's easy to blame others for why things don't get done. So take a hard look at what you are doing. Is your time spent wisely? What have you really accomplished? Do an internal audit of your own effectiveness. Buckets of time can be wasted on internal procedures, government briefings, revisiting the same old issues.

Find something that could really help caribou on the land and focus on that, rather than fretting over everything and accomplishing nothing. It could be protecting a local habitat, getting young people out hunting and doing it properly, reducing the cow harvest. Set yourself the goal of accomplishing that one thing and see if you can do it.

Bridging the science/TK divide

Co-management has a foot in both camps and therefore is in the best position to create ways for scientists and the communities to have meaningful discussions. Some pioneering in this field has been done by the the Selkirk First Nation in the Yukon. Working with industry, SFN prepared a list of geological exploration terms in Northern Tutchone. It also has its own 'Consultation Protocol' based on traditional principles that spells out each step (and style) for engaging with the community. It hosts an annual 'May Gathering' taken from traditional practice where three First Nations pool their harvest data and knowledge of the land to determine management actions for the coming year. The YTG regional biologist is a welcome participant.

If you are looking for something to sink your teeth into this may be one of the most worthwhile areas for co-management attention. Getting people together is one thing – having them understand and respect each other is something else. It may not directly affect caribou but greater cooperation and less friction in the future is bound to have some benefits on the land.

Well, the past 25 years looks pretty bleak. Hopefully, greater aboriginal involvement through new boards and new governments will improve matters. But the status quo is a tough barrier to break through. As an aging veteran of co-management, all I can say is:

1. fight the good fight,
2. never be satisfied with your own performance,
3. don't be afraid of government,
4. and always, always, remember the caribou.

The 13th North American Caribou Workshop
Winnipeg, Manitoba, Canada
25–28 October, 2010

Symposium

Innovative approaches to woodland caribou management

The 13th North American Caribou Workshop
Winnipeg, Manitoba, Canada
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Towards a Manitoba Hydro boreal woodland caribou strategy: Outcomes from Manitoba Hydro boreal woodland caribou workshop

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Abstract: Manitoba Hydro is responsible for the continued supply of energy to meet the needs of the province and is committed to protecting the environment when planning the construction and operation of its facilities. Corporate policy dictates ongoing improvement of Environmental Management Systems (EMS) in order to meet or surpass regulatory requirements. Environmental objectives are reviewed annually and programs are modified when necessary to address improvements in environmental performance. Manitoba Hydro plans and constructs major transmission projects throughout northern Manitoba which includes areas occupied by boreal woodland caribou. In recognition of the potential issues associated with hydro transmission construction in boreal caribou range, Manitoba Hydro hosted an expert workshop on May 8, 2007 to provide objective advice in the development of a draft corporate strategy that effectively directs targeted monitoring and research for environmental assessment and mitigation. The workshop focused on assessing the potential threats to boreal woodland caribou from a transmission line construction and operation perspective, and identifying appropriate approaches in site selection and environmental assessment (SSEA) and long-term monitoring and research. A total of nine threat categories were reviewed to determine the degree and magnitude of potential effects that may result from transmission construction and operation; and of the original nine, five final threat categories were delineated. The main elements of the workshop provided strategic approaches for proactive pre-construction monitoring, research on recruitment and mortality for local populations impacted by ROWs and control areas, and various habitat monitoring, management, and mitigation techniques. Research and monitoring priorities have been identified and continued collaboration with Manitoba Conservation and other land users were also identified.

Key words: boreal woodland caribou; Delphi; Manitoba Hydro; threats; transmission line right-of-ways.

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Introduction

Boreal woodland caribou (*Rangifer tarandus caribou*) are a valued ecosystem component of Manitoba's boreal forest, and have been designated as a threatened species under Canada's Species at Risk Act (COSEWIC, 2010) and the Manitoba Endangered Species Act (Manitoba Conservation, 2010a). In Manitoba, boreal caribou and their habitat are impacted by both natural and anthropogenic disturbance. Wildfire constitutes the majority of disturbance on boreal caribou ranges in Manitoba; however, human activities such as logging, right-of-way (ROW) development (including seasonal and all-weather roads), and hydro-electric transmission can potentially affect the conservation status of local boreal woodland caribou populations (Manitoba Conservation, 2010b). Manitoba Hydro recognizes the need to address the potential impacts of ROW construction and operation on local boreal woodland caribou populations and collaborates with Manitoba Conservation on collaring and tracking studies and other monitoring required for both planning and long-term monitoring of effects. Data from these studies are being utilized in assessing the effects of previously constructed ROWs on boreal caribou range use and movement as well as in the routing of new transmission ROWs in order to mitigate negative effects, to the extent possible, by avoiding core use areas and critical habitat. These data provide opportunities to enhance the existing knowledge on the potential effects on local caribou populations due to transmission lines and other linear features. These data are also providing direction on future research and monitoring by identifying data gaps and additional information needs.

In order to enhance and refine the collaborative research and monitoring efforts, Manitoba Hydro undertook a threat-based assessment using Delphi methods and outside boreal caribou experts. The Delphi process involved workshops and discussions with the goal of reaching agreeable conclusions on the specific topic, with the premise that: 1) opinions of experts are justified as inputs to decision making where absolute answers are unknown; and 2) a consensus of experts will provide a more accurate response to a question than a single expert (Crance, 1987). The Delphi exercise has been adapted to develop expert-opinion–based suitability indexes for wildlife habitat (Crance, 1987) and was utilized in conducting the threat-based assessment of hydro transmission ROWs on boreal woodland caribou to guide Manitoba Hydro's Site Selection and Environmental Assessment (SSEA) process. Five threat assessment categories were identified based on literature supporting potential issues as a result of transmission ROW development. These included forage, habitat, predation, pathogens, and human interactions (i.e., hunting). The following is a summary of the main threat categories used in the threat assessment.

Forage and habitat

Boreal woodland caribou utilize large tracts of functioning habitat that contain adequate space for foraging, predator avoidance, and reproduction. They are generally associated with mature coniferous forests and fen/bog complexes, though this can vary from one location to the next (James & Stuart-Smith, 2000; Hins *et al.,* 2009). The presence of boreal caribou is a function of the ecosystem state at a regional or landscape scale. Fragmentation is generally understood to have negative effects on caribou as this species is associated with contiguous forest.

Effective habitat loss resulting from avoidance behaviours can be a consequence of the construction and operation of a transmission line ROW. James & Stuart-Smith (2000) found that individual caribou differ in their response to linear corridors, but on average caribou avoided corridors. The type and density of linear development within a local caribou range combined with the terrain conditions may or may not reduce the amount of available habitat as linear corridors represent a small fraction of habitat required for sustaining local populations. Studies have indicated that the avoidance of human developments increases as the level of activity increases (Dyer *et al.,* 2001); however, low levels of human activity, such as those most commonly associated with transmission line ROWs, have also been found to cause avoidance of developments by caribou. Reduction in abundance of caribou in the vicinity of various human developments has been reported to range from 1 to 5 kilometers (Weir *et al.,* 2007). Movement and habitat use response of caribou to all-weather logging road development across core winter range have been observed with the effect dissipating as distance to the disturbance increases, resulting in a potential loss of functional habitat up to 1 kilometre (Schindler *et al.,* 2006). Linear corridors specifically may also be avoided by caribou as a means to reduce risk of predation. James & Stuart-Smith (2000) found that caribou mortality attributed to wolf predation was closer to linear corridors than live caribou locations and wolf predation sites were found to be 55 meters closer to corridors than random points.

Predation

In Canada, the impact of wolf predation on caribou is considered a factor limiting the size of certain caribou herds (Hayes & Gunson, 1995). Caribou and wolves have been found to typically occupy different habitat types, creating a spatial and temporal separation between prey and predators, thereby reducing predation (James *et al.,* 2004; Courbin *et al.,* 2009). However, fragmentation of the boreal forest and avoidance of disturbances has the potential to concentrate caribou into progressively smaller areas of remaining habitat, which can make caribou vulnerable to predation (Dyer *et al.*, 2001; Courbin *et al.*, 2009). Boreal caribou exist at low densities compared to other boreal forest ungulates, thereby reducing predation risk as low caribou densities will not support predators in the absence of alternative prey (Thomas, 1995; Dyer *et al.*, 2001). Habitat conditions strongly influence the interaction between prey and predator (Peek, 1986), and spatial separation from other ungulates and conspecifics have been hypothesized as an anti-predation strategy of caribou (Thomas, 1995; James *et al.,* 2004; Courbin *et al.,* 2009). Finally, it has been previously found that linear corridor development in remote regions can increase wolf access and mobility in formerly inaccessible caribou habitat, thus increasing wolf–prey contacts and interactions (Thomas, 1995; James & Stuart-Smith, 2000; Courbin *et al*., 2009).

Disease and parasites

In the southern portion of Manitoba where boreal caribou range may overlap with white-tailed deer (*Odocoileus virginianus*), there may be potential for linear development to have a cumulative effect on the infection rates of caribou by meningeal worm (*Parelaphostrongylus tenuis).* This parasite is common throughout deciduous mixed-hardwood forests of eastern North America, and has been reported as far west as Manitoba (Wasel *et al.,* 2003). While the intermediate host (white-tailed deer) can tolerate the parasite, it is fatal to caribou and may be a contributing factor in declining caribou populations (Thomas, 1995). Human disturbances or fragmentation of forests which facilitate the migration of deer onto caribou range can lead to disease spread within caribou populations. There is little information to support linear development as a mechanism for increased transmission of meningeal worm to caribou in Manitoba.

Human interactions

The creation of transmission line ROWs can increase public access to remote areas and potentially lead to increased human recreational activity in caribou habitat. Such recreational activities may include snowmobiling, all-terrain vehicles (ATVs), hiking, and hunting. Harassment by humans may displace cow–calf pairs, and cause caribou to avoid the disturbance stimuli, leave optimal forage areas, alter periods of activity, alter home ranges, and increase energy expenditure. Such stresses can result in death from malnutrition or predation (Seip, 1995).

Methods

Manitoba Hydro, on May 8, 2007, hosted an expert—or Delphi (Crance, 1987) workshop on boreal caribou focusing on electrical transmission planning, construction, and operation. The workshop goal was to provide advice to Manitoba Hydro in the development of monitoring, research, and mitigation opportunities that would form the basis of a draft corporate boreal caribou strategy. Participants included Manitoba Hydro staff, Manitoba Hydro consultants, and outside authorities known for expertise in boreal caribou research, conservation, and recovery.

The opinions expressed and discussed at the expert workshop were summarized and classified according to the guidelines developed by Environment Canada (Environment Canada, 2007) entitled *Species at Risk Guidance: Guidelines on Identifying and Mitigating Threats to Species at Risk*. These guidelines were intended to aid in the identification and management of threats to species at risk by providing nationally consistent and evidence-based practices, therefore contributing to assessment of the conservation status of species, as well as to recovery planning and implementation. This document defines separate designations of threats to a species at risk. *Threat Categories* were defined as broad categories which indicate the type of threat, and include such categories as Habitat Loss or Degradation, Accidental Mortality, and Disturbance or Harm (Environment Canada, 2007). *General Threats* were defined as the general activity causing the specific threat, and *Specific Threats* were defined as the specific factor or stimulus causing stress to the population (Environment Canada, 2007). *Stress* from an identified threat was defined as an impairment of a demographic attribute of a population, or a physiological or behavioural attribute of an individual in response to an identified or unidentified threat that results in a reduction of its viability (Environment Canada, 2007). Indicators that a population of a certain species at risk is stressed include reduced population size or reduced population viability, small population size, or poor reproductive success (Environment Canada, 2007).

Threat attributes define how a threat acts upon a species, and provides an indication of where measures may be used to manage or mitigate the threat (Environment Canada, 2007). The *Extent* of a threat was defined as indicating whether the threat was widespread, localized, or unknown across the species range. The *Occurrence* of a threat was defined as the indication of whether the threat was historic, current, imminent, anticipated, or unknown (Environment Canada, 2007). *Threat Frequency* was defined as whether the threat was a one-time occurrence, seasonal, continuous, recurrent, or unknown (Environment Canada, 2007). *Causal Certainty* of a threat was defined as indication of whether the best available knowledge about the threat and its impact on population viability was high, medium, or low, and should be a general reflection of the degree of evidence that was known for the threat, which in turn provides information on the risk that the threat has been misdiagnosed (Environment Canada, 2007). The *Severity* of a threat was defined as indication of whether the level of severity of the threat is high, medium, low, or unknown (Environment Canada, 2007). The *Level of Concern* of a threat was defined as indication of whether managing the threat was an overall high, medium, or low concern for recovery of the species, taking into account all of the above factors, and may take into account the ability to mitigate or eliminate the threat (Environment Canada, 2007). The Occurrence of a threat, Threat Frequency, Causal Certainty of a threat, and the Severity of a threat can also indicate whether the threat attribute differs between 'local' populations (a specific site or narrow portion of the range of the species), or if the threat attribute applies to the full 'range-wide' distribution (applicability to the whole distribution or large portion of the range of the species) (Environment Canada, 2007).

Nine threat categories were reviewed at the expert workshop to determine the degree and magnitude of potential effects that may result from transmission construction and operation. These specific threat categories were reviewed and in some cases amalgamated or revised based on the expert discussion. A threat classification table (Environment Canada, 2007) was used to organize information on each threat to prioritize and allow action to be taken to manage the identified threats to boreal caribou from the construction and operation of a transmission line and ROW.

Results and discussion

Loss of forage during construction and long-term vegetation management

Forage availability is typically not a limiting factor for sustaining boreal woodland populations (Bergerud, 1996). Although the direct effects of construction and ongoing vegetation management in high quality boreal caribou range could potentially result in a loss or degradation of caribou forage on the transmission line ROW, the magnitude of this impact is small within the context of the overall range requirements for security and forage for boreal caribou (Table 1).

It was found via the workshop that activities associated with ROW clearing and vegetation management could result in a change from conifer/lichen associations to shrub/herb–rich habitat. As lichens are shade intolerant and are known to respond to increased sunlight conditions, there may be opportunities to maintain or enhance caribou forage along transmission lines in high quality range. Vegetation management practices that promote lichen reproduction could be enhanced and incorporated into vegetation management planning.

Loss of functional habitat and range fragmentation during construction and operation

The extent of avoidance of transmission lines by boreal caribou during construction or operation is not well understood. There are complex ecological and human-caused interactions that could influence the

Table 1. Implications of threat categories for Site Selection and Environmental Assessment determined during Manitoba Hydro Boreal Woodland Caribou Workshop addressing destruction/degradation of boreal woodland caribou forage (lichens) located along transmission line right-of-ways.

Construction		Threat Information	
Threat Category	Forage loss and degradation	**Extent**	Local
General Threat	Right-of-way clearing/ Access Roads: Destruction of lichen-rich habitat during construction and operation	**Occurrence**	Current
		Frequency	One Time (Construction) Periodic (Veg. Management)
Specific Threat	Direct loss of forage resulting in reduced resource availability, increased energetics, decreased health and reduced recruitment	**Causal Certainty**	Low
		Severity	Low
Stress	Decreased fitness and reproductive success, decreased population size	**Level of Concern**	Low

extent of animal or herd avoidance of transmission line ROWs. These include disturbance from human activity (i.e., primary and secondary access), increased predation by wolves and bears, and other ecological influences directly or indirectly related to human activities in proximity to right-of-ways (e.g., forestry, mining, outdoor recreation,).

It was generally agreed through the workshop that potential effects of ROWs include reduction in forage availability as a result of sensory avoidance and displacement of animals away from high quality habitat into less suitable and less secure habitat away from the ROWs (Table 2). The effects of right-of-ways on individual animal movement compared to the population/range response may be significantly different in that population response is more critical than an individual animal response. Although individual animals may illustrate a movement response to a linear corridor (such as faster movement rates near the corridor) but still cross and utilize their original range, illustrates no effect at the range scale. It was therefore determined that measuring the gradient effect of linear density to determine at what point there is range fragmentation as a result of transmission lines would be an appropriate goal in a Manitoba Hydro strategy. It was also agreed that this may be very difficult to define as a population effect based on thresholds of linear density and effect is dependent upon the types (roads versus ROWs) combined with local terrain conditions (bog versus rock or mineral soil). The natural range of variability of animal movement and range occupation through time and space also needs to be addressed. The effects of natural barriers such as predator-rich riparian areas associated with large rivers and lakes (during summer) may play a greater role in the natural fragmentation of range and needs to be studied.

Manitoba Hydro has acquired significant volumes of boreal woodland caribou location and movement data through both collaborative and corporate-led research and monitoring. Detailed animal-borne GPS data have been gathered in the east, northwest, and

Table 2. Implications of threat categories for Site Selection and Environmental Assessment determined during Manitoba Hydro Boreal Woodland Caribou Workshop addressing boreal woodland caribou reduced use of habitat (less forage availability) away from right-of-ways due to sensory disturbance (human and ecological interactions).

Construction		Threat Information	
Threat Category	Range Fragmentation	**Extent**	Local
General Threat	Right-of-way clearing/ access: Reduced use of high quality habitat from construction and ongoing human activity.	**Occurrence**	Current
		Frequency	One time (construction) Continuous (Veg. Management)
Specific Threat	Avoidance of T-Line and displacement of animals. Loss of functional habitat and foraging opportunities due to sensory disturbance resulting in range isolation, reduced resource availability, increased energetics, decreased health, reduced recruitment	**Causal Certainty**	Low (expected)
		Severity	Intuitively thought to be low, however where secondary use exists (i.e., provide access to other areas from the T-Line) there may be long-term chronic effects. Overall severity and extent is unknown (gap in research knowledge)
Stress	Decreased fitness and reproductive success, decreased population size	**Level of Concern**	Intuitively thought to be low Unknown severity and extent (gap in research knowledge)

northeast regions in Manitoba. These data continue to be assessed in examining animal movement and population response to transmission lines. These data have also been synthesised into a Manitoba Hydro corporate database for analysis relative to the threats identified.

Prior to conducting analysis of transmission line avoidance at both the individual animal and range population scales, the data must be evaluated to determine its utility for various scientific and management questions. It was found through the workshop that sample size and replication issues could include the number of collared animals, number of years collared, proximity of animals to transmission lines and other linear features (e.g., rail ways, roads), and availability of other disturbance information. Opportunities for region- or province-wide comparisons (i.e., general trends in animal movement) should be assessed. Habitat evaluation/comparisons will also need to be incorporated into any analysis.

The response of experts regarding the effect of activities associated with transmission line construction and operation suggests it will be extremely challenging to associate effects from these activities alone on boreal caribou, or on a specific subset of larger cumulative landscape effects. There is a need for long-term strategic research and monitoring to assess the effects of ROWs through boreal caribou range. It is likely that overshadowing anthropogenic and natural events and processes (i.e., fire, wind, insects, forestry, roads, wolves, alternate prey, etc.) have a much greater effect on boreal woodland caribou than transmission line construction and operation alone. The time lag response of caribou population decline to these natural and cumulative human-caused disturbances can take years or decades to detect and/or quantify, and documenting an effect and conclusively attributing the cause to transmission line activities will require a significant corporate commitment. Avoidance of a transmission line may restrict an individual animal's choice at the local level while not restricting a population's access to its overall range. Based on the current information, the notion of establishing a "threshold" measure of disturbance that equates to when population decline commences is not feasible at this time. Describing and managing an acceptable "gradient" of disturbance may be a more appropriate goal in mitigating potential negative impacts of transmission lines.

Transmission lines constructed in areas occupied by boreal caribou are generally in areas where access is limited, particularly during the post-construction and operation period. As such, it was found by the experts that human access–related direct sensory effects are expected to be less than those associated with all-weather or winter roads. When new transmission lines parallel existing linear development, there would be little to no additive effect expected, however comparisons between multiple linear features has not been objectively assessed. Indirect ecological impacts from transmission lines are also intuitively thought to be minor compared to those associated with other human-caused or natural landscape disturbances. Research on sensory disturbance and ecological effects has been undertaken in Alberta, Labrador, and Manitoba (Frid & Dill, 2002; Schindler *et al.,* 2006; Weir *et al.,* 2007) and it will be important to assess these affects relative to transmission line ROWs and the cumulative effect that may result in areas already fragmented by other anthropogenic disturbance. The cumulative effects of transmission line construction and operation as a factor responsible for a decline are not clearly understood, but are expected to be minor in most cases.

Increased predation

Boreal caribou populations are maintained when long-term recruitment trends compensate for ongoing annual mortality (Seip, 1995; Harris *et al*., 2008). Survival of productive adult females is critical to the conservation and recovery of this species. Boreal caribou are sensitive to even small reductions in reproductive potential, such as reduced number of breeding females in the population. In some populations, the additional loss of a few adult females annually (<5) over a period of a few years could lead to local population decline. High wolf densities do not necessarily imply reduction of caribou populations in a given range, however relocation of predators from adjacent areas to linear corridors may increase prey–predator interactions.

The experts found that these interactions could potentially result in increased mortality or displacement away from transmission line ROWs to avoid predators (Table 3). Boreal woodland caribou have an inherent predator avoidance strategy that may result in avoidance of linear features used by predators or humans (Thomas, 1995; James & Stuart-Smith, 2000). Depending on habitat suitability within the range, displacement away from the transmission line ROWs may be a relatively minor issue from a forage perspective (gradient effect issue). Also, if there is no real effect on caribou populations (range-wide), increased predator travel along transmission lines may not be a limiting factor.

It is generally accepted that there is increased probability of caribou mortality with increased use of transmission lines by wolves (Thomas, 1995; James

Table 3. Implications of threat categories for Site Selection and Environmental Assessment determined during Manitoba Hydro Boreal Woodland Caribou Workshop addressing boreal woodland caribou predator movement along right-of-ways due to access and habitat change leading to increased mortality.

Construction or Operation		**Threat Information**	
Threat Category	Predation	**Extent**	Local or Range-Wide
General Threat	Mortality from wolves	**Occurrence**	Current
		Frequency	Continuous
Specific Threat	Increased predation by wolves and bears using transmission corridors (linked to increased mortality from displacement into predator-rich habitat and human effects)	**Causal Certainty**	High
		Severity	Intuitively thought to be low Unknown severity and extent (gap in research knowledge) Potential for concern in some areas or circumstances
Stress	Loss of breeding females, decreased population size	**Level of Concern**	Medium–High

Table 4. Implications of threat categories for Site Selection and Environmental Assessment determined during Manitoba Hydro Boreal Woodland Caribou Workshop addressing expansion of deer range due to increased forb and shrub habitat along transmission line right-of-ways and possible transmission of brainworm to boreal woodland caribou.

Construction or Operation		**Threat Information**	
Threat Category	Natural Process or Activities	**Extent**	Local or Range-Wide
General Threat	Disease and Parasites: Deer movement northward from T-line development.	**Occurrence**	Current–Future (Climate Change)
		Frequency	Continuous
Specific Threat	T-lines as corridors for deer movement and transmission of *P. tenuis* or other pathogens	**Causal Certainty**	Intuitively thought to be low Unknown severity and extent (gap in research knowledge) Potential concern in some areas or circumstances
		Severity	Unknown
Stress	Decreased population size	**Level of Concern**	Unknown

& Stuart-Smith, 2000; Courbin *et al.*, 2009); however, more research is required on predator density and use of linear development in Manitoba. Comparisons of predator activity for different linear features in the Manitoba context (such as roads and snowmobile trails) are specifically recommended. Differences in animal movement and population range characteristics between industrial developed areas versus remote areas should be researched to allow for objective comparison to determine potential impacts. Clear monitoring and research objectives will also need to be developed.

Deer movement and increased occurrence of Parelaphostrongylus tenuis and other pathogens

Boreal caribou are susceptible to various pathogens, of which the meningeal worm is a significant threat if infected deer invade boreal woodland caribou range (Table 4) (Thomas, 1995). It was found through the workshop that transmission lines may have some effect on the distribution of deer in the boreal forest. Other pathogens, such as Chronic Wasting Disease (CWD), may also be a factor. Monitoring the spread of wildlife disease relative to transmission line ROWs will require collaboration with Manitoba Conservation.

Hunting by humans

The susceptibility of boreal woodland caribou populations to decline from loss of breeding females is potentially significant (Table 5). Manitoba Conservation is responsible for determining appropriate protection of boreal woodland caribou and does not permit recreational hunting. First Nations subsistence hunting is a mortality factor, but the extent and significance is not well documented. Stewardship approaches for boreal caribou must consider and respond to the level and distribution of subsistence harvest. It was found by the experts that Manitoba Hydro should cooperate with Manitoba Conservation on appropriate stewardship initiatives. Access management, as part of Manitoba Hydro's construction and operation of new transmission lines, is an important mitigation tool and should be used in boreal caribou range in Manitoba where appropriate and in consultation with communities and Manitoba Conservation.

Recommendations

The following research/monitoring programs have been recommended to Manitoba Hydro based on results of the May 2007 Boreal Woodland Caribou Workshop:

- Most issues related to construction and vegetation management can be mitigated through site selection and routing processes. Locating transmission lines in areas providing least risk would be a constructive and positive mitigation measure. Conduct pre-project collaring and monitoring of boreal caribou to determine critical local range components including calving and calf-rearing areas and winter core use areas.
- Conduct long-term monitoring of recruitment and mortality in local ranges where transmission line ROWs and other linear development exists. Assess differences in lambda among varying disturbance and linear density regimes and compare with control populations in areas where there is little or no anthropogenic disturbance.
- Specific research is required regarding interactions between transmission lines and the behaviour/density of predators and their impacts on boreal woodland caribou. Key elements to consider include monitoring of select wolf populations, examination of how snowpacks influence the movement and behaviour of wolves, and study of the winter frequency/distribution of wolves through track surveys along transmission lines in comparison to natural areas, other

Table 5. Implications of threat categories for Site Selection and Environmental Assessment determined during Manitoba Hydro Boreal Woodland Caribou Workshop addressing hunting of boreal woodland caribou.

Construction or Operation		Threat Information	
Threat Category	Direct Mortality from Humans	**Extent**	Local or Range-Wide
General Threat	Hunting/ Recreation	**Occurrence**	Current
		Frequency	Periodic
Specific Threat	Poaching, subsistence hunting	**Causal Certainty**	High
		Severity	Unknown
Stress	Loss of breeding females, decreased population size	**Level of Concern**	Unknown

linear features (i.e., rivers, snowmobile trails), and access points to transmission lines. Monitoring should also include the use of trail cameras to document transmission line use by predators, ATVs, and snowmobiles.

- Utilize existing data to demonstrate and document the effects of transmission line ROWs on caribou habitat use and range fragmentation. This will require assessment of movement patterns and habitat use of individuals, and assessment of the overall population response at the landscape level. Elements of consideration include habitat assessment, other linear features, comparisons of areas with transmission lines to areas with no transmission lines, assessment of temporal and spatial variability in use, assessment of possible gradient effects, and DNA evidence of possible range fragmentation.
- Monitoring the presence of primary prey species (deer/moose) of predators is required as part of the environmental monitoring of transmission line ROWs in boreal woodland caribou range. This includes long-term monitoring to assess trends related to the presence and abundance of deer.
- Future monitoring of transmission line use by humans in boreal woodland caribou range must include long-term studies and documentation of all users of the area (e.g., trappers, hunters). Documentation must also include vehicle use along lines and the broader footprint of these lines (e.g., forestry trails leading on to transmission line right-of-ways) to assess and quantify effects of transmission line construction and operation.
- Monitor and document caribou use/activity, season and timing, population demographics and habitat use of primary prey (moose/deer) within and adjacent to transmission line ROWs. This must also incorporate traditional and local knowledge.
- Conduct post-construction monitoring such as aerial transect surveys, standard VHF and GPS telemetry collaring.
- Mitigation strategies should be investigated for assessing mode of access for vegetation management to minimize potential increased use by predators as a result of snowpack. Timing of maintenance during the frost-free period could also be considered. The human access effect or analysis of “spin-off” access to and from transmission lines should be considered in future siting of transmission lines.
- Examination of the effects of transmission lines on black bear populations, particularly near potential and existing caribou calving areas, is required to determine if transmission ROWs in calving complexes contribute to calf mortality.
- Integration of lichen monitoring into proposed long-term vegetation monitoring programs on transmission line right-of-ways to determine the extent of change in conifer/lichen associations into shrub/herb habitats.
- Development and implementation of a vegetation management strategy which encourages lichen production in high quality boreal caribou range.
- Conducting pre-construction surveys to identify lichen-rich habitat in high-quality boreal caribou range.
- Examination of gastropod distribution in Manitoba and varying habitat types to assess the potential risk to caribou populations is required. This includes deer pellet analysis for *P. tenuis*.

Conclusions

The cumulative effects of transmission lines need to be put in context with other natural and anthropogenic disturbance events. Collaboration with Manitoba Conservation, other land users and stakeholders on population monitoring is important to Manitoba Hydro. Due to the multiple vectors of decline and the time lag response of boreal caribou populations to disturbance, it is essential that long-term monitoring of populations through recruitment and mortality studies be undertaken to understand the cumulative effects of linear development on boreal caribou recruitment and mortality. The long-term goal of such research is to determine if there is a gradient effect of transmission line ROWs relative to range occupation and recruitment and if there is a negative response as a result of ROW development. This is a critical component and ties the proposed monitoring and research to an end effect, and will also contribute to determining if and where the effects of transmission lines are significant or additive to an existing linear disturbance density effect.

Comprehensive review of historical distribution of boreal caribou, fire history, and habitat and human disturbance in the form of a retrospective analysis will demonstrate the dynamic nature of caribou distribution through time and space. This will assist in identifying and rationalizing major transmission line routing options in some cases by avoiding future intact habitat complexes or paralleling existing linear infrastructure. Reviews of historical data should also include analysis of forest succession and use of habitat by boreal caribou through time and space.

The difference in environments and how populations use habitat must also be investigated (e.g., bog versus forest populations).

Integrated collaborative research and monitoring efforts need to be established in the context of overall provincial boreal caribou recovery activities where Manitoba Hydro should be a partner. Manitoba Hydro is assessing the recommendations and has incorporated many of the major components into an internal draft corporate boreal woodland caribou strategy. Collaborative projects are being undertaken with Manitoba Conservation and university graduate studies are underway. Manitoba Hydro will continue to participate in collaborative research and monitoring initiatives with Manitoba Conservation towards the collective goal of achieving self sustaining boreal caribou populations in Manitoba, while ensuring a safe, reliable and environmentally friendly source of energy vital to the economy of Manitoba.

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The 13th North American Caribou Workshop
Winnipeg, Manitoba, Canada
25–28 October, 2010

Mountain caribou recovery plan for British Columbia

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Mountain caribou are an ecotype of woodland caribou (*Rangifer tarandus caribou*) that live in the mountains of south-eastern British Columbia. The mountain caribou ecotype live in an area of deep snow which precludes digging for forage under the snow, and consequently they feed almost exclusively on arboreal lichens in old-growth forests during winter. These caribou are part of the nationally Threatened woodland caribou population in the Southern Mountains National Ecological Area. The caribou have experienced significant population declines and range reduction leading to them being Red-listed or "Endangered" in British Columbia The primary cause of population declines is predation, but excessive levels of predation appear to be associated with human caused landscape change. There is also concern about disturbance and displacement of caribou by snowmobiles and heli-skiing. The British Columbia government endorsed the Mountain Caribou Recovery Strategy in 2007. The strategy includes: Protecting 2.2 million hectares of core habitat from logging and road-building; managing recreation to reduce disturbance of caribou through closures and best-management practices; Managing predators and alternate prey species to reduce predation on caribou; Transplanting caribou to supplement very small herds; and ongoing monitoring and adaptive management. Implementation and monitoring of the plan are ongoing.

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The reintroduction of boreal caribou as a conservation strategy: A long-term assessment at the southern range limit

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Abstract: Boreal caribou were extirpated from the Charlevoix region (Québec) in the 1920s because of hunting and poaching. In 1965, the Québec government initiated a caribou reintroduction program in Charlevoix. During the winters of 1966 and 1967, a total of 48 boreal caribou were captured, translocated by plane, and released within enclosures; only their offspring (82 individuals) were released in the wild. Between 1967 and 1980, a wolf control program was applied to support caribou population growth. The caribou population, however, remained relatively stable at 45–55 individuals during this period. During the 1980s, the population grew slowly at a rate of approximately 5% each year to reach a peak of 126 individuals in 1992. At that time, Bergerud & Mercer (1989) reported that the Charlevoix experiment was the only successful attempt at caribou reintroduction in the presence of predators (in North America). Afterwards, the population declined and since then it has been relatively stable at about 80 individuals. Here we reviewed the literature regarding the ecology and population dynamics of the Charlevoix caribou herd since its reintroduction, in an attempt to critically assess the value of reintroduction as a conservation tool for this species. Indeed, the Charlevoix caribou herd is now considered at very high risk of extinction mostly because of its small size, its isolation from other caribou populations, and low recruitment. The Charlevoix region has been heavily impacted by forestry activities since the early 1980s. Recent studies have indicated that these habitat modifications may have benefited populations of wolves and black bears—two predators of caribou—and that caribou range fidelity may have exposed caribou to higher predation risk via maladaptive habitat selection. As females are ageing, and females and calves suffer high predation pressure from wolves and bears respectively, we suggest that the future of this reintroduced herd is in question and that they are facing a high probability of extinction in the near future if further action is not taken.

Key words: boreal caribou reintroduction; Charlevoix herd; conservation tool; decline and extirpation; landscape disturbance; predator-prey relationships.

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Introduction

Throughout North America, woodland caribou (*Rangifer tarandus*) have undergone severe population declines and range recession in the last century (Vors & Boyce, 2009). Numerous local populations have been extirpated, essentially because of overhunting and poaching, but also due to anthropogenic habitat modifications such as forest harvesting and road networks—both of which locally favour large predator populations (Schaefer, 2003; Racey & Arsenault, 2007; Vors *et al.*, 2007). Now recognized as a threatened species by COSEWIC, woodland caribou receive much political attention and are considered of high conservation value (Mallory & Hillis, 1998; Environment Canada, 2008a).

In the past decades, several jurisdictions have advocated caribou reintroduction as a conservation strategy to support declining populations or to reestablish extirpated herds. Bergerud & Mercer (1989) published a critical review of caribou reintroduction experiments in which they identified a series of factors influencing the success of these reintroductions. Namely, they attributed failures to high predation pressure (e.g., in St. Ignace, Ontario and northern Minnesota) and to low lichen supplies (e.g., in Cape Breton, Nova Scotia and Mt. Katahdin, Maine). They also highlighted that the presence of white-tailed deer (*Odocoileus virginianus*), which may transmit a meningeal worm (*Parelaphostrongylus tenuis*) infection to caribou, may be an important factor limiting the success of caribou reintroductions.

Other factors reported as potentially compromising successful ungulate reintroductions include an incomplete understanding or characterisation of historical distributions, husbandry practices, patterns of space use, feeding habits, habitat relationships, population structure (age and sex), number of animals that should be released, mitigation of the extirpation causes, site/range fidelity and dispersal capacities, individual experience or naivety of animals vs. local risks of mortality, guilds of predators and competitors, parasitism, genetic diversity and the evolution of genetic polymorphism of the reintroduced animals (Griffith *et al.*, 1989; Wolf *et al.*, 1996; Fischer & Lindenmayer, 2000; Komers *et al.*, 2000; Larter *et al.*, 2000; Armstrong & Seddon, 2007; Frair *et al.*, 2007; Kidjo *et al.*, 2007; Bell & Dieterich, 2010).

As elsewhere across the historical range of caribou in North America, caribou in Québec underwent severe declines beginning in the early 1800s. The most important declines occurred at the southern edge of the boreal forest, close to human settlements. Range recession towards the north resulted in three isolated herds south of the continuous species range, namely the relict herds of Gaspé National Park, Val-d'Or, and Charlevoix. The Val-d'Or herd is a remnant of the larger herds which historically inhabited the boreal forest near the Québec–Ontario border. The status of this herd is now critical, with only 25 individuals remaining (MRNF, unpubl. data). The herd associated with the summits of Gaspé National Park contains about 150 individuals and represents the last vestige of the populations once occupying the southern shore of the St. Lawrence River, from New England to Nova Scotia (Ouellet *et al.*, 1996). The last of these three isolated herds is unique in that the herd was reintroduced in the Charlevoix region, north of Québec City, during the late 1960s. Interestingly, Bergerud & Mercer (1989) reported that the Charlevoix experiment was the only successful attempt at caribou reintroduction in the presence of predators (in North America). Although the Charlevoix herd managed to persist until now, recent findings suggest that it might face new threats in the near future.

Here we review the history of the Charlevoix caribou herd, focusing on the population dynamics since the reintroduction. We review the causes of their original decline and extirpation, describe habitat modifications and population surveys, and synthesize the results from past and recent research projects. We demonstrate that, even 40 years following reintroduction, population persistence is not ensured. Ultimately, we discuss the feasibility and potential limitations of using caribou reintroduction as a conservation strategy.

Description of the Charlevoix region

The area traditionally used by the Charlevoix caribou herd covers approximately 5500 km^2 and is located ~50 km north of Québec City (Québec, Canada). The range overlaps the Laurentides Wildlife Reserve and three protected areas—Jacques-Cartier National Park (670 km^2), Grands-Jardins National Park (310 km^2), and Hautes-Gorges-de-la-Rivière-Malbaie National Park (225 km^2) (Fig. 1). Located within the Jacques-Cartier ecoregion, the area is characterised by broken topography, a coniferous-dominated forest cover, and an important current and historical habitat disturbance regime (Li *et al.*, 1997). The forest is dominated by balsam fir (*Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* Mill.), white birch (*Betula papyrifera* Marsh.), and trembling aspen (*Populus tremuloides* Michx.). An important wintering area of the Charlevoix caribou herd is found in Grands-Jardins National Park, in a section characterised by alpine tundra vegetation and a highly-rugged topography with some of the highest peaks in southern Québec (up to 1100 m) (Li *et al.*, 1997). The Charlevoix region is subject to harsh weather conditions. Mean annual temperatures range between -2.5 and 0.0 °C, with a daily minimum of -15 °C in January and a maximum of 15 °C in July (Environment Canada, 2008b). The region typically receives 1000 to 1600 mm of precipitation annually, with 400 to 700 mm falling as snow. Mean snow depth reaches ~150 cm each year.

The forested landscape of the study area has been frequently modified by natural disturbances. Since

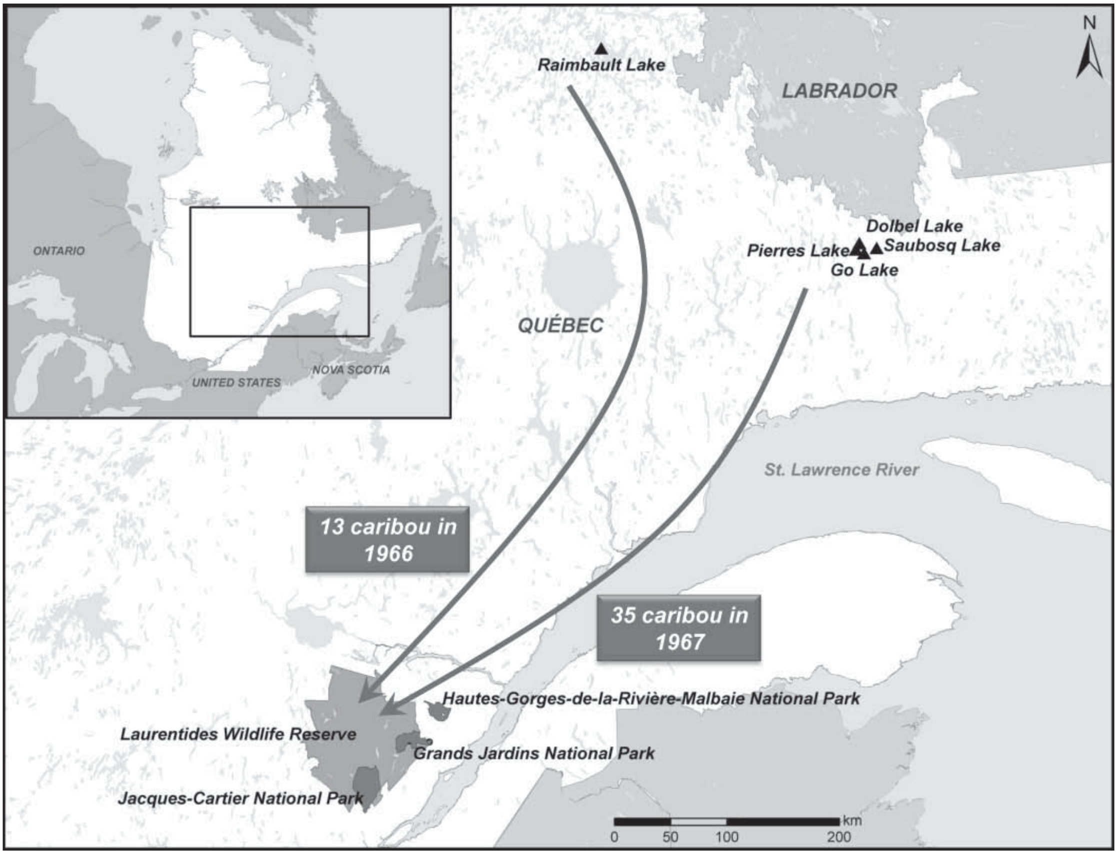

Fig. 1. Location of the sites where caribou were captured for reintroduction in the Charlevoix area in 1966 and 1967. The current location of the Laurentides Wildlife Reserve, the Jacques-Cartier National Park, the Grands-Jardins National Park and the Hautes-Gorges-de-la-Rivière-Malbaie National Park is also indicated (adapted from Sebbane *et al.*, 2008).

the reintroduction of caribou, four major forest fires (1977, 1991, 1996, and 1999) have affected approximately 100 km^2 of habitat frequented by caribou (Jasinski, 2004). In Grands-Jardins National Park alone, at least 13 different forest fires have burned across about 40% of the park's area (~120 km^2) since the beginning of the 20th century. In addition, two severe spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks occurred in 1976–1977 and in 1981–1985, with considerable impact on the balsam fir stands in the region (Jasinski, 2004). Logging activity began at the end of the 19th century, but it became more important in the early 1940s, and since the 1970s the forestry industry has had a strong presence in the region. For instance, when Grands-Jardins National Park was created in 1981, around 40% of the territory was composed of early seral stage forests as a result of logging activities that occurred between 1942 and 1967 (Jasinski, 2004). Today, the area frequented by the Charlevoix caribou herd is considered to be one of the most heavily impacted areas inhabited by forest-dwelling caribou in Québec (Faille *et al.*, 2010), with the most important habitat modifications occurring during the last four decades (see details below).

Causes of decline and extirpation

Similar to other woodland caribou populations (Vors & Boyce, 2009), the Charlevoix caribou herd underwent a rapid and continuous decline at the end of the 19th century. The population size decreased from an estimated 10 000 individuals (Potvin, 1945) in the 19th century to a complete extirpation in the early 1920s. The most important sources of mortality were hunting and poaching. During the first few centuries of European colonization in the province of Québec, caribou harvest was rather low—likely due to the use of high plateaus by caribou during the winter and their ability to move through deep snow with ease (Martin, 1980). At the end of the 19th century, caribou harvest rates increased rapidly in association with the use of repeating rifles and increased access to hunting territory (as road and railway networks were developing). The rapid expansion of human settlements, logging, and clearing of forested areas for agriculture also resulted in degraded habitat conditions for caribou and changes in predator-prey relationships (Gaudreault & Fortin, 1988; Jolicoeur *et al.*, 1993).

An increase in predation mortality is the second most important factor explaining the decline of the Charlevoix caribou herd. Habitat modifications, such as logging and natural disturbances, increased the abundance of early successional stands in the area—this change in forest structure and composition provided moose (*Alces alces*) with more high-quality habitat (Courtois *et al.*, 1998; 2007). As reported by pioneer naturalists, and in the harvesting records of the Charlevoix region, moose densities began to increase in the late 1890s (Jolicoeur *et al.*, 1993). Increased prey (i.e., moose) availability for wolves (*Canis lupus*) translated into increased wolf density and, indirectly, increased predation risk for caribou (Bergerud & Elliot, 1986; Seip, 1992; Rettie & Messier, 1998; Wittmer *et al.*, 2007). Anthropogenic habitat modifications also favoured the northward expansion of white-tailed deer range and an increase in beaver (*Castor canadensis*) densities. The increase in density of these prey species likely resulted in higher wolf numbers and a consequent increase in predation pressure on caribou (Latham *et al.*, 2011).

Reintroduction of caribou

Following the extirpation of the Charlevoix caribou herd in the 1920s, the Québec government decided to reintroduce the species in the region in the late 1960s. Two capture sessions were organized approximately 700 km northeast of Québec city, along the Québec–Labrador border. Thirteen individuals were captured in March 1966 near Raimbault Lake, while 35 individuals were captured in March 1967 near Pierres, Dolbel, Go, and Saubosq Lakes (Fig. 1). Individuals were captured by being herded by aircraft towards nets on a frozen lake. All captured caribou were adults and were temporarily maintained within a small enclosure prior to transportation to the reintroduction site.

The caribou were transported to Charlevoix via plane, followed by a short trip by truck to the relocation site. Prior to travel, caribou were chemically immobilised with succinyl chlorine, physically restrained with a harness in a sternal position, and blindfolded. They were first released in a 0.5-ha enclosure (Lake Turgeon, Grands-Jardins National Park) and then in a 2.1-ha enclosure (Grand Lac Jacques-Cartier, Laurentides Wildlife Reserve). Despite all the precautions taken, 7 of the 48 caribou died from myopathy soon after their release. For 3 years caribou were kept in captivity and fed daily with 8 kg of lichens (wet weight) and 2 kg of a specially prepared animal feed. The caribou reproduced successfully in captivity, increasing their numbers within the enclosure to 102 (both adults and calves) in the summer of 1969. Only captive-born offspring were released because translocated individuals were expected to exhibit site fidelity toward their native range and could potentially return there. A total of 83 caribou were released in the wild on three different occasions between 1969 and 1972 (Table 1).

Wolf control program

The Québec government conducted a wolf control program from 1967 to 1979 in the area to be frequented by the reintroduced caribou (Jolicoeur *et al.*, 2005). It is not obvious from the population survey data whether the wolf control program had a significant positive impact on caribou demography. Surprisingly, caribou abundance only started to increase shortly after the end of the control program (Ban-

Table 1. Characteristics of the 83 caribou released in Charlevoix between 1969 and 1972, following breeding in captivity.

Year	Number of caribou	Sex		Age class		
		Male	Female	Adult	Yearling	Calf
1969	42	19	23	18	19	5
1971	23	14	9	12	11	0
1972	18	6	12	0	7	11
Total	83	39	44	30	37	16

ville, 1998) (Figure 2). Even if the link between caribou increase and wolf control was not obvious, the Québec government has continued to encourage wolf harvest by local trappers (Banville, 1998). Special training was even offered to trappers in an attempt to increase trapping efficiency (Sebbane *et al.*, 2008).

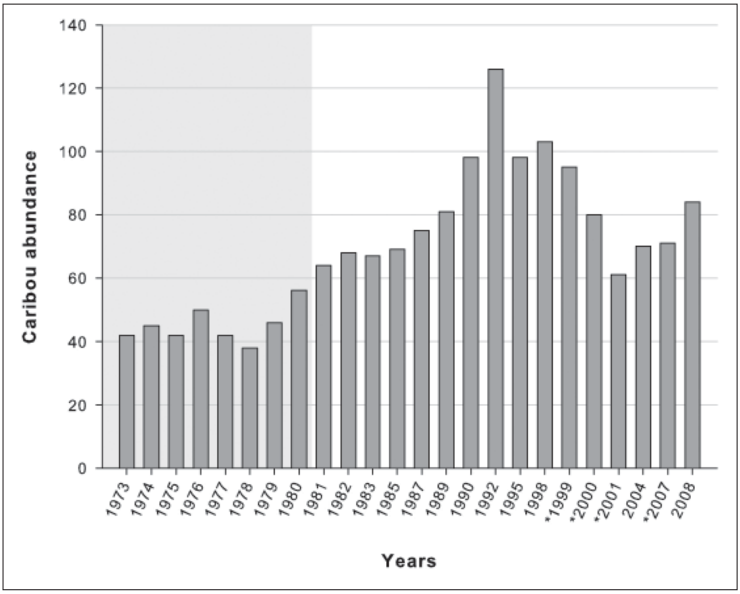

Fig. 2. Variation in abundance of the reintroduced caribou herd estimated from aerial surveys conducted in Charlevoix between 1973 and 2008. An asterisk (*) identifies years when caribou abundance was estimated rather than counted by aerial surveys.

New data, however, suggest that wolf abundance may have increased substantially in recent decades (Sebbane *et al.*, 2003). For example, the density of the wolf's primary prey species, moose, is estimated to have increased from 0.6 to 2.2 individuals/10 km^2 between 1978 and 1994 (Crête & Dussault, 1987; St-Onge *et al.*, 1995; Sebbane *et al.*, 2008), reaching 4.1 moose/10 km^2 in 2009 (MRNF, *unpubl. data*)–a density considered by Bergerud (2007) to be far too high to maintain caribou. Despite a high wolf harvesting rate between 1995 and 1998 (estimated at 41%, Jolicoeur, 1998), there are still seven packs inhabiting the Charlevoix region, several of which have a territory overlapping the caribou distribution area; and recent data suggest that wolf harvest is still high in the region (about 40%; Dussault & St-Laurent, *unpubl. data*). Although the predation rate of wolves on the caribou population has not been evaluated precisely, Tremblay *et al.* (2001) have estimated that the summer diet of wolves in the Charlevoix region in 1996–1997 was composed of 29 to 92% moose, 1 to 24% caribou, and 7 to 73% beaver.

Population monitoring

Caribou abundance and population structure have been monitored regularly by aerial survey since the reintroduction. The abundance of the reintroduced caribou population remained stable at around 50 individuals during the 1970s and increased rapidly from 38 animals in 1978 to 126 animals in 1992 (Fig. 2). Between 1978 and 1992, recruitment—defined here as the proportion of calves in the population during late winter—was high (18–30%), as were annual survival rates of both adults (87–95%) and calves (79%). Following the peak abundance of 126 individuals recorded in 1992, the population declined steadily to a minimum of 61 in 2001 (Fig. 2). During the decline, recruitment was low (~15 %) and annual survival rate of adults was low (69%); and lower in winter (77%) than in summer (90%; Sebbane *et al.*, 2003). Based on a telemetry survey, Sebbane *et al.* (2003) noted that 46% of the females fitted with a VHF collar died from natural causes (e.g., predation, cliff falls, malnutrition, and calving complications).

Woodland caribou are known to have low productivity and high mortality rates, which often result in stable or slightly declining population trends (Bergerud, 1980; Stuart-Smith *et al.*, 1997; Rettie & Messier, 1998; Mahoney & Virgl, 2003). The high mortality rates observed in Charlevoix since 1992 illustrate the precarious state of this reintroduced population. Between 1992 and 2008, the annual growth rate (λ) was estimated at 0.95 (see methods in Akçakaya *et al.*, 1997), indicating an approximate 5% decline in caribou abundance annually. Since 2004, the Charlevoix caribou population appears to be relatively stable at approximately 75–80 individuals (Sebbane *et al.*, 2008; Fig. 2).

Although the Charlevoix caribou herd has managed to persist in a human-altered landscape since its reintroduction, it has exhibited a relatively low population growth rate. Further, it was troubling to note that following 1992 the status of the herd deteriorated. Possible explanations for this apparent stabilization of the population at a low density suggest the interaction of several aspects of caribou ecology, such as genetics, fecundity, forage quality and availability, habitat modifications, and relationships with predators. In the following sections, we synthesize the results of several research projects conducted on the reintroduced Charlevoix herd to assess the different hypotheses raised to explain the precarious status of the population.

Population intrinsic hypotheses

Although food is usually not a major limiting factor for forest-dwelling caribou in the boreal forest (Bergerud & Mercer, 1989), it may become more important or interact with other limiting factors in highly managed landscapes (Briand *et al.*, 2009; Hins *et al.*, 2009). Caribou consume about 5.0 kg and 3.5 kg of lichen every day in winter and summer, respectively, for a total of 1135 kg/yr (Cumming, 1992). Consequently, open lichen woodlands and coniferous forests rich in lichens have been identified as important habitat types in Charlevoix (Charbonneau, 2011) as elsewhere in eastern Canada (Mahoney & Virgl, 2003; Briand *et al.*, 2009; Hins *et al.*, 2009). To determine whether caribou could be limited by food availability in Charlevoix, Sebbane *et al.* (2003) estimated the winter carrying capacity in the herd's distribution area, based on terrestrial (TL) and arboreal lichen (AL) biomass produced in open lichen woodlands (4160 kg/ha for TL and 7–14 kg/ha for AL) and in other coniferous stands (588–609 kg/ha for TL and <1.4 kg/ha for AL). Considering annual lichen production and lichen damage caused by caribou trampling, they estimated that terrestrial lichens could support 117 individuals and arboreal lichens could support 17 individuals, which is similar to the maximum abundance of the reintroduced herd in 1992 (n = 126). Although we have no precise information on caribou body condition since the reintroduction, we could hypothesize that food – at least lichen – may have partially limited the growth of the Charlevoix caribou herd; but lichen abundance alone cannot explain why caribou abundance has remained so low since 2001. Food abundance could, however, interact with other limiting factors such as habitat loss and fragmentation (i.e., food accessibility) or predation.

Another plausible hypothesis to explain the decline of the Charlevoix herd is low genetic diversity (i.e., heterozygosity). Genetic analyses confirmed that the reintroduced caribou were of the forest-dwelling ecotype, and that the Charlevoix herd exhibited lower genetic diversity than larger populations inhabiting the continuous range (Courtois *et al.,* 2003). However, the number of alleles per locus and expected heterozygosity for the reintroduced herd were twice as high as those of the insular Svalbard reindeer (Côté *et al.*, 2002). Courtois *et al.* (2003) thus concluded that the genetic diversity of the Charlevoix herd was sufficient to prevent problems with productivity and/or mortality, at least on a short-term basis. They concluded that the Charlevoix herd was more likely vulnerable to extinction caused by stochastic variation in population dynamics than to inbreeding, a situation observed in many isolated animal populations (Caughley, 1994; Levin, 1995).

The last hypothesis that could explain the observed decline in the Charlevoix population is related to fecundity problems. Pinard *et al.* (2012) estimated the calving rate at approximately 80% between 2004 and 2007. They reported that this was a similar rate to those observed elsewhere in the continuous caribou range of Québec (e.g., Courtois *et al.*, 2007) and consequently discarded this hypothesis.

Habitat degradation

The forest structure and composition within the range of the Charlevoix herd has been greatly modified since their reintroduction. By comparing caribou behaviour during two distinct time periods using VHF telemetry surveys (1978–1981 and 1998–2001), Sebbane *et al.* (2008) demonstrated that these habitat modifications resulted in the expansion of the herd's range and influenced habitat selection patterns. Between the late 1970s and late 1990s, the herd's range almost doubled, increasing from 1185 km^2 to 3127 km^2. Caribou expanded their population range and their individual home ranges to include open coniferous forests (Sebbane *et al.*, 2008), a behaviour recognized recently as an anti-predator strategy (Charbonneau, 2011; Pinard *et al.*, 2012). In comparison, closed-canopy coniferous stands, which were selected for by caribou in the late 1970s, were avoided in the late 1990s.

An ongoing GPS telemetry monitoring program (2004–present) showed that the Charlevoix herd is now occupying a range of approximately 6500 km^2, which is heavily disturbed by logging (Fig. 3). Even though 16% of the herd's range is found within protected areas (i.e., national parks), most of the range (71%) overlaps a wildlife reserve where logging is permitted. Consequently, their range is essentially dominated by disturbed stands (48%) with 18% of clearcuts being < 20 years old. Nearly half of the herd's range (46%) is composed of mature forests (>50 years old) suitable for caribou, but these suitable patches are dispersed in a highly fragmented landscape intersected by numerous forest roads (0.97 km/

km^2; Fig. 3a). Regenerating stands (mainly old clearcuts, 20-50 years old) occupy 25% of the distribution range, while natural disturbances (insect outbreaks, fires, and windthrows) account for only 4% of the range (Fig. 3b). Recreational infrastructure (both private and commercial cabins) are also well-distributed across the landscape (0.14/km^2), suggesting that the road network is active.

Finally, the Charlevoix caribou range is fragmented (cut almost in half) by Highway 175 (density of 0.03 km/km^2; Fig. 3a), an important paved road linking two major cities, Québec City and Ville Saguenay (total population >500 000). Though caribou are sometimes involved in collisions with vehicles, the barrier effect of the highway on caribou movements may have a much greater impact on population dynamics. Caribou are found on both sides of the highway and, as they usually avoid it (Leblond *et al.*, 2011), the already small population could become subdivided into even smaller units. The fragmenting effect of the highway has become an even greater concern for wildlife managers since 2006 when a very large roadwork project aimed at

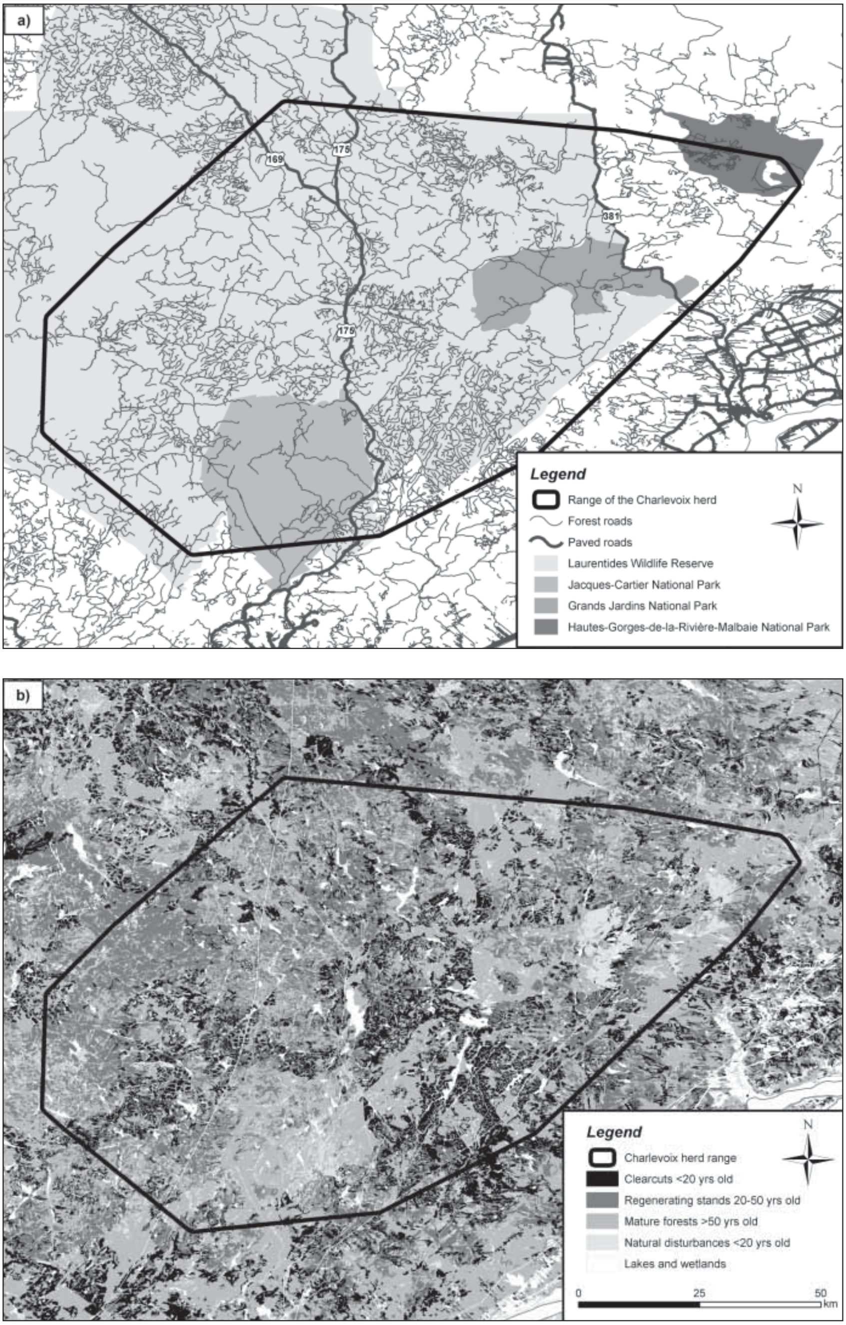

Fig. 3. Characterisation of the range occupied by the reintroduced caribou herd in Charlevoix between 2004 and 2010 (MCP 100%). Habitat characteristics were determined using ecoforest maps updated in 2009 by the Ministère des Ressources naturelles et de la Faune du Québec (MRNF). (a) Map showing road density (both paved and forest roads) and boundaries of the Laurentides Wildlife Reserve, Jacques-Cartier National Park, Grands-Jardins National Park and Hautes-Gorges-de-la-Rivière-Malbaie National Park. (b) Map showing the abundance and configuration of clearcuts, regenerating stands, mature forest and naturally disturbed forest stands.

rebuilding the highway from a two-lane highway into a four-lane dual carriageway was initiated.

Changes in the predator – prey system

The apparent competition hypothesis (Bergerud & Elliot, 1986; Seip, 1992)—that links changes in forest age and structure following timber harvest and fire to increases in moose and wolf abundance—is now well accepted in the literature as one of the mechanisms involved in the North American caribou decline (James *et al.*, 2004; Wittmer *et al.*, 2005; Vors & Boyce, 2009). This hypothesis stipulates that caribou populations suffer from increased predation risk when wolf populations are maintained at high levels by alternative prey (Wittmer *et al.*, 2007), a precarious situation for endangered populations (DeCesare *et al.*, 2010).

In Charlevoix, the situation is slightly different as caribou demography is more constrained by black bear (*Ursus americanus*) predation on calves than by wolf predation on adults. Indeed, results of the telemetry surveys conducted since the caribou reintroduction indicate a variable annual survival rate for adults (69–95%; Cantin, 1991; C. Dussault, unpubl. data) but aerial surveys indicate relatively low recruitment for several years. In agreement, calf survival rate was estimated to be 61% between 1973 and 1990, and only 47% between 2004 and 2007. A recent study has indicated that bears were responsible for the majority (96%) of calf predation events and 65% of overall calf mortality, while wolves were responsible for only 3% of calf mortalities (Pinard *et al.*, 2012). Throughout the caribou range, black bears are often recognized as a major threat for neonates and calves (Adams *et al.*, 1995; Mahoney & Virgl, 2003). Although it is not known whether black bears have long been an important predator of calves in Charlevoix, it is possible that high bear predation pressure is linked to the considerable increase in early successional stands in the area, as these provide a high biomass of berries (Brodeur *et al.*, 2008; Mosnier *et al.*, 2008a), an important black bear food. Black bear density was estimated at 2.2 individuals/10 km^2 in the study area in 1989 (Jolicoeur, 2004) but more recent data are not available. However, few bears (< 10) were annually harvested until the late 1980s, whereas total annual harvest increased up to 24 individuals thereafter (Sebbane *et al.*, 2008), suggesting that the bear population may have increased since then. Wolf density is moderate in the Charlevoix caribou herd range (0.44 wolf/100 km^2; Jolicoeur, 1998) and caribou anti-predator strategies appear to be effective in avoiding them (Pinard *et al.*, 2012). As demonstrated by Frair *et al.* (2007) for elk (*Cervus elaphus*), we believe that in Charlevoix, caribou were not able to adapt quickly to new threats (i.e., growing bear density) in their environment and that this naivety might have resulted in the recruitment problems currently observed.

A recent study conducted in Charlevoix demonstrated that most black bears are not actively seeking caribou calves during spring, when calves are most vulnerable (Bastille-Rousseau *et al.*, 2011). Instead, they appear to move between vegetation-rich areas, and their frequent movements result in high rates of opportunistic encounters with caribou neonates. The overall impact of black bears on caribou recruitment may be substantial given the suspected high bear density in the heavily logged landscape of Charlevoix. Such opportunistic predation on calves by bears could be exacerbated by the high range fidelity observed for caribou in Charlevoix (Faille *et al.*, 2010), which could have two possible consequences. First, higher calf and female caribou survival could result from increased familiarity with food distribution, escape cover, and predation risk. However, high range fidelity in a modified landscape could also result in an ecological trap because predation risk increases in early successional forests that are attractive to black bears (Brodeur *et al.*, 2008). We strongly believe that this latter situation occurred in Charlevoix, where range fidelity led to high calf mortality. We therefore suggest that the decline of the Charlevoix herd could be explained, in part, by maladaptive habitat selection behaviour (i.e., range fidelity in an unsuitable habitat matrix; Faille *et al.*, 2010).

Uncertain future

Although caribou are still present in the Charlevoix region approximately 40 years after their reintroduction, it would be hasty to conclude that this reintroduction was a complete success, based on recent findings and as suggested by Bergerud & Mercer (1989). Continuous adaptive measures must be implemented to ensure population persistence. Indeed, this case-study exemplifies the fragile equilibrium between habitat, predators, and caribou. Caribou is a highly-adaptable species that may persist for a long time in adverse environments (Vors *et al.*, 2007); however, long time periods (> 40 years) are required for harvested stands to become unattractive to wolves and bears, and to become a suitable lichen-rich caribou habitat again. Telemetry flights recently revealed that many adult caribou in Charlevoix have died during the last few years, most of them from wolf predation. The Charlevoix herd has been experiencing low recruitment over a long period of time, and many reproductive females are reaching the end of their effective reproductive life. For instance, several females have been followed via telemetry for >12 years, and we believe that these older females may become senescent and more vulnerable to predation, a situation that could lead to rapid population extirpation. Wittmer *et al.* (2010) underlined the negative impact of an increasing proportion of early successional forest stands on both adult female survival rate and caribou density, suggesting that caribou populations might face extinction within < 200 years.

Our review of the Charlevoix reintroduction supports the conclusions of many researchers regarding the proximate (i.e., numerical response of alternative prey and predators) and ultimate (i.e., profound habitat modifications) causes of the observed decline (Bergerud & Mercer, 1989; Racey & Arsenault, 2007; DeCesare *et al.*, 2010). Accordingly, we strongly suggest that immediate action be taken to preserve the reintroduced caribou population in Charlevoix. Both logging and recreational activities that are well established throughout the herd's range are resulting in a functional loss of suitable habitat for caribou while simultaneously favouring predator and alternative prey populations. Preserving caribou in a landscape such as in the Laurentides Wildlife Reserve, where human activities are entrenched, will require socio-economical and ecological compromises. A crucial step was recently taken by the Québec government with the publication of a caribou habitat management plan (Lafleur *et al.*, 2006). This plan is now in action and forest companies are requested to follow some important guidelines. It specifically aims to protect critical caribou habitat, maintain a minimum amount of suitable caribou habitat within the herd's range, and limit human disturbance and the development of road networks within critical caribou areas. Considering that recent research identified black bear as the most important threat to caribou recruitment in Charlevoix, we believe that the management plan could be complemented by requesting outfitters to increase bear harvest and forest managers to control deciduous species, especially grasses and berry-shrubs, within regenerating stands. Because wolf harvest is still important in this area and as wolves currently have only a slight influence on caribou recruitment according to Pinard *et al.* (2012), we do not believe that more pressure on the wolf population is necessary at this time. Similar to Environment Canada (2008a), we think that there is a habitat disturbance threshold above which the conservation of a small isolated herd like that of Charlevoix might become very difficult. We believe that the conservation of the Charlevoix caribou cannot be ensured solely by protection in protected areas, as exemplified by the recent extirpation of caribou in Banff National Park (Alberta, Canada; Hebblewhite *et al.*, 2010; see also Brashares, 2010).

As previously mentioned, the development of the road network continues in the Charlevoix caribou range—one of the largest roadwork projects in Canada in recent years. The overall impact of this road construction has yet to be explored in detail. In addition, a substantial proportion of the new right-of-way will be fenced to prevent moose–vehicle collisions, further limiting connectivity among caribou groups. An ongoing research project aims to assess the impacts of this new highway and fence on the Charlevoix caribou herd. We can only hope that current mitigation measures such as wildlife passages will allow caribou to move safely from one side to the other, thereby allowing access to some highly suitable winter habitats and, more importantly, increase connectivity between groups on both sides of the highway. Considering the above-mentioned threats, it is obvious that the reintroduced caribou herd of Charlevoix is facing an uncertain future and, if action is not taken soon, it is at high risk of being extirpated in the coming decades.

Lessons from the Charlevoix experiment

Improving the likelihood of a successful caribou reintroduction requires consideration of several very important factors. First, we believe that caribou reintroduction (as any other conservation effort) must be based on a rigorous, *a priori* estimation of the costs and probability of success (Schneider *et al.*, 2010), and must be supported by population viability analyses to assess the relative need for and benefits from animal translocation (DeCesare *et al.*, 2011). We judge that most reintroductions would be compromised if conducted in areas where predator and alternative prey populations are abundant and diversified, especially if translocated animals have not experienced similar predation risk and predator diversity (Frair *et al.*, 2007). Second, it is imperative to support reintroduction with a habitat management plan that will protect suitable caribou habitat, prevent habitat modifications favouring predator and alternative prey populations, and favour restoration of caribou habitat. Indeed, reintroduction success increases substantially when the causes of the original decline are removed (IUCN, 1987; Fischer & Lindenmayer, 2000; DeCesare *et al.*, 2011). Finally, if a reintroduction is attempted in a highly disturbed landscape, we consider that reducing predator (Bergerud, 2007)—and even alternative prey (Latham *et al*., 2011)—populations might be necessary. Predator control, although logistically difficult to implement and ethically sensitive in the public opinion (Latham *et al*., 2011), has already proven efficient in increasing caribou recruitment in northern British Columbia (Seip, 1992) and in eastern Québec (Mosnier *et al*., 2008b), at least on a short-term basis; it is also less expensive (relatively speaking) than protecting and restoring areas (Schneider *et al*., 2010). Even though wolves are usually recognized as the main predators of caribou throughout the species' range, we urge managers not to overlook the role of bears as calf predators. We recognize that predator removal can be an effective short-term strategy to release pressure on an endangered prey species, but stress that it should be accompanied by suitable habitat management to dampen the influence of habitat alteration (an ultimate factor of caribou decline) on a long-term basis (DeCesare *et al*., 2010). Moreover, wolf and bear control–if applicable–needs to be supported by detailed information on predator populations and pursued until the landscape becomes suitable to caribou and unsuitable to predators, which is hardly achievable on large territories. Despite difficulties inherent in applying such exceptional measures, we believe that conservation efforts should not be limited only to protection and restoration of habitats in highly disturbed landscapes (Bergerud, 2007). Because low recruitment is often a problem, reintroduced caribou populations will age and declines will likely ensue.

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The 13th North American Caribou Workshop
Winnipeg, Manitoba, Canada
25–28 October, 2010

Woodland caribou management and industrial development in West Central Alberta: Can we have both?

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Since 2005, the Foothill Landscape Management Forum (FLMF) has been operating under the umbrella of the Foothills Research Institute (FRI) to proactively influence industrial development within two Alberta woodland caribou ranges. The FLMF represents 16 energy and forest companies that have overlapping dispositions within caribou ranges. The supporting members recognize that their resource extraction activities can have an impact on caribou and other values. As part of the development and implementation of caribou recovery plans, industry is concentrating its efforts on what they have direct control over such as anthropogenic footprint (amount and type) and vegetation (habitat) spatially and temporally. The FLMF is leading the way in advancing integrated land management, partnering with government, collecting data, supporting research, and monitoring to support an adaptive management approach to caribou management. This talk will outline some of the forums initiatives, challenges, and scenario modeling that support the concept of "learn while doing" for caribou.

The 13^{th} North American Caribou Workshop
Winnipeg, Manitoba, Canada
25–28 October, 2010

An ATK-based approach to management of critical caribou ranges in northern Alberta

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Information gathered from Little Red River Cree Nation (LRRCN) elders shows how current map depictions of critical caribou habitat around Wood Buffalo National Park could be misleading. LRRCN proposes that Aboriginal Traditional Knowledge (ATK) about caribou migration through critical range areas can help to frame a collaborative approach to the establishment of a conservation management strategy in support of caribou recovery. This approach to caribou recovery would use WBNP as an "anchor" and set aside large portions of provincial crown forest lands in protected areas and conservation management areas in order to protect the critical habitat for the Red Earth, Bistho, Yates, and Caribou Mountain herds. To support this strategy, LRRCN is undertaking a collaborative monitoring initiative within the "blank" areas which divide these existing identified caribou habitat areas.

The 13th North American Caribou Workshop
Winnipeg, Manitoba, Canada
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Caribou conservation and recovery

The 13th North American Caribou Workshop
Winnipeg, Manitoba, Canada
25–28 October, 2010

Caribou conservation and recovery: development and implementation of the Caribou Conservation Plan

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Abstract: The range of Ontario's woodland caribou (*Rangifer tarandus caribou*) (forest-dwelling ecotype) has receded northward substantially over many decades, leading to its current Threatened designation. Ontario released its Caribou Conservation Plan (CCP) in the fall of 2009. This policy responded to public input and recommendations from the Ontario Woodland Caribou Recovery Team and the Caribou Science Review Panel, and outlines conservation and recovery actions to conserve and recover caribou. Within an adaptive management framework, the CCP builds upon a recent history of managing at large landscape scales in Ontario to implement a range management approach as the basis for recovery actions. These commitments and actions include enhanced research and monitoring, improved caribou habitat planning at the landscape scale, an integrated range analysis approach using advanced assessment tools to evaluate thresholds of habitat amount, arrangement and disturbance, the assessment of probability of persistence, consideration of cumulative effects, meeting forest management silvicultural performance requirements, consideration of caribou recovery implications when managing other wildlife, an initial focus on the southern edge of caribou distribution where threats are most significant, improved outreach and stewardship, and consideration of Aboriginal Traditional Knowledge in recovery actions. Implementation of the CCP signifies a long-term provincial commitment to caribou recovery, initially focusing on identified priorities within the CCP.

Key words: woodland caribou; Ontario; conservation; policy; recovery; range management; adaptive management.

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Introduction

The range of Ontario's woodland caribou (forest-dwelling ecotype, boreal population) has receded northward substantially over many decades, dating back to the late 1800s (Harris, 1999). Although interest in caribou recovery and conservation has increased considerably over recent decades, the concern is not new. deVos (1949) noted that "Of all the game animals in Ontario today, the one most in danger of extinction is the woodland caribou...Only drastic protection measures…can save the species from complete extermination". Based on this long-term, apparently permanent range recession and the associated population decline, the forest-dwelling ecotype was designated as 'Threatened' in 2004.

There has been increasing emphasis on caribou conservation and management in Ontario since the early 1990s, including a status assessment report (Harris, 1999). A provincial Caribou Recovery Team was established, and produced a provincial Caribou Recovery Strategy (Ontario Woodland Caribou Recovery Team, 2008). Under Ontario's Endangered Species Act, 2007 (ESA), recovery strategies are considered "advice to government", which require a government response statement outlining the actions the government intends to take to recover the species (Government of Ontario, 2007). The Caribou Conservation Plan (CCP) was released by the Ontario Ministry of Natural Resources (OMNR) in 2009 as the Government policy response to recommendations from the Ontario Woodland Caribou Recovery Team and the Ontario Woodland Caribou Science Review Panel (Suffling *et al.*, 2008), and outlines conservation and recovery actions Ontario is taking to recover caribou.

The CCP and some potential limitations were discussed in part in a debate article by Wilkinson (2010). The purpose of this paper is to more fully describe the development of the CCP, clarify and expand on some of the issues raised by Wilkinson (2010), and address initial implementation of the CCP, while recognizing that full implementation of the CCP will be a long-term and ongoing process.

Public consultation and engagement

There was a substantial amount of public input involved in the long-term development of Ontario's caribou conservation and recovery approach. Racey & Armstrong (1996) summarized some of the early consultation efforts that were focused on the development of a caribou habitat management approach for northwestern Ontario. A stakeholder advisory panel provided key advice as part of this process (Greig & Duinker, 1996). A provincial Woodland Caribou Recovery Team was subsequently established to develop a Recovery Strategy, and a Caribou Advisory Committee provided relevant recommendations and advice. The Recovery Strategy was finalized and made available in 2008 (Ontario Woodland Caribou Recovery Team, 2008), considerably changed from and addressing many of the criticism directed at the draft strategy (Wilkinson, 2008).

An external Woodland Caribou Science Review Panel was established to provide independent advice on the content and recommendations of the Recovery Strategy (Suffling *et al.*, 2008). Based on the Recovery Strategy and Science Review Panel report, a discussion paper was developed to solicit public input to support development of the CCP (OMNR, 2008a). Public consultation efforts specific to the CCP included several stakeholder consultation sessions in fall 2008 and winter 2009 (OMNR, 2008b), and invitations to participate through posting on Ontario's Environmental Registry (Government of Ontario, 2009).

A wide range of public comments and interests was submitted, and many people and stakeholders expressed interest in the topic, support for caribou conservation and/or concern about the implications of caribou conservation to northern communities and natural resource management. Public input was considered during the development of both the draft and final CCP. The CCP was released in the fall of 2009 (OMNR, 2009a), at which point the focus shifted to its multi-year implementation.

Ontario's caribou conservation goal

The goal of Ontario's Woodland Caribou Conservation Plan is "To maintain self-sustaining, genetically-connected local populations of woodland caribou (forest-dwelling boreal population) where they currently exist, improve security and connections among isolated mainland local populations, and facilitate the return of caribou to strategic areas near their current extent of occurrence" (OMNR, 2009a). The focus is on maintaining caribou within the area where they are currently distributed, and seeking opportunities to improve their prospects in and adjacent to this area.

Geographic scope of the Caribou Conservation Plan

Caribou occur relatively continuously over much of northern Ontario, where the vast majority of land is under Crown management control. The CCP applies across the entire mapped area of continuous caribou distribution in Ontario (Fig. 1). This reflects both the current distribution of the forest-dwelling ecotype in Ontario and immediately adjacent areas where there is the potential for future caribou re-occupancy. Areas of continuous distribution to the north and along coastal Lake Superior are separated by an area of discontinuous caribou distribution, where caribou live in isolated populations or only on a temporary basis. Some specific elements of the CCP also apply to this area of discontinuous caribou distribution, although the CCP does not broadly apply.

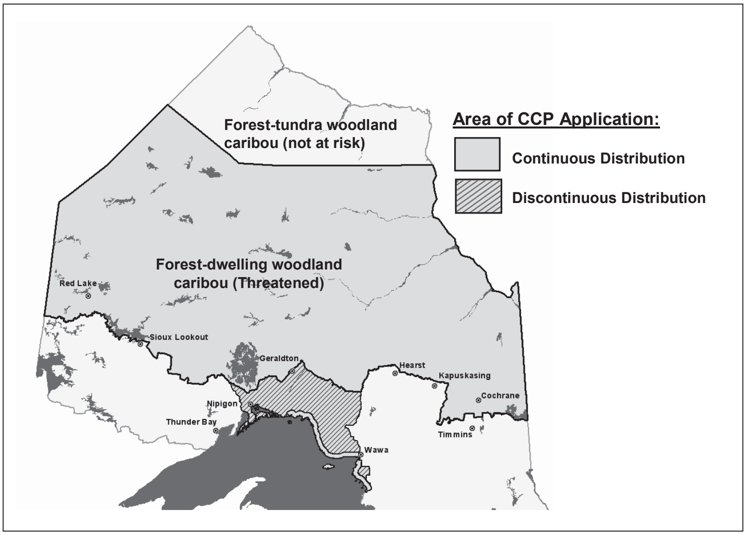


Fig. 1. Area of application of the Caribou Conservation Plan (as revised from OMNR, 2009a).

Key elements of the Caribou Conservation Plan

The CCP contains a number of principles to guide its development and implementation. One of the overarching principles was a commitment to the adaptive management process, involving the "ongoing scientific review and evaluation of progress on management actions, and the use of new science and management information to continually review and improve management" (OMNR, 2009a; as adapted from Baker, 2000).

The eight main strategies of the CCP, each with associated actions, are:

1. Enhance caribou science;
2. Adopt a range management approach;
3. Improve planning;
4. Enhance caribou habitat;
5. Manage the wildlife community;
6. Focus on geographic priority areas;
7. Improve outreach and stewardship; and
8. Integrate Aboriginal Traditional Knowledge.

Each of these strategies contain a variable number of specific action items and commitments; more detail on some of the major commitments and actions are outlined in the following sections.

1.0 Enhanced research and monitoring

The CCP recognized both the significant value of existing scientific information to support caribou recovery in Ontario, and the need to address a number of key scientific uncertainties. One of the key commitments of the CCP was met by the initiation of a long-term collaborative caribou research program that has been under development for some time. A number of previous workshops and assessments involving government (federal and provincial, including neighbouring provinces) and non-governmental individuals (university academics, industry representatives, and non-government environmental organizations) had been undertaken to identify key research questions, develop a research approach and experimental design, and to identify candidate research study areas (Rodgers *et al.*, 2007; 2008; 2009). Key identified uncertainties related to the direct and indirect effect of habitat disturbance, principally forest management, on caribou persistence. Based on a survey of a wide range of resource professionals with interest and/or expertise in caribou, three key research questions of relevance to caribou recovery in Ontario were identified:

1. Evaluation of the effects of landscape disturbances caused by forest management on caribou populations, including impacts on population parameters, habitat selection and changes in the broader wildlife (predator-prey) community;
2. Determination of the mechanisms driving caribou population dynamics in modified landscapes; and
3. Determining thresholds of disturbance for caribou occupancy of disturbed landscapes (Rodgers *et al.*, 2007).

This enhanced research program, involving the Centre for Northern Forest Ecosystem Research (CNFER), the Forest Ecosystem Science Co-op, the University of Guelph, and the Canadian Forest Service was initiated in 2009-10 with the designation of study areas, initiation of silvicultural research, and the radio-collaring of caribou and gray wolves (*Canis lupus*) in three large (22 500 km^2) landscapes in northern Ontario with contrasting levels of habitat disturbance, including road densities, predator densities and abundance of alternate prey, mainly moose (*Alces alces*).

One of the major issues raised during public consultation on the CCP was the concern that the Ontario government's habitat management approach to caribou appeared to be unduly reliant upon the ability to harvest forests within caribou range and subsequently successfully renew them to a condition where they again became suitable as caribou habitat. This was seen by many members of the public, and by the Caribou Science Review Panel, as an untested hypothesis (Suffling *et al.*, 2008). Thus, a significant commitment was also made to a broad science program implemented by CNFER in co-operation with the partners listed above to test this hypothesis and examine the 3 identified key research questions. In areas where caribou appear to have re-occupied logged habitat, researchers will test for differences in habitat conditions between occupied and available stands, and between logged and naturally disturbed habitats across a range of forest ages. Other efforts to further document case studies of demonstrated caribou reoccupancy of logged habitats will also continue (e.g. Racey *et al.*, 1996).

The CCP further committed to an expanded provincial caribou monitoring program that included an annual range monitoring program and a provincial caribou database to maintain all current and historical caribou inventory data. A provincial caribou monitoring plan is currently under development to coordinate monitoring activities consistent with an adaptive management approach, negating Wilkinson's (2010) concern that the lack of a monitoring plan will lead to an inability to determine if the program is achieving its objectives. Population monitoring was initiated for two ranges in 2009-10, and is being continued under the CCP commitment for the monitoring of one to two ranges annually. Additionally, caribou occurrence and population surveys were completed during the winter of 2010-11, the final year of a 4 year endeavour to survey caribou over the entire Far North planning area, which represents the northern 42% of the province. Caribou collaring to support these population monitoring efforts is occurring in the ranges currently being assessed and across the Far North planning area.

A Provincial Caribou Technical Committee was established to provide science expertise and advice on implementation of the CCP. This will build on the successful outcome of the Caribou Science Review Panel, which contributed significantly to the development of the final CCP.

2.0 Adoption of a range management approach

One of the most significant commitments within the CCP was the adoption of a range management approach to caribou recovery. Founded on an adaptive management framework, the CCP builds on a recent history of managing at large landscape scales in Ontario to implement the range management approach as the primary basis for many recovery actions. This entails the delineation of the area of continuous caribou distribution into smaller units of analysis or conservation based on the local population range concept (see Environment Canada, 2008). These ranges provide the spatial and ecological context for the assessment of the condition of the caribou population and its habitat, and the conservation actions expressed through resource management and land use decisions. This approach is consistent with the range-based concept of critical habitat proposed by Racey & Arsenault (2007), which identified the need for consideration and management of caribou habitat at a range of scales if caribou recovery is to be successful. The extent of Ontario's caribou distribution is believed to be essentially continuous (Racey & Armstrong, 1998; Ontario Woodland Caribou Recovery Team, 2008), an observation supported by both the documentation of occupied range and the results of early studies of radio-collared caribou. There is no indication that Ontario's extent of caribou occurrence can be delimited by geographically explicit and spatially separated "herds" or populations as in some other jurisdictions, with the exception of the Lake Superior islands and mainland.

It was recognized that the ecological and biological information on which to delineate ranges is never fully adequate or complete. However it was also recognized as important to begin to delineate ranges in the area considered most at risk to provide a basis for long-term planning, using criteria identified by Environment Canada (2008). Therefore, preliminary ranges were delineated across the southernmost extent of the continuous distribution. Delineation criteria included:

1. animal movement and occupancy patterns;
2. large spatial extent;
3. geographic features;
4. common ecological expressions of functions and behavioural responses;
5. predominant risk factors; and
6. ecological and administrative boundaries.

Subsequent to release of the CCP, there were adjustments to the number and boundaries of these preliminary ranges based on new information (Fig. 2). It is anticipated that these preliminary ranges may be further adjusted over time as additional information and interpretations become available, consistent with an adaptive approach. Ranges were not initially delineated for the more northern areas within the extent of caribou occurrence (Fig. 2), given that development pressures were perceived to be lower and that there was time to await additional information that is forthcoming from current studies of radio-collared caribou. However, rapidly increasing interest in planning and natural resource development in this northern part of the province have accelerated the need for northern range delineation.

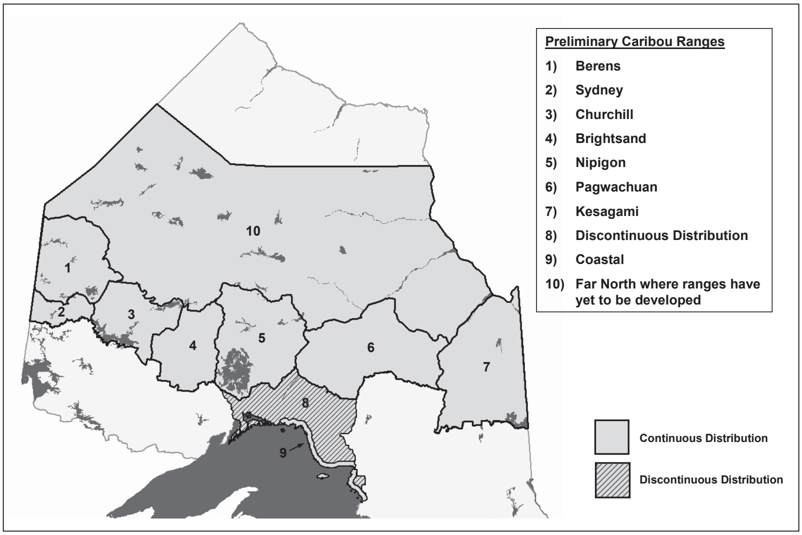


Fig. 2. Preliminary delineation of caribou ranges along the southern edge of the provincial extent of occurrence (as revised from OMNR, 2009a)

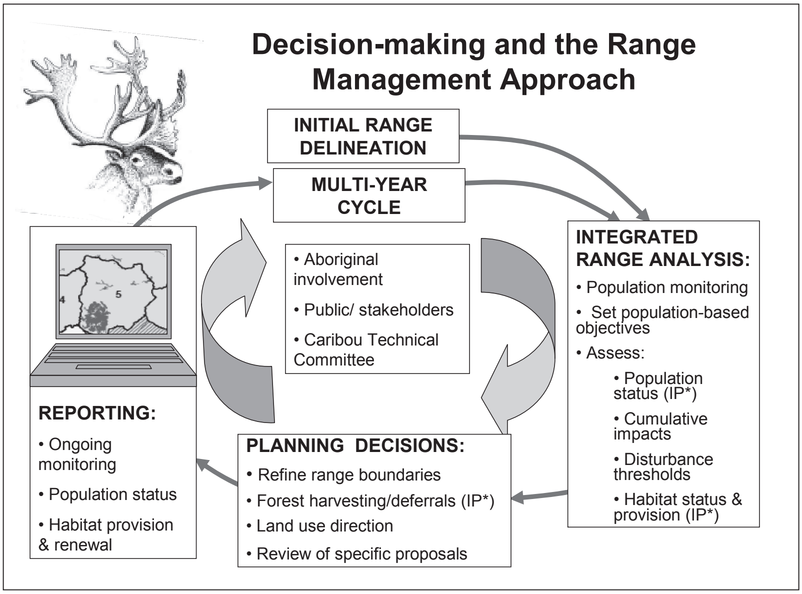


Fig. 3. Relationship between integrated range analysis outcomes and the subsequent CCP decision-making environment (from OMNR, 2009a)

Integrated range analyses using advanced assessment tools to evaluate the condition of caribou habitat and populations are an integral component of the range management approach. Each individual range will be periodically assessed (1-2 ranges annually) following a standardized monitoring protocol. Landscape analysis tools, two-stage aerial surveys, and studies of radio-collared caribou are collectively being used to identify habitat condition, landscape disturbance levels, distribution, probability of occurrence, probability of persistence, and population health parameters (e.g. intrinsic rate of increase, population trends, calf survival) (Ontario Woodland Caribou Recovery Team, 2008). This information will support the evaluation of planning alternatives in light of overall range condition. The status of caribou habitat and populations at the range level will guide decisions on resource management proposals, potential mitigation and the need for recovery measures (Fig. 3).

In the context of range management, the CCP recognized the need to work with the adjacent provinces of Manitoba and Quebec, Parks Canada, and Environment Canada, for recovery to be successful. Caribou ranges on the eastern and western boundaries of Ontario are contiguous and continuous with ranges in the adjacent jurisdiction (e.g., Manitoba Conservation, 2005), and the CCP commits Ontario to working collaboratively with those jurisdictions to effectively recover caribou.

While the CCP applies to the entire area of continuous caribou distribution, only some elements apply to the zone of discontinuous distribution (see Fig. 1). While this area is not known to support a permanent caribou presence and has limited opportunity for full recovery as caribou range, it is recognized as having an important role to play in providing potential genetic and landscape connectivity between the isolated Lake Superior coastal range and continuous range to the north. The CCP committed to the development of a strategy for this area that will identify opportunities for enhancing this connectivity to improve the long-term prospects for population security and the probability of persistence of the coastal population.

The range management approach is central to Ontario's caribou recovery program. The CCP identified the need to develop a range management policy to integrate all range-related guidance within a single coordinated policy, and to ensure a consistent and common approach to implementation of the range management approach. Initiation of policy development was an early priority of the CCP.

3.0 Actions to improve planning for caribou at the landscape scale

The greatest number of recovery actions identified in the CCP are those related to the improvement of planning processes, to more comprehensively consider caribou values in the wide range of resource and land use activities that take place on Crown land. The primary focus of these planning tools and processes is reliance on the probability of caribou persistence as a key determinant of appropriate management decisions and actions.

A significant amount of public input from very diverse perspectives was associated with this component. Many respondents felt that it was essential to identify caribou habitat that would be "protected", in the sense that it would be set aside from resource development and exploitation as a protected area. Wilkinson (2010) similarly expressed the concern that there is little direction in the CCP on what and how much habitat will be protected. It was difficult to reconcile this perspective with the view that caribou conservation requires the consideration and management of entire landscapes over large spatial and temporal scales, and that entire ranges represent important habitat (Racey & Arsenault, 2007). Across the broad boreal forest landscape of northern Ontario, parks and protected areas can clearly be important reserves of caribou habitat, although it does not appear that they can ever be sufficiently large and robust to be relied upon solely as isolated islands of habitat in the absence of integrated management with the adjacent connecting landscape; the experience of caribou population and habitat trends in the Prince Albert National Park area appear to support this conclusion (Arlt & Manseau, 2011). This is particularly important to recognize given that even very large protected areas in the boreal forest can be rendered largely unsuitable for caribou for several decades by wildfire or other natural disturbances. The CCP recognized that parks and protected areas can be important contributors to caribou habitat conservation, but on their own are insufficient to ensure the long-term persistence of caribou; the entire landscape must be managed with caribou habitat considerations in mind. New protected areas were not created as part of the CCP; instead, the focus was on appropriate resource management and land use planning to ensure suitable habitat conditions across the landscape and over time, with an appropriate caribou conservation focus in management plans for protected areas within the extent of caribou occurrence. The CCP committed to significant consideration of caribou conservation values in the designation of new protected areas (at least 225 000 km^2) announced for the Far North Planning Area (Office of the Premier, 2008).

The CCP supported amendments to existing land use planning mechanisms to increase commitments to caribou conservation in planning designations and processes. This includes the amendment of the Crown Land Use Policy Atlas, so that designations reference caribou presence and the need to consider caribou values in all land use decisions, and the review of designated Fish and Wildlife Enhanced Management Areas to assess and improve their effectiveness in support of caribou recovery. These are longer term commitments that have not yet been initiated.

Under the Endangered Species Act, 2007 (ESA), habitat can be defined either through a habitat regulation that prescribes the habitat of the species, or more generally as the area on which the species depends, directly or indirectly, to carry on its life processes (Government of Ontario, 2007). As one of the transition provisions of the ESA, general habitat provisions for woodland caribou take effect 5 years after the act is enacted (i.e. 2013) unless a habitat regulation is put into effect sooner. Habitat "protection" is a challenging concept for a landscape species, such as woodland caribou, which requires extensive areas of refuge habitat, and inhabits dynamic boreal forest habitat that will at some point in the successional cycle become unsuitable habitat for several decades after large disturbances such as wildfire. The CCP committed to development of a caribou habitat regulation, within a landscape approach, that will provide sufficient amount and arrangement of habitat over time to sustain caribou populations. The policy direction in the CCP and the legislated habitat protection afforded by the habitat regulation, which is currently under development, will work together to support caribou conservation and recovery.

Much of the southern extent of caribou occurrence in Ontario has been allocated for forest harvesting and management. Enhanced caribou habitat management through forest management planning requires the development of habitat provision plans that will ensure a sufficient amount and spatial arrangement of caribou habitat through time; the CCP requires that all forest management units provide sufficient habitat over time and the renewal of that habitat through the development of "dynamic caribou habitat schedules", integrated across adjacent management units. These schedules are similar to and build on the former caribou "habitat mosaics" applied in northwestern Ontario (I. Armstrong *et al.*, 1998; T. Armstrong *et al.*, 2000). These dynamic caribou habitat schedules are intended to ensure a long-term habitat supply, and are based on the premise that logged areas that formerly provided suitable habitat can be regenerated through intensive silviculture to again provide future caribou habitat in large tracts of mature coniferous forest.

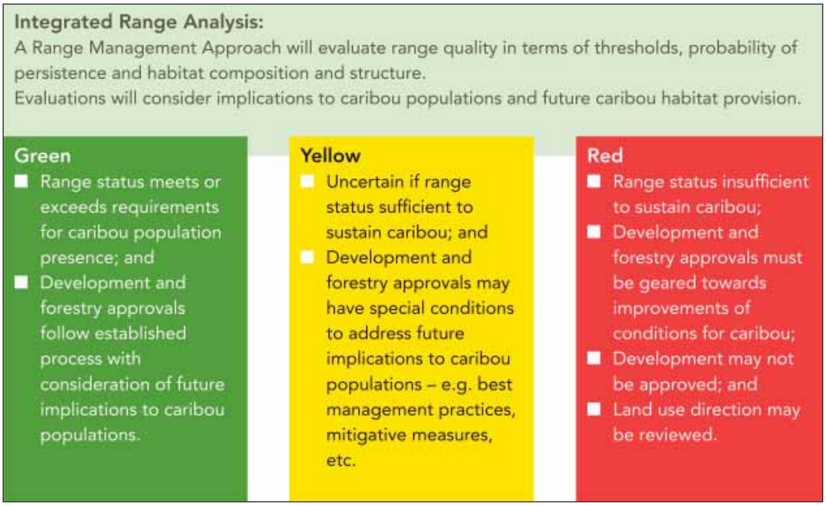
As noted in the CCP, "Adjustments to forest management practices in northwestern Ontario since the early 1990s appear to have had some initial success at retaining caribou and caribou habitat near the southern edge of range… Although the evidence is not conclusive, short-term caribou well-being and management options for the future are probably greater due to the deferral of large tracts of mature forest at the southern edge of range" (OMNR, 2009a). Although there is some evidence to support this suggestion based on repeated observations of habitat use through time, it is recognized that there are some uncertainties around the effectiveness of silvicultural practices to renew habitat conditions similar to those that follow wildfire and thus support caribou reoccupancy (OMNR, 2008a), sometimes referred to as an "untested hypothesis" (Suffling *et al.*, 2008; Wilkinson, 2010). While this perspective is to some extent valid, it is also clear that past approaches to the management of boreal landscapes in the absence of caribou considerations were decidedly unsuccessful at retaining caribou (Racey & Armstrong, 1998); positive management adjustments based on forest ecology and caribou science are expected to have a much higher likelihood of success at retaining caribou, particularly when enacted within an adaptive management framework.

In part to address this uncertainty, and to ensure that there will be sufficient amount and arrangement of future caribou habitat, a caribou habitat "insurance policy" is being implemented in areas allocated for forest harvesting. Recognizing that the forest landbase must be planned with caribou habitat needs in mind over the entire rotation of the forest, this "insurance policy" stipulates that deferral areas (areas that are not scheduled for harvest for 20 years or more) will not be harvested in future unless three broad habitat and population criteria are met:

1. there must be sufficient amount and arrangement of both currently suitable habitat and future habitat;
2. harvested areas that do not yet provide habitat must be tracking towards a suitable future habitat condition, based on silvicultural monitoring; and
3. the local caribou population must be stable or increasing at the range level, based on an assessment of caribou presence, population size and population trend.

The development of detailed policy guidance to implement and interpret this "insurance policy" is an early priority of the CCP.

The range management approach provides the key framework for land use planning and resource management decisions, integrating well with the adaptive management framework (Fig. 4). The CCP commits to the development and use of new planning tools, including the evaluation of cumulative effects. The cumulative effects of natural and human disturbance at a landscape scale are being assessed relative to the overall disturbance footprint within a range, comparable to the range disturbance concept applied in Environment Canada (2008). An initial assessment of range condition based upon this approach was completed for each preliminary range as an early CCP priority. A screening tool is being developed to assess the potential implications of proposed development proposals on caribou ranges, and to support planning and mitigation decisions. This tool will evaluate the projected disturbance footprint of the proposed development including existing disturbance levels within the range, proximity to the southern edge of continuous distribution, and adjacency to specific habitat values such as calving and nursery areas. These planning tools and integrated range assessments will define the decision-making environment and support decision-making (Fig. 3). Additional research and policy development on a roads management framework is underway to provide guidance on managing densities of roads and other linear features and the decommissioning of roads to support persistence of caribou.



Integrated Range Analysis:

A Range Management Approach will evaluate range quality in terms of thresholds, probability of persistence and habitat composition and structure.

Evaluations will consider implications to caribou populations and future caribou habitat provision.

Green

- Range status meets or exceeds requirements for caribou population presence; and
- Development and forestry approvals follow established process with consideration of future implications to caribou populations.

Yellow

- Uncertain if range status sufficient to sustain caribou; and
- Development and forestry approvals may have special conditions to address future implications to caribou populations – e.g. best management practices, mitigative measures, etc.

Red

- Range status insufficient to sustain caribou;
- Development and forestry approvals must be geared towards improvements of conditions for caribou;
- Development may not be approved; and
- Land use direction may be reviewed.

Fig. 4. Application of the CCP range management decision-making framework within the adaptive management context (from OMNR, 2009a).

4.0 Enhanced caribou habitat management

While closely related to enhanced planning approaches (3.0), the CCP contains a specific section on the enhancement of caribou habitat through additional guidance in the application of various natural resource planning processes, and in particular forest management planning. These approaches build on recent advances in forest planning guidance, including the release of guidelines to manage caribou habitat across northwestern Ontario (Racey *et al.*, 1999). Forest management practices will fully consider both current and future caribou habitat needs for all forest management units within the extent of continuous caribou distribution. Tools will include enhanced silviculture, the scheduling of harvest and deferral areas, caribou-specific objectives for forest planning, and the use of science-based models. One such model helps to plan for sufficient amount and spatial arrangement of caribou habitat over time within the range of natural variation, by establishing the desired range of variation in levels of habitat composition and texture over the entire managed forest landbase (Elkie *et al.*, 2010).

There is a particular emphasis on silviculture within the CCP, given the need to ensure that harvested forests within the extent of caribou occurrence are renewed to suitable future caribou habitat. This emphasis on effective silviculture is essential to avoid successional shifts towards more mixedwood or hardwood-dominated forests after harvesting. Forest management silvicultural performance requirements specific to caribou habitat renewal will need to be met. The CCP requires a caribou-based objective for silviculture in every forest management plan, more rigorous assessment of the effectiveness of silvicultural programs to renew caribou habitat, and monitoring to ensure that regenerating logged areas are tracking towards a suitable future forest condition for caribou habitat, to meet the tests of the "insurance policy".

An immediate priority of the CCP was the review of all forest management plans to ensure that CCP commitments were met, or schedules developed for revisions and amendments, to address silvicultural objectives, dynamic caribou habitat schedules, habitat management and roads management. Where not currently in place, dynamic caribou habitat schedules were directed to be developed within the first year of CCP implementation.

5.0 Consideration of caribou recovery implications when managing other wildlife species

A broad ecosystem approach and perspective is important to the successful delivery of a caribou conservation and recovery plan. The CCP recognizes that caribou recovery actions will not be successful in isolation of the consideration and management of other boreal wildlife species. For example, an important consideration within this ecosystem approach is a focus on the management of predators and alternate cervid prey. This is particularly important because of the apparent relationship between habitat disturbance, resulting higher densities of moose and white-tailed deer (*Odocoileus virginianus*), and subsequent higher densities of predator numbers, which in turn may lead to increased and unsustainable predation pressure on caribou (Bergerud, 1974; Bergerud & Ballard, 1988; Schwartz & Franzmann, 1989).

Moose distribution overlaps with that of caribou for most of northern Ontario, and the species have historically co-existed for at least several centuries (Fritz *et al.*, 1993). A number of concurrent wildlife initiatives within OMNR provide convergent direction to strive to maintain natural predator-prey densities within the extent of caribou occurrence, including relatively low moose densities similar to what would occur naturally across much of the conifer-dominated boreal forest. The Cervid Ecological Framework provides direction to maintain low moose densities (0-20/100 km^2) in the majority of the area of continuous caribou distribution (OMNR, 2009b), and the guidance for establishing moose population objectives similarly recommends that "in areas where caribou are the primary focus of management, moose should be managed to a low density to reduce predation pressure on caribou" (OMNR, 2009c). Based upon Bergerud *et al.* (2007), OMNR (2009c) further suggests that "maintaining or restoring caribou populations may mean managing to ≤10 moose per 100 km^2". The CCP reinforces this direction, recognizing the need to develop objectives for maximum moose densities within the extent of caribou occurrence. There is also the need for a temporal perspective when managing moose densities, as moose typically increase in the short-term after disturbance.

In recent decades white-tailed deer range and populations in northern Ontario have been increasing and expanding northward, raising concern about the potential implications for the predator-prey balance and potential brainworm (*Parelaphostrongylus tenuis*) transmission (Trainer, 1973). Concurrent with finalization of the CCP, new deer hunting seasons were implemented in 2009 in northern wildlife management units that did not yet have a season to help slow the advance of deer range expansion, although it is recognized that any effect on deer numbers will be modest. Efforts are underway to increase monitoring of deer numbers in northern Ontario to track population trends, and to standardize the monitoring and documentation of incidences of brainworm.

Predator numbers are intended to be managed primarily through the management of habitat, with the objective of maintaining naturally occurring low densities of alternate prey and predators (OMNR, 2009a). The CCP commits to a review of the feasibility and effectiveness of directly and indirectly managing predator numbers, and the development of criteria and guidelines. Despite the concerns expressed by Wilkinson (2010) that this is ecologically indefensible and would open the door to the culling of wolves, this will be a comprehensive, ecologically-based review that will consider a range of predator management options including habitat management.

A final important wildlife management action is the commitment to a review of the feasibility of caribou translocations as a recovery tool for unique recovery situations, such as coastal Lake Superior (Bergerud and Mercer, 1989). This review is anticipated to address many of the same considerations as those addressed by Jordan *et al.* (1998), including habitat availability and suitability, and densities of white-tailed deer, gray wolves, black bears (*Ursus americanus*) and moose. This will be a collaborative review with Parks Canada, who are also evaluating the feasibility of a caribou translocation to augment the Pukaskwa National Park caribou population along the Lake Superior coast (Euler, 2010; Allen *et al.*, 2011).

6.0 An initial recovery focus on geographic priority areas

The CCP places a priority on immediate recovery actions focused on the most at-risk populations along the southern edge of continuous distribution. This includes the area of continuous distribution where preliminary ranges have already been delineated, and the Lake Superior coast population (Fig. 2). An increasing number of pending and potential development proposals further north, including mineral exploration and development, renewable energy projects, utility corridors, and road access development have all emphasized the urgency of completing preliminary range delineation in the far north, and applying all planning tools and actions within the CCP to the entire zone of continuous distribution in the near future.

7.0 Improved outreach and stewardship

Improved public engagement and outreach, and enhanced stewardship of the caribou resource by public and stakeholders, are important objectives of the CCP. Specific communications products are being developed including several natural resource-specific 'best management practices' (BMPs) to increase the awareness amongst natural resource users of caribou ecology and conservation practices, and to help mitigate some of the impacts of resource development; these will include BMPs directed towards mineral exploration and development, tourism and outdoor recreation, forestry, and roads and linear feature planning. OMNR will also produce a "State of the Woodland Caribou Resource Report" to coincide with the 5-year review of CCP implementation in 2014. This report will provide results of range assessments (population and habitat condition), research results and progress towards achieving the commitments and targets set in the CCP.

A concern has been raised that the CCP did not make a commitment that any BMPs will be posted on the provincial Environmental Registry for public notification and comment (Wilkinson, 2010). To increase public awareness and support for caribou stewardship, it is essential that these documents be widely circulated and publicly available. Posting on the Environmental Registry will be one means of ensuring that this occurs.

8.0 Consideration of Aboriginal Traditional Knowledge in recovery actions

The CCP contains a commitment to the consideration and incorporation of Aboriginal Traditional Knowledge (ATK), where available, in caribou conservation and recovery. This includes considering ATK in the delineation and refinement of caribou range boundaries, and seeking additional information on caribou populations and habitat to support caribou recovery. The CCP also includes a commitment to work in partnership with Aboriginal people to share information, increase mutual knowledge and awareness of caribou and caribou conservation, and identify opportunities for shared research and recovery actions.

Documented Aboriginal Traditional Knowledge related to caribou is limited, although efforts are underway to increase the awareness and availability of ATK for conservation and recovery planning purposes. O'Flaherty *et al.* (2008) described a positive outcome of an attempt to consider both indigenous and science knowledge in the development of a caribou conservation approach for the Whitefeather Forest in northwestern Ontario. A number of pilot studies, led by First Nations, are being conducted to document traditional knowledge in several areas of both northeastern and northwestern Ontario.

CCP Implementation

The CCP has an initial focus on identified priorities. Not all recovery actions can be initiated simultaneously, requiring the setting of priorities to allocate funds and resources. The CCP contained specific target dates (6 months to 5 years) for some specific actions. Initial CCP implementation is focussed on the one to three year commitments specified within the CCP. Although not all commitments were assigned a specific timeframe, all are expected to be initiated within the first 5 years of implementation. A multi-year implementation plan has been developed to guide implementation, incorporating all commitments within an adaptive management framework (Fig. 3).

Discussion

There has been growing recognition of the decline and 'Threatened' status of woodland caribou in Ontario in recent decades, although concerns about their decline were expressed as early as the mid-20th century (de Vos, 1949; de Vos & Peterson, 1951). Increasing attention began to be directed towards caribou conservation and recovery during the 1980s (Darby *et al.*, 1989). In Ontario, particularly northwestern Ontario, intensive conservation efforts generally began in the early 1990s. Recent efforts have included direction to begin to consider caribou habitat values during the preparation of forest management plans in northwestern Ontario in the early 1990s, the development of forest management guidelines for northwestern Ontario (Racey *et al.*, 1999), a regional caribou conservation strategy for northwestern Ontario (OMNR, 1999), the establishment of some large provincial parks with high caribou conservation value (Cumming, 1987; Duinker *w* ., 1998), and an enhanced standardized caribou database. A more detailed chronology of some key conservation initiatives in Ontario can be found in OMNR (2008a).

The Caribou Conservation Plan builds upon these earlier conservation efforts to provide a comprehensive and coordinated approach to caribou conservation and recovery. It addresses science and information needs, planning approaches, habitat management, management of the broader wildlife community, public outreach and stewardship, and Aboriginal engagement. This reflects the complexity of the challenge of caribou recovery, and provides the greatest opportunity to conserve caribou, rather than relying on only a few very specific measures such as the designation of protected areas.

Caribou occur relatively continuously across northern Ontario, thus requiring integrated management actions across both protected areas and managed landscapes where resource development activities will occur. Our challenge is to ensure suitable quality, quantity and distribution of intact caribou habitat at a landscape scale, both now and into the future, while also recognizing and integrating recovery actions with other authorized natural resource uses. It is important that the entire northern landscape remain in a condition that is capable of providing suitable habitat over time, so that provincial range is not fragmented or isolated by permanent impairment of habitat quality. The range management approach, applied in an adaptive management context, is an important measure to ensure no further loss of caribou range in Ontario and to strengthen caribou prospects and the probability of caribou persistence. New information on caribou ecology, populations and their habitat, and caribou response to various ecological and anthropogenic factors, is continually and increasingly being gathered. This new information will continue to inform and refine our caribou recovery approaches through the adaptive management approach as it becomes available.

A recurring concern of Wilkinson's (2010) analysis was that the CCP lacks sufficient detail about how various policies will be implemented, and is thus open-ended and lacks the commitment for follow-through. The CCP is clearly a high-level strategic policy, and given the comprehensive nature of the actions being committed to, it is not feasible to articulate in detail the specific approaches and responsibilities for every policy commitment. Thus there are a number of commitments to further develop more detailed operational policies within the framework of the CCP to address such aspects as road density thresholds, how new protected areas in the Far North will align with caribou conservation values, and the details on implementation of the caribou insurance policy. This is a necessary approach to policy development, but the overall government commitment to achieve every commitment within the CCP is clear.

As a legally required government response under the Endangered Species Act, 2007, the CCP represents a significant long-term commitment to caribou recovery and conservation. The authors view the Caribou Conservation Plan, released in October 2009, as a significant step forward in both a commitment to, and progress towards, caribou recovery and conservation in Ontario. In this regard, we do not agree with the assessment of Wilkinson (2010) that this plan avoids the tough policy choices, fails to take a precautionary approach, holds more uncertainty for stakeholders, and defers many policy decisions to the future. This is a very clear policy commitment, backed by legislation, to establish and implement a number of science, policy, planning and stewardship initiatives that will collectively support caribou conservation and recovery and enhance the long-term probability of caribou persistence in Ontario.

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Delineating demographic units of woodland caribou (*Rangifer tarandus caribou*) in Ontario: cautions and insights

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Abstract: Delineating demographic structure across an organism's range can reveal the extent to which population dynamics in different geographic areas are driven by local or external factors and can be crucial for effective conservation and management. Obtaining optimal data for such analyses can be time and resource-intensive and impending development and resource extraction pressures may necessitate the examination of existing data, even when they are less than ideal. We analyzed a historic telemetry dataset containing satellite radio-collar locations of 73 forest-dwelling woodland caribou in northern Ontario to determine demographic structure. We applied several clustering methods (i.e., agglomerative, divisive and fuzzy *k*-means) to median seasonal locations. Results were used to distinguish demographic units and minimum convex polygons and fixed-kernel density estimates were used to delineate unit boundaries and core areas. For areas where sampling was considered representative of the distribution of caribou on the landscape, we assessed demographic distinctness by evaluating intra-individual variation in cluster membership, membership strength and distance between boundaries and core areas of adjacent units. The number and composition of clusters identified was similar among methods and caribou were grouped into 6 general clusters. The distinctions between the three clusters identified in the central portion of the province (i.e., Lac Seul, Wabakimi, Geraldton) and the two clusters identified in the eastern portion of the province (i.e., Cochrane and Cochrane-Quebec) were determined to represent demographic structuring. Additional distinctions in other areas (i.e., between The Red Lake and Lac Seul clusters in the west and between the central and eastern clusters) may just be artifacts of the original sampling effort. Amongst demographic units, there was no evidence of individual flexibility in cluster membership and average membership strength was very high. There was little to no overlap between boundaries and core areas of adjacent units, but distances between adjacent unit boundaries were relatively low. Additional sampling effort is needed to further delineate demographic structure in Ontario caribou.

Key words: cluster analysis; demographic units; Ontario; population delineation; population monitoring; *Rangifer tarandus caribou*; woodland caribou

Rangifer, Special Issue No. 20: 159–181

Introduction

Determining population structure is a critical step for developing effective wildlife conservation and management strategies (Bethke *et al.*, 1996; Thomas & Kunin, 1999; Schaefer & Wilson, 2002; Edwards *et al.*, 2008; EC, 2008). If discrete local populations exist, their boundaries can serve as an ecologically meaningful basis for determining abundance and rates of population change (Bethke *et al.*, 1996; Schaefer *et al.*, 2001; Taylor *et al.*, 2001; EC, 2008) — information that is essential for standard assessments of population viability (Akçakaya & Sjögren-Gulve, 2000). If data on survival, pregnancy and recruitment are summarized over areas that fail to correspond with the spatial distribution of demographically distinct groups of individuals, then the resulting estimates of vital rates may be inaccurate and unreliable for conservation and management purposes (Bethke *et al.*, 1996; Edwards *et al.*, 2008). Unreliable estimates of population sizes and trends could have serious consequences for long-term population viability, particularly for organisms whose long-term persistence is threatened.

The northern region of Ontario encompasses approximately 18% of the extant range of what the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) refers to as the "boreal population" (Thomas & Gray, 2002) of the forest-dwelling ecotype of woodland caribou (*Rangifer tarandus caribou*). The boreal population has exhibited long-term patterns of range retraction and population decline (Racey & Armstrong 2000; Schaefer, 2003) and these trends have resulted in a "threatened" species designation under Canada's federal *Species at Risk Act* (2004) and Ontario's *Endangered Species Act* (2007). Consequently, there have been several recent national and provincial efforts to develop conservation and recovery strategies for woodland caribou (e.g., MC, 2005; EC, 2008; OWCRT, 2008; OMNR, 2009).

The Scientific Review for the Identification of Critical Habitat for Woodland Caribou (*Rangifer tarandus caribou*), Boreal Population, in Canada (EC, 2008) recommended that each jurisdiction currently occupied by the boreal population of woodland caribou undertake efforts to delineate local populations and ranges and use these as units of analysis for assessing population trends and probability of persistence. Due to the difficulties associated with inferring demographic structure from genetic indicators (Avise, 1992; Cronin, 1993; Moritz, 1994; Esler *et al.*, 2006; Palsbøll *et al.,* 2007; Frantz *et al.,* 2009), the *Scientific Review* recommended that telemetry-based analyses of individual space use and movement patterns of forest-dwelling woodland caribou be used to delineate meaningful demographic units (i.e., "local populations") throughout the ecotype's current range (EC, 2008: Appendix 6.2).

The ideal dataset for such analyses would be obtained via a uniform distribution of sampling effort throughout the current range of forest-dwelling woodland caribou (e.g., Schaefer *et al.*, 2001; McLoughlin *et al.*, 2002). Sample sizes would be sufficiently large and study duration sufficiently long (e.g., 20 years - EC, 2008: Appendix 6.2) to capture spatial and temporal variability in movement behaviour and radiocollar deployments would be representative of the distribution of caribou across the landscape (e.g., uniform, patchy). For wide-ranging, long-lived species like woodland caribou, obtaining such an optimal dataset would require extensive resources and considerable time. In situations where resource extraction and development pressures are high, it will sometimes be necessary to evaluate existing data and if adequate, analyze them to derive preliminary assessments of demographic structure, which can be used to make conservation and management decisions that cannot be deferred until more comprehensive datasets are available. While such analyses should not be used as a substitute for initiating more comprehensive studies, they can be used to inform management decisions until more appropriate sources of information are available.

In Ontario, there have been several research and local management-based projects over the past 15 years that have deployed satellite radiocollars on forest-dwelling woodland caribou. For much of this time period, collars were only deployed near the southern margin of the ecotype's continuous range within the province and even within this general area, sampling efforts were not evenly distributed and the temporal extent of data coverage differs substantially between regions. While these data are not ideal for delineating population structure, industrial pressures within the continuous range are high and will likely increase as development (e.g., roads, utility lines) and resource extraction activities (e.g., mining and forestry) expand northwards (OMNR, 2008). Thus, there is justification for evaluating existing telemetry data for Ontario's woodland caribou as a means of obtaining preliminary insights into demographic structure in the portion of their range where they are considered at greatest risk of extirpation (Racey & Armstrong, 2000; Thomas & Gray, 2002; Schaefer, 2003).

In this study, we applied the same general methodology used in several other studies of species' demographic structure (e.g., Bethke *et al.*, 1996; Schaefer *et al.*, 2001; Taylor *et al.*, 2001; McLoughlin *et al.*, 2002; Edwards *et al.*, 2008) to delineate preliminary demographic units of forest-dwelling woodland caribou at the southern limits of their continuous range in Ontario.

First, we inspected the distribution of deployment locations to determine which regions of the province had data that were adequate for delineating demographic units. Second, we applied several different cluster analysis techniques to satellite telemetry data to determine whether there is evidence for spatial population structure amongst these woodland caribou. Third, we used home range estimators to delineate the boundaries and core areas of use associated with identified groups. Fourth, we looked at evidence for immigration/emigration and the proximity of boundaries and core areas amongst adjacent groups to determine whether they are demographically distinct. Finally, we discuss the implications of the results for identifying areas where additional research and monitoring are needed to develop effective conservation and management strategies for forest-dwelling woodland caribou in Ontario.

Material & methods

Study area

The study area (Fig. 1) was located in northern Ontario, Canada. It was approximately 236 000 km^2 in size, spanning a 1185 km distance from east to west (78°36'W to 95°13'W longitude), and a 255 km distance from north to south (51°48'N to 49°36'N latitude). It encompassed eastern and western sampling regions, which were separated by an area (spanning approximately 320 km from east to west) where no sampling was conducted.

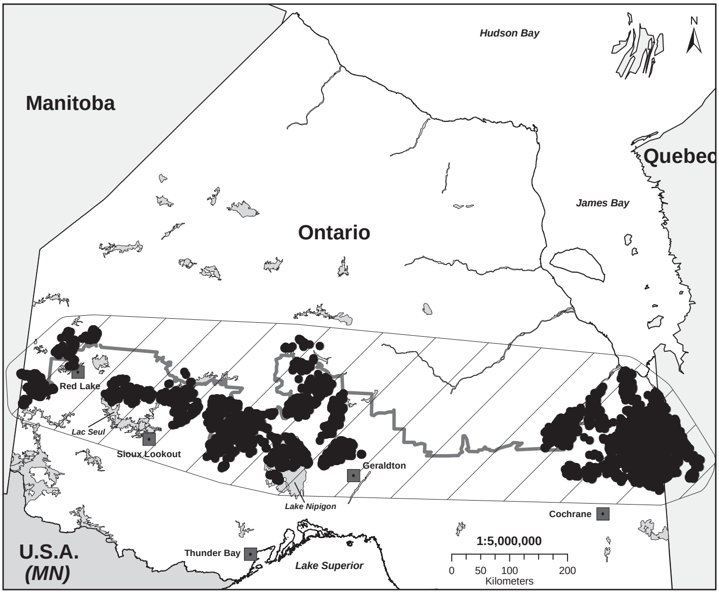

Fig. 1. Study area and locations of sampled individuals. Hatched polygon delineates the general study area, defined by a buffered (25 km) 100% Minimum Convex Polygon. Black circles represent all sub-sampled locations recorded from 1995-2008, for the 73 woodland caribou (*Rangifer tarandus caribou*) included in our analyses. Thick gray line depicts the northern boundary of commercial logging during the time period when location data were collected.

The western sampling region fell within Canada's boreal shield ecozone (Wiken *et al.*, 1993) and was located almost entirely within the region subjected to commercial logging. It is described in detail by Ferguson & Elkie (2004a, 2004b, 2005). Forest cover was dominated by jack pine (*Pinus banksiana*) and also contained black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*) (Rowe, 1972). The topography has been characterized as rolling and relatively low relief, featuring well-drained soils, sand and gravel deposits and rocky uplands and outcrops (Rowe, 1972). The landscape contained numerous bogs, fens, rivers and lakes, including a few larger waterbodies such as Lake Nipigon and Lac Seul (Rowe, 1972). The primary source of natural disturbance was wildfire, with return intervals ranging from 80 to 200 years (Li *et al.*, 1996 cited in Ferguson & Elkie, 2004a).

The eastern sampling region straddled the boundary between Canada's boreal shield ecozone in the south and the Hudson Plains ecozone to the north (Wiken *et al.*, 1993). It was located in the "clay belt" region of north-eastern Ontario (Rowe, 1972) and is described in detail by Brown *et al.* (2003, 2006, 2007). Forests in the southern half of the region fell within the area of the province where commercial logging was permitted, while forests in the northern half were not subject to this disturbance type. The topography in this sampling region is relatively flat, soils are dominated by water-worked tills and lacustrine materials and forest cover is dominated by lowland black spruce stands, interspersed with numerous treed bogs, sedge fens and sphagnum-heath bogs, but relatively few lakes (Rowe, 1972; Brown *et al.*, 2007). Species such as tamarack (*Larix laricina*), trembling aspen, willow (*Salix* spp.), balsam fir and white birch co-occur with black spruce in early successional stands, while mixedwood or jack pine-dominated stands sometimes occurred in drier sites (Rowe, 1972; Brown *et al.*, 2007). The primary sources of natural disturbance were wildfire and insect infestation (Carleton & Maycock, 1978), with fire return intervals estimated at approximately 263 years (Ter-Mikaelian *et al.*, 2009).

Animal capture and telemetry

Capture and handling procedures

In the western sampling region, a total of 53 forest-dwelling woodland caribou (40 adult females, 13 adult males) were captured and collared by Ontario Ministry of Natural Resources (OMNR) staff from 1995 to 2005. Animals were captured using net-guns during winter (n=31) or while swimming during spring and summer (n=22). Fifty caribou were fitted with an Argos radiocollar that contained both satellite (UHF) and VHF transmitters (Telonics, Inc., Mesa, AZ, U.S.A.) and three caribou were fitted with

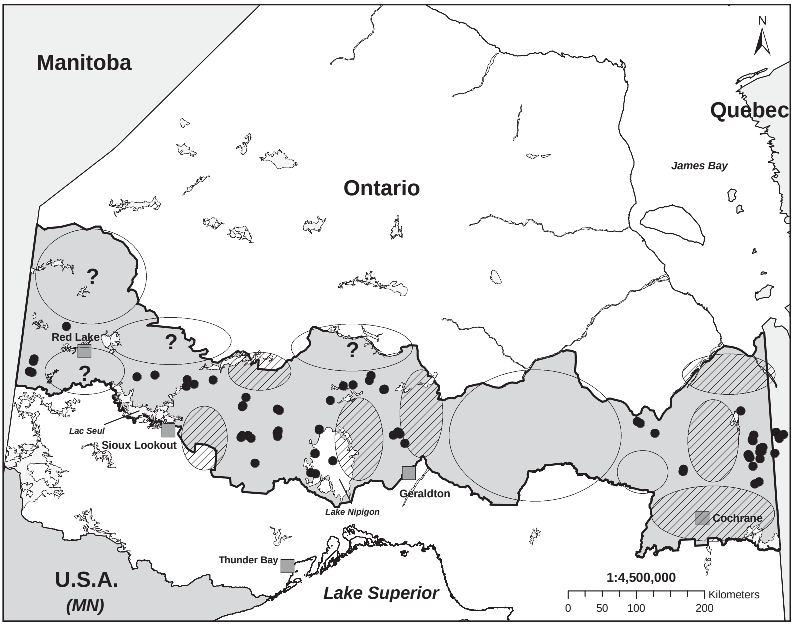

Fig. 2. Approximate deployment locations (black circles) of radio collars placed on forest-dwelling woodland caribou in Ontario from 1995 to 2008. Only deployment locations of individuals included in the cluster analysis (n = 73) are depicted. The gray polygon is bounded by the southern boundary of the ecotype's continuous distribution in the province (OMNR 2009) and the approxmate northern extent of historic sampling efforts in the province. The hatched ellipses represent areas where spatial gaps in deployment locations correspond with apparent low density areas for caribou (assessed during winter). Hollow ellipses without question marks represent areas where spatial gaps in deployment locations are known to be artefacts of inadequate sampling efforts. Hollow ellipses with question marks represent areas where further sampling efforts are needed to determine whether spatial gaps in deployment locations reflect low caribou density or whether they are artefacts of inadequate sampling effort.

GPS "store on board" radiocollars (Lotek Wireless Inc., Newmarket, ON, Canada).

In the eastern sampling region, a total of 36 female caribou (32 adults and 4 yearlings) were captured and collared by OMNR staff. Thirty collars were deployed in the Detour Lake area in 1998 and 1999 (Brown *et al.,* 2003) and in 2006, six additional collars were deployed just west of the region sampled during the first period (Gauthier, 2007). All animals (n=36) were captured during winter and were herded into nets using a helicopter and ground crew (Brown *et al.*, 2003; Gauthier, 2007). Once captured, each caribou was fitted with an Argos radiocollar that contained both satellite (UHF) and VHF transmitters (Telonics, Inc., Mesa, AZ, U.S.A.) Capture and handling procedures for all 89 collared caribou followed several similar protocols, all of which were approved by the OMNR Animal Care Committee.

Sampling efforts

As mentioned above, sampling efforts were not evenly distributed throughout the study area. In some cases, efforts were made to distribute radiocollars in a manner that represented the distribution of caribou on the landscape, while in others, sampling was concentrated in areas of local management concern or sample sizes were simply too small to obtain adequate regional coverage. The approximate deployment locations of radiocollars on caribou included in our analyses (see "Cluster Analysis" below) are depicted in Fig. 2.

In the central-west and the eastern-most sections of the study area the distribution of deployment locations was relatively even (Fig. 2). Additionally, based on the average annual home range sizes for woodland caribou in the boreal shield ecozone in northwestern Ontario (i.e., 1148 km^2 ± 109 km^2 SE – derived from generating 100% MCPs using the annual telemetry data of each individual analyzed here) and the boreal clay plains ecozone in northeastern Ontario (i.e., 4026 km^2 ± 29 km^2 – Brown *et al.,* 2003), we determined that sampling resolution in most areas was sufficient to allow for potential home range overlap between adjacent collared animals. Despite these generalities, there are some areas in these regions where there were spatial gaps in the distribution of deployment locations—immediately east of Lake Nipigon and immediately northeast of Geraldton, east and north east of Sioux Lookout and Lac Seul, as well as the northern and central portions of the area north of Cochrane (Fig.e 2: hatched polygons). However, recent efforts to distribute radiocollars as uniformly as possible in each of these general areas confirmed the absence of caribou or, at best, occurrence at extremely low densities (A. Rodgers, OMNR, unpubl. data, 1 April 2011; L. Walton, OMNR, pers. comm., 25 March 2011). This indicates that the patchiness of historic collar deployments in the specific areas described above is likely representative of the distribution of individuals across the landscape during sampling and not due to lack of effort.

In contrast, there were other areas where inadequate sample sizes and/or spatial contagion in sampling effort made it impossible to infer demographic structure from the available telemetry data (Fig. 2). Specifically, there was a total absence of historic sampling effort in a large area between the eastern region and the central region of the study area (Fig. 2: hollow polygons, no question marks) and recent sampling efforts in this area resulted in several collar deployments (L. Walton, OMNR, pers. comm., 25 March 2011), indicating that caribou are currently present and likely had a historic presence in this area.

Small sample sizes and spatially clustered deployments in the western-most section of the study area (i.e., the area to the north and west of Lac Seul and the Red Lake area – Fig. 2: hollow polygons with question marks) also made it difficult to draw demographic inferences using the telemetry data collected in this region. Consequently, fine scale analyses of core areas and proximity (see below) were not undertaken for either of these areas. Additional collaring efforts are needed in this latter group of areas to determine whether the spatial gaps in deployment locations highlighted in Figure 2 represent areas of low caribou use or whether they are artefacts of inadequate sampling efforts.

Observations made during recent collaring efforts (L. Walton, OMNR, pers.comm., 25 March 2011) indicate that the historic collar deployment locations north of Cochrane are generally representative of the winter distribution of caribou in this region (Fig. 2). However, the sample size in the western portion of this general area was considered to be too small to complete fine scale analyses of core areas and proximity using historic data. Thus, only coarse delineations of range boundaries and assessments of boundary proximity were conducted in this area.

Radiocollar transmission schedules

Collars were scheduled to transmit or store caribou locations at time intervals that varied greatly among individuals (i.e., daily to every 10 days) and for 65 of the caribou with Argos satellite collars, between seasons (i.e., every two days for spring and autumn, every 7 days for late winter and summer). For both the Argos satellite and GPS collars, multiple locations were often estimated during each day in which data transmission or storage occurred. A total of 60 403 locations were obtained from the original 89 collared individuals.

Cluster analyses

Data preparation

Since the analysis focused on identifying demographic structure amongst woodland caribou in Ontario, we excluded any individuals with collaring periods that were too short to provide representative location information throughout the course of the annual cycle (e.g., McLoughlin *et al.*, 2002). The length of the collaring period for each individual was calculated and only those individuals with collaring periods ≥ 0.75 years (n = 73) were included in subsequent analyses. Of the 73 individuals (64 females, 9 males) that remained, 34 individuals were collared for two full years and seven were collared for three full years, yielding a total of 121 individual-years of location data.

Next, the locations for the remaining individuals were screened for accuracy and all locations with relatively high error estimates were excluded from further analyses. For the Argos satellite data, only locations with Argos location quality index values of 3 (NQ < 250 m) or 2 (250 m ≤ NQ < 500 m) (CLS, 2008) were retained, while for the GPS data, only those locations with error estimates < 50 m were kept. Error estimates for GPS locations were based on position dilution of precision (PDOP) values and the number of dimensions associated with each position (i.e., 2D or 3D). Finally, in circumstances where individuals had multiple locations per transmission/storage period that met accuracy requirements, only the location with the highest accuracy was retained. If multiple locations met this criterion, the location associated with the earliest time of day was selected.

Both Argos satellite and GPS collars recorded location information using decimal latitude-longitude coordinates. To prepare the data for use in subsequent analyses, each location was "flattened" or scaled to a common x,y grid (Bethke *et al.*, 1996; Taylor *et al.*, 2001). A Lambert Conformal Conic (LCC) projection was chosen because it retains the relative Euclidean distance between points (Taylor *et al.*, 2001). ArcGIS (v. 9.2, ESRI, Inc.) was used to reproject the geographic dataset in the LCC format.

Seasonal median locations

Forest-dwelling woodland caribou in Ontario exhibit seasonal changes in movement behaviour and habitat selection (Cumming & Beange, 1987; Bergerud *et al.*, 1990; Brown *et al.*, 2003; Ferguson & Elkie, 2004a). To account for the seasonal shifts in spatial location that this might produce, we used the behavioural season definitions derived by Ferguson and Elkie (2004a) for woodland caribou in northwestern Ontario, to divide the location data into different seasons. Ferguson and Elkie (2004a) made a distinction between five different seasons based on temporal changes in movement rates: early winter, late winter, spring, calving and post-calving. However, because we wanted to minimize the ratio between observations and variables included in the cluster analysis and because spatial displacement and differences in movement rates between the calving and post-calving seasons were relatively low (Ferguson & Elkie, 2004a), we decided to lump these two seasons together. This produced a total of four different seasons: early winter (Nov. 15 – Jan. 20), late winter (Jan. 21 – Mar. 5), spring (Mar. 6 – May 5) and snow-free (May 6 – Nov. 14).

The start and end dates of these behavioural seasons did not correspond with the start and end dates used to set the seasonal transmission schedules that were applied to most of the deployed Argos collars. Therefore, for the 65 caribou with seasonally variable location intervals, location data were sub-sampled within seasons to ensure equal time intervals between sequential locations. After sub-sampling, median easting and northing values were estimated for each season, for each individual, for each year of location data, as recommended by Bethke *et al.* (1996), Taylor *et al.* (2001) and Schaefer *et al.* (2001). Thus, for every full year that an individual was collared, a total of eight variables (i.e., a median easting and northing value for each of four seasons) were derived to represent its general geographic location. For the 41 individuals that were collared for multiple years, calculating seasonal median locations separately for each complete year of data enabled each unique individual-year combination (i.e., "caribou-years") to be treated separately in the cluster analyses. Using caribou-year combinations as experimental units in the cluster analyses allowed us to detect migration between demographic units by allowing for the possibility of cross-classification of individuals to different clusters in different years (Taylor *et al.*, 2001; McLoughlin *et al.*, 2002).

Data analyses

To determine whether there was evidence for demographic structuring amongst forest-dwelling woodland caribou in Ontario, we performed cluster analyses on the seasonal median location data for each caribou-year. Clustering is a classification technique that forms groups of objects based on a measure of dissimilarity with respect to the independent variables included in the analysis (Romesburg, 1984; Kaufman & Rousseeuw, 1990). In this case, clusters of caribou-years were formed based on similarity in geographic location (i.e., their spatial proximity to one another).

Since the independent variables consisted of the geographic coordinates of an individual's position in space (east-west or north-south) during a particular season and year, Euclidean distance was selected as the measure of dissimilarity for the cluster analysis (Ferguson *et al.*, 1998; Schaefer *et al.*, 2001, Taylor *et al.*, 2001; McLoughlin *et al.*, 2002). Standardization of independent variable values to the zero mean is recommended in situations where independent variable values are measured in different units and/or the researcher wants to assign equal weight to variables with unequal variances (Romesburg, 1984; Gotelli & Ellison, 2004). Marked differences in the breadth of the study area along the east-west and north-south axes meant that variances in median easting values were substantially higher than variances in median northing values. However, since there was no *a priori* rationale for treating Euclidean distances between median locations along the north-south axis differently than Euclidean distance along the east-west axis and since all variables were measured using the same units of measurement, cluster analyses were performed using an unstandardized data matrix.

There are many different clustering methods that can be used to classify objects into groups. They differ in several respects, including (1) the basic type of clustering algorithm applied (e.g., partitioning, hierarchical), (2) the specific clustering procedure used (e.g., 'top-down' hierarchical divisive routines, 'bottom-up' hierarchical agglomerative routines), (3) the amalgamation or linkage rules for joining or separating hierarchical clusters and (4) whether cluster membership is absolute or partial (Anderberg, 1973; Romesburg, 1984; Kaufman & Rousseeuw, 1990). Some approaches are better suited to particular types of data than others (Romesburg, 1984), but applying multiple appropriate clustering methods and comparing results can serve as a test of whether the cluster structure identified is robust to methodological differences (Romesburg, 1984; Bethke *et al.*, 1996). With this in mind, we performed cluster analyses of the seasonal median location data using five different methods. These included the hierarchical divisive method, three hierarchical agglomerative methods (unweighted pair- group method with arithmetic mean [UPGMA], Ward's minimum variance method and the complete linkage method), and a partitioning clustering method (fuzzy *k*-means clustering). All hierarchical clustering methods were implemented in S-Plus v.6 (Insightful Corp., Seattle, WA, U.S.A.) and fuzzy *k*-means clustering was conducted using FuzME v.3.5b (Minasny & McBratney, 2002).

Fuzzy *k*-means analysis permits objects to have partial membership across multiple clusters (Bezdek *et al.*, 1984; Odeh *et al.*, 1992). To set the fuzziness of the resulting classification, a weighting exponent (m) must be specified (Bezdek *et al.*, 1984; Schaefer *et al.*, 2001). We ran the analysis with the weighting exponent set at $m = 1.5$ to produce a low-to-moderate level fuzzy classification. Repeating the analysis with different values of m (changed in increments of 0.1) for $1 < m \leq 2$ (e.g., Schaefer *et al.*, 2001) produced results that were qualitatively consistent in terms of cluster number and cluster membership.

Hierarchical clustering methods continue lumping or splitting objects into clusters until no new groups are possible, while partitioning methods require *a priori* specification of the total number of clusters (k) to be defined (Romesburg, 1984). Both approaches are associated with different options for determining the appropriate number of clusters. For the hierarchical methods applied, we determined the number of meaningful clusters based on notable changes in linkage distance when new 'splits' (for the divisive method) or 'lumps' (for the agglomerative methods) were formed (Schaefer *et al.*, 2001). For the fuzzy k-means analysis, we ran the analysis for $k = 2$, up to $k = 15$ and inspected values of separate fuzzy validity (S), the fuzziness performance index (FPI) and modified partition entropy (MPE) to identify the appropriate number of clusters (Reyniers *et al.*, 2006).

Once the appropriate number of clusters was determined, the results for each clustering method were compared to assess the robustness of cluster structure to changes in methodology. Comparisons were based on the number of meaningful clusters identified and cluster membership (i.e., the specific caribou-years assigned to each cluster). In cases of discrepancy between results produced by different methods, we determined final cluster structure by examining all location data for each caribou-year assigned to the affected clusters and considered the relative reliability of different clustering methods. For the location data, we calculated the distance between caribou-years in different clusters and determined the direction and extent of individual movements at cluster boundaries. For the methodological assessment, we considered the findings of previously published simulation studies that compared the performance of different clustering methods.

Under optimal sampling conditions, a cluster analysis of data from an unstructured panmictic population (i.e., the null hypothesis) would yield no significant clusters. However, inadequate sampling in two regions of the study area (i.e., between the eastern and central regions and between the Lac Seul and Red Lake areas – Figure 2) were expected to produce significant clustering even if the underlying population structure was panmictic. Thus, using the dataset described here, the null hypothesis was predicted to produce a three cluster solution (i.e., dividing the study area into western, central and eastern clusters). Under the alternative "demographic structure" hypothesis, cluster analysis was predicted to result in the detection of ≥ 4 significant clusters.

Delineating demographic units: boundaries and "core areas"

Selection of range estimators

To delineate demographic unit boundaries and identify areas of more intensive use (i.e., "core areas") within them, we pooled the location data for each caribou-year assigned to a specific cluster and applied two different home range estimators to the data for each cluster—Minimum Convex Polygons (MCPs) and Kernel Density Estimators (KDEs). We calculated 100% MCPs for each cluster because they provide an estimate of the total area used by sampled demographic unit members (Powell, 2000). Consequently, all locations analyzed are included within the resulting boundary and as such, the MCP can be viewed as a conservative estimator of the range associated with a given demographic unit (EC, 2008: Appendix 6.2). In comparison, ranges delineated using a KDE approach are generally smaller and outlying locations are not necessarily encompassed by isopleth boundaries (Powell, 2000; EC, 2008: Appendix 6.2). However, the resulting utilization distributions are based on information contributed by all locations and provide an estimate of the probability of occurrence of sampled demographic unit members within a range (White & Garrott, 1990; Seaman & Powell, 1996). This enables the delineation of boundaries and core areas for each demographic unit based on areas of frequent use.

For some clusters, limited sampling efforts restricted the extent to which clusters could be considered representative of demographic units and home range estimates could be considered representative of demographic unit boundaries and core areas. While we still applied MCP and KDE estimators to the sub-sampled telemetry data for these clusters, we only present 100% MCPs and 95% isopleths for these clusters. These are interpreted as providing a very preliminary indication of the minimum spatial extent of forest-dwelling woodland caribou demographic groups in these areas.

Data preparation

Since there was considerable variation in sampling intensity between caribou-years, we attempted to standardize the location data so that each caribou-year contributed a comparable number of locations per season. To accomplish this, we followed a protocol similar to the one described by Edwards *et al.* (2008). First we calculated the mean number of locations per season for the 65 caribou that were sampled at the coarsest time intervals (i.e., every seven days during summer and every two days during autumn and spring). Then, for the seven caribou that were sampled more frequently, we chose a random subsample of locations per season, per year for each caribou that was equal to the mean number of locations that we calculated for each season using the coarsely sampled individuals.

For KDE-based delineations of demographic unit boundaries and core areas, there was some concern that the results of analyses that included location data from every caribou-year would be unduly influenced by the geographic affinities of the 41 individuals who were collared for multiple years. To avoid this potential source of bias, we randomly selected one caribou-year per individual for inclusion in each cluster-specific analysis and excluded the data from other caribou-years. Since MCPs are delineated based on information from outer-most locations only, the inclusion of data for multiple years for the same caribou in a cluster-specific analysis was not considered problematic. Consequently, all of the data recorded for each individual were retained for the MCP-based delineations of demographic unit boundaries.

Data analyses

We used Hawth's Tools (Beyer, 2004) in ArcGIS v. 9.2 (ESRI, Inc. Redlands, CA, U.S.A.) to generate a 100% MCP for each identified cluster, using the sub-sampled location data for each caribou-year assigned to a given cluster during the cluster analysis. Fixed-kernel density estimates (Wand & Jones, 1995; Seaman & Powell, 1996; Taylor *et al.*, 2001) of demographic unit boundaries and core areas were derived using the Home Range Tools extension v. 1.1 (Rodgers *et al.*, 2007) in ArcGIS v. 9.2. Utilization distributions were derived using all of the sub-sampled data for each cluster that met the constraints outlined above (i.e., one randomly selected year, per individual, per cluster). A cell size of 150 x 150m was used to calculate the probability density of caribou locations for each demographic unit and 95% and 50% isopleths derived from the density function were used to delineate range and core boundaries, respectively.

KDE-based utilization distributions can be sensitive to choice of smoothing parameter and there is no general agreement on the optimal smoothing technique (Silverman, 1986; Gitzen & Millspaugh, 2003; Millspaugh *et al.*, 2006; Edwards *et al.*, 2008). To avoid under-smoothing or over-smoothing the utilization distributions, we used an *ad hoc* approach (e.g., Berger & Gese, 2007; Edwards *et al.*, 2008) to select cluster-specific smoothing parameters. For each demographic unit the "reference" smoothing parameter (h_{ref}; Silverman, 1986) was calculated, the resulting value was used as a starting h value and then h was increased or decreased by computing different proportions of h_{ref} in sequential increments of 0.01 until the minimum value of h that still produced a continuous, lacuna-free 95% isopleth, was identified (Silverman, 1986; Berger & Gese, 2007; Edwards *et al.*, 2008). The h value ($h_{ad\ hoc;}$ Berger & Gese, 2007) identified for a given demographic unit served as the smoothing parameter for the utilization distribution constructed for that unit.

Assessing distinctness of demographic units

Our objective was to determine whether there was evidence for the existence of discrete demographic units. We applied two basic criteria to assess whether demographic units identified and delineated using cluster analysis and home range estimates could be considered demographically distinct from one another. The first criterion focused on the strength and consistency of caribou-year classification in the cluster analyses. To assess the level of uncertainty in the cluster membership assignment for each caribou-year, we examined the fuzzy membership coefficient values generated by the fuzzy k-means analysis. Additionally, to determine whether there was any evidence of migration between clusters, we conducted within-individual evaluations of cluster membership assignments amongst individuals collared for multiple years to identify between-year differences in cluster membership (e.g., Taylor *et al.*, 2001).

The second basic criterion that we applied to assess the demographic "distinctness" of identified clusters focused on the degree of geographic separation between boundary and core areas delineated for adjacent groups of caribou (EC, 2008: Appendix 6.2). First, we used the equation developed by Lazo (1994) to calculate the proportion of overlap between the MCP and KDE-based boundaries of adjacent clusters. Next, for core areas and boundaries that didn't overlap, we measured the minimum distance between the respective core areas and boundaries of adjacent clusters.

Assessing reliability of demographic units

Environment Canada (2008: Appendix 6.2) suggested that when the relationship between number of observations and cluster size is plotted, the presence of an asymptote indicates that corresponding cluster boundaries have a high probability of accuracy. Given the general fidelity that woodland caribou tend to exhibit at the home range scale (Ouellet *et al.*, 1996; Schaefer *et al.*, 2000; Rettie & Messier, 2001; O'Brien *et al.*, 2006), incremental changes in the number of locations based on the addition of data collected for single individuals appeared to be the most appropriate approach for evaluating this association. To assess the extent to which identified clusters could be considered representative of existing demographic structure, we applied an adapted version of the protocol suggested by Environment Canada (2008: Appendix 6.2). For each cluster, we randomly selected a single individual and calculated the area of the 100% MCP generated using their location data. We added the locations for each additional individual assigned to the cluster (in random order) and calculated the area of the corresponding 100% MCPs each time a new, randomly selected individual was included. The process was repeated until the locations for all individuals assigned to a cluster were included in the home range area calculations. Then, for each cluster, we inspected the relationship between 100% MCP size and the number of individuals that contributed to the corresponding estimate to determine if sampling efforts were sufficient for obtaining an accurate depiction of the size and location of cluster boundaries and cores.

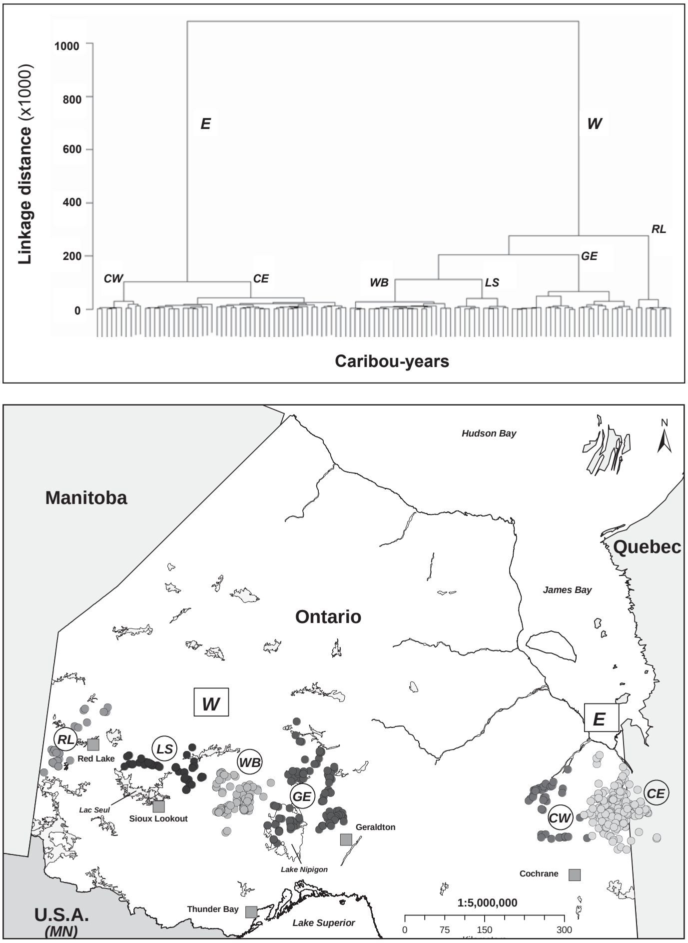

Fig. 3a-b. Cluster dendrogram formed from Euclidean distances between means of last clusters joined using the sum of squares (i.e., "Ward's") method (a) and geographic extent of corresponding clusters (b), depicted using the seasonal median locations of classified woodland caribou (n=73). Each terminal point in (a) represents one object (i.e, caribou-year), which include 1 full year of location data for a single individual. In both figures, the western and eastern sampling regions are labeled "W" and "E", respectively. The six clusters delineated were: Red Lake = "RL", Lac Seul = "LS", Wabakimi = "WB", Geraldton = "GE", Cochrane West = "CW", Cochrane East = "CE".

Results

Cluster analyses

General

Each of the different clustering methods yielded similar results with respect to cluster composition and the appropriate number of clusters. A dendrogram that depicts the results obtained when Ward's algorithm was applied to the seasonal median location data is depicted in Fig. 3a, to serve as an illustrative example of the groups demarcated by the different methods. Fig. 3b displays the geographic locations of the clusters detected using Ward's algorithm.

For all methods, the 3-cluster solution corresponded with the null hypothesis (i.e., panmictic population structure). The first split separated caribou in the east from caribou in the west and the second split separated caribou in the Red Lake area from other western groups (e.g., Fig. 3a), which corresponded with the cluster structure expected as an artifact of incomplete sampling efforts. Given the lack of sampling on the landscape between these clusters, it was impossible to determine the extent to

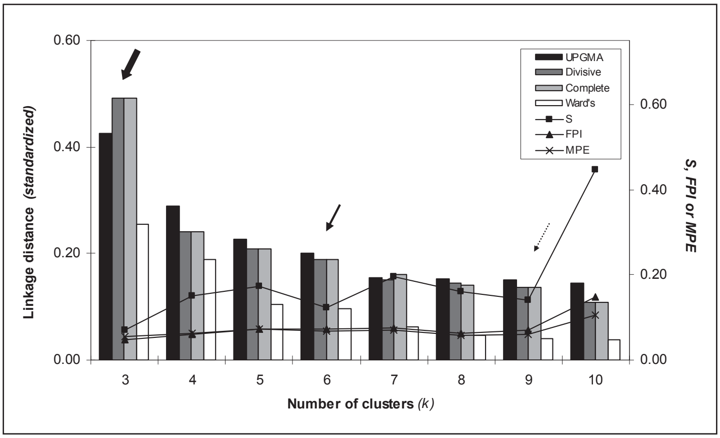

Fig. 4. Linkage distance (standardized across hierarchical methods) and fuzzy *k*-means performance measures in relation to number of clusters (*k*). Fuzzy performance measures include separate fuzzy validity (S), the fuzziness performance index (FPI) and modified partition entropy (MPE). The large solid arrow indicates the solution (*k* = 3) that corresponds with the null hypothesis (i.e., panmixia). For the hierarchical methods, the decline in linkage distance reached a plateau at *k* = 5 or 6 (indicated by the small solid arrow). Minimum values for the three fuzzy performance measures were observed at *k* = 3, with local minima at *k* = 6 and 9 (indicated by the small dashed arrow).

which these distinctions were representative of actual demographic structure. Consequently, we restricted our evaluation of the results and our demographic inferences to solutions with more than three clusters.

The relationship between the number of clusters and the different metrics used to identify the appropriate stopping point for different clustering solutions is depicted in Fig. 4. The minimum values for the 3 fuzzy indices corresponded to a 3 cluster solution (Fig. 4). For more complex solutions, FPI and MPE remained close to this minimum value until increasing at *k* > 9 (Fig. 4). In comparison, S was considerably higher than the minimum value for most of the more complex clustering solutions, increasing substantially when *k* > 9 (Fig. 4). Exceptions occurred at *k* = 6 and 9, where S reached local minima (Fig. 4).

For the hierarchical methods, the 3 cluster solution size was also associated with relatively high linkage distance, yet the decline in linkage distance continued as the number of clusters increased with all methods, indicating a general plateau in linkage height for solutions with more than 5-6 clusters (Fig. 4). Since all three fuzzy clustering indices were close to minimum values at 6 clusters and the S exhibited a local minimum when *k* = 6, clustering solutions that included 6 clusters appeared most appropriate for delineating demographic structure (Fig. 4).

The clusters delineated were relatively consistent across methods in terms of the location and composition of cluster solutions that contained 3 through to 6 clusters. Amongst the 6 cluster solutions, all methods delineated the same groups of caribou-years in the Red Lake area, Lac Seul area and the Cochrane area (which was subdivided into separate eastern and western groups) (Fig. 5).

The central area of the province was the only region where there were discrepancies among classifications produced by different methods. Specifically, cluster solutions differed in terms of how caribou-years with median locations in the immediate vicinity of Lake Nipigon were classified. The UPGMA and divisive method clustered them to the west (with caribou-years in the Wabakimi Provincial Park area), Ward's method and the complete linkage methods clustered them to the east (with caribou-years in the Geraldton area) and the fuzzy *k*-means method divided the Lake Nipigon caribou-years in two-clustering half to the west (i.e., Wabakimi) and half to the east (i.e., Geraldton). To determine which cluster structure was most appropriate for classifying caribou-years in the Lake Nipigon area, we evaluated the proximity of the Lake Nipigon caribou to adjacent groups (i.e., Wabakimi and Geraldton), their general space use patterns and the relative reliability of the different clustering methods we applied.

Lake Nipigon

The seasonal median locations of Lake Nipigon caribou-years were slightly closer to those of the Wabakimi caribou-years, with an average distance of 105 km and an average minimum distance of 63 km, compared to an average distance of 113 km and an average minimum distance of 67 km in relation to the Geraldton caribou-years. The actual minimum distance between a seasonal median location of a caribou-year in the Lake Nipigon area and a caribou-year in Wabakimi was 25 km, while the shortest distance between a seasonal median location of a Lake Nipigon caribou-year and that of a Geraldton caribou-year was almost double that distance at 41 km.

All sub-sampled locations from caribou located in the general vicinity of Lake Nipigon (i.e., those assigned to either the Geraldton or the Wabakimi clusters) are displayed in Fig. 6. When the proximities of all caribou locations were compared, the average distance between locations recorded for Lake Nipigon caribou-years and those recorded for Wabakimi caribou-years was slightly higher (i.e., 123 km) than it was for Geraldton caribou-years (i.e., 110 km). However, the average and actual minimum distances between Lake Nipigon caribou-years and Wabakimi individual years were much lower than those recorded for caribou-years in the Geraldton area (i.e., 43 km and 6 km respectively, compared with 70 km and 22 km). Thus, in general, Lake Nipigon caribou appeared to be closer to caribou in the west (i.e., Wabakimi) than they were to caribou in the east (i.e., Geraldton).

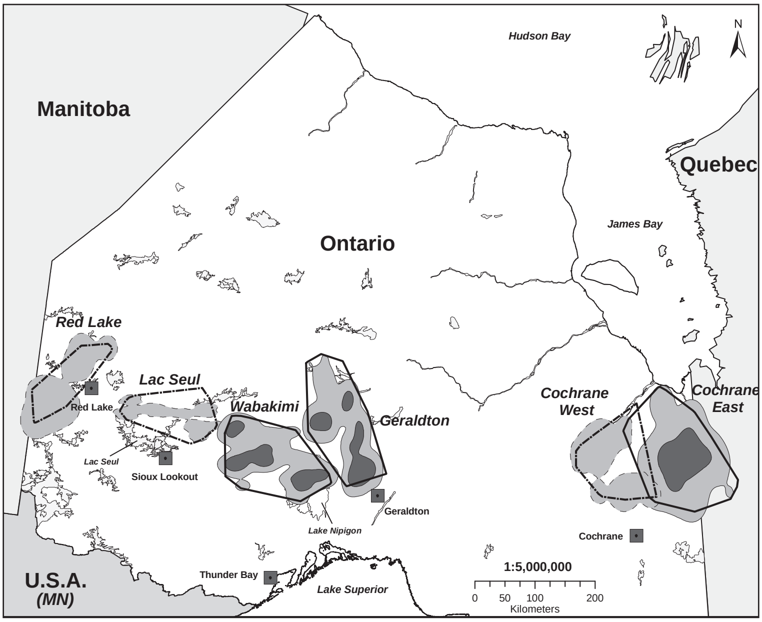

Fig. 5. Demographic unit boundaries and core areas of forest-dwelling woodland caribou (*Rangifer tarandus caribou*) at the southern limit of the ecotype's continuous distribution in Ontario. Angular polygons outlined in black represent 100% Minimum Convex Polygons generated using all the subsampled locations of the caribou assigned to each cluster. Light gray polygons represent boundaries defined using the 95% isopleth from kernel density estimates of the utilization distributions for caribou assigned to each cluster. Polygons with dashed outlines were generated using location data from a small sample of individuals. Isopleths generated using data from relatively large, broadly distributed samples of individuals have solid outlines (i.e., Wabakimi, Geraldton and Cochrane East clusters), while isopleths generated using data from a small samples of individuals have dashed outlines (i.e., Red Lake, Lac Seul, Cochrane West). Dark gray polygons represent core areas defined using the 50% isopleth from cluster-specific kernel density estimates of the utilization distribution. These core areas were only generated for clusters with large, well-distributed samples of individuals (i.e., Wabakimi, Geraldton and Cochrane East).

An evaluation of the space use patterns of the Lake Nipigon caribou suggests that these individuals were not only closer to individuals in the west, but they also made their greatest inland movements from the north-western shore of Lake Nipigon. The majority of the locations recorded for each caribou-year in the Lake Nipigon area were distributed either within the Lake (i.e., on islands or frozen lake waters) or immediately adjacent to the lakeshore (Fig. 6). The majority (i.e., 68%) of all caribou locations recorded near the eastern, north-eastern and north-central shores of the lake (n = 184) were located within 1 km of the lakeshore. The only exceptions were locations recorded on a large peninsula that extends into the lake (i.e., the North peninsula, near Ombabika Bay—Fig. 6). The 147 locations recorded near the south-western shore exhibited similar patterns—95% were located within 1 km of the shoreline and the few that were further from the lake shore were located on points and peninsulas that extended into the lake.

In comparison, in the vicinity of the north-western shore of Lake Nipigon there were several instances where Lake Nipigon caribou traveled a considerable distance inland, in the general direction of the Wabakimi caribou. Specifically, one individual spent spring of 2005 and winter and spring of 2006 approximately 5 km inland from English Bay, along the western shore of Lake Nipigon. An adult male and female that spent summers in the Ombabika Bay area along the eastern coast of Lake Nipigon, spent the late winter and spring of 2002 in a general area located approximately 8 km north-west of Windigo Bay (at distances that ranged from 5 to 11 km), on the northwest shore of Lake Nipigon. The female returned to the same general area during the winter of 2003.

An evaluation of the space use patterns of the Wabakimi and Geraldton caribou indicated that

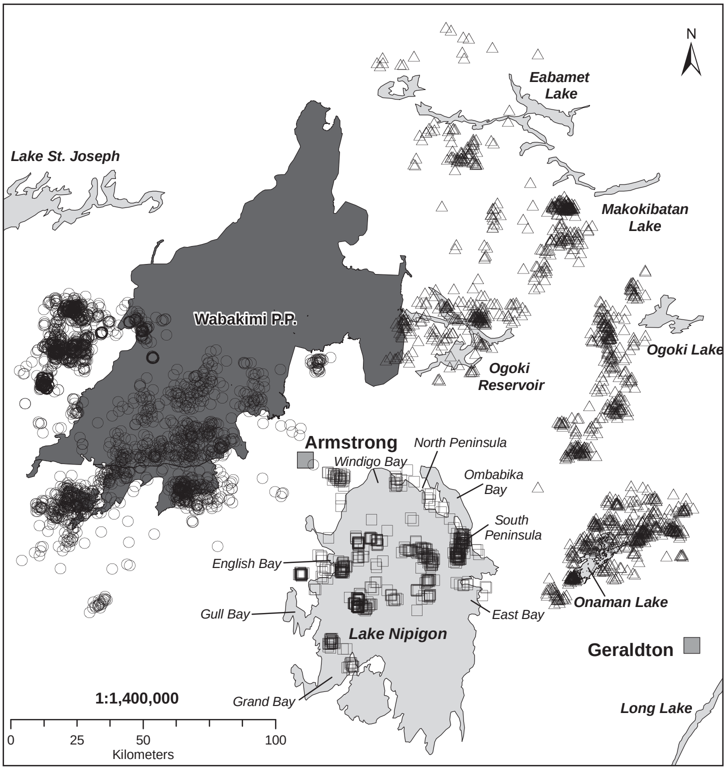

Fig. 6. Distribution of locations for collared caribou (*Rangifer tarandus caribou*) that occurred in and around the shores of Lake Nipigon (open squares) and for caribou that inhabited adjacent areas to the east (open triangles) and west (open circles). All subsampled locations recorded from 1995-2008 for individuals assigned to either the Geraldton or Wabakimi clusters are depicted. Light gray polygons represent major waterbodies. The dark gray polygon located to the west of Lake Nipigon depicts the boundaries of Wabakimi Provincial Park.

most sampled individuals from both groups did not travel closer than roughly 30 km (or more) from the Lake Nipigon shoreline. However, the nearest locations of the closest individual from each group differed considerably. Specifically, one individual from the Wabakimi area spent time in an area less than 4 km from the north-western shoreline of Lake Nipigon and the closest location recorded for a Geraldton caribou was approximately 20 km from the shoreline.

Finally, an evaluation of evidence regarding the relative reliability of different clustering methods favoured the UPGMA and divisive hierarchical methods and the fuzzy *k*-means method over Ward's and the complete linkage method (Cunningham & Ogilvie, 1972; Milligan & Isaac, 1980; Kaufman & Rousseeuw, 1990). Both Ward's and the complete linkage methods perform well when a dataset produces a spherical distribution (Kuiper & Fisher, 1975; Aldenderfer & Blashfield, 1984) but are less effective when clusters have different diameters, numerous outliers or are ellipsoidal in shape (Everitt, 1977; Aldenderfer & Blashfield, 1984; Kaufman & Rousseeuw, 1990). Since the clusters produced from our data by all methods were mostly ellipsoidal in shape (e.g., Fig. 5), the classification of the Lake Nipigon caribou-years under Ward's method and the complete linkage method were considered to be the least reliable. Consequently, given the proximity of Lake Nipigon caribou-years to Wabakimi, the presence of notable inland movements from Lake Nipigon to the north-west and the greater reliability of the methods that clustered all (i.e., UPGMA and divisive) or several (fuzzy *k*-means) of the Lake Nipigon caribou-years to the west, our results suggest grouping Lake Nipigon caribou-years with caribou-years in the Wabakimi cluster when delineating preliminary demographic units.

Cochrane

For all methods, the 6 cluster solution delineated two groups of caribou-years in the Cochrane area (i.e., east and west). However, for most methods (*n*=4) this distinction was not present in the 5 cluster solution. Thus, of all recognized groups, the distinction between the two Cochrane groups was the weakest. Due to the relatively low level of dissimilarity between the two Cochrane clusters and the small sample size (i.e., 5 individuals / 10 caribou-years) of the western group, we decided to look at all the location data from the Cochrane area caribou to determine whether individual space use and movement behaviour supported the distinction between groups. There was very little overlap in space use between caribou-years from the eastern and western groups. Six out of 10 caribou-years (3 out of 5 individuals) had relatively small home ranges (based on a 100% MCP), which were located in an area approximately 35 km west of the closest eastern individual. Only one wide-ranging female had ranges (*n*=2) that overlapped slightly with those estimated for some caribou-years in the eastern group. Given the low level of overlap and in some cases, considerable distance between home ranges of caribou-years assigned to the different groups, we decided to retain the east-west distinction in the Cochrane area when delineating preliminary demographic units.

Demographic unit boundaries and core areas

Based on the results of cluster analyses and the resolution of differences between the cluster structures delineated by different methods, each caribou-year was assigned to one of six clusters: Red Lake (n = 5 caribou, 8 caribou-years), Lac Seul (n = 6 caribou, 12 caribou-years), Wabakimi/Lake Nipigon (n = 21 caribou, 29 caribou-years), Geraldton (n = 11 caribou, 19 caribou-years) Cochrane West (n = 5 caribou, 10 caribou-years) and Cochrane East (n = 5 caribou, 10 caribou-years). The precise locations and geographic extents of each demographic unit (as delineated by the MCP and kernel density-based estimates of cluster "ranges") are depicted in Figure 5. Three clusters had relatively low sample sizes, particularly for the KDE analysis: Red Lake, Lac Seul and Cochrane East. For these clusters, only the 100% MCP and the 95% isopleth from the KDE are displayed in Figure 5. The 50% isopleths generated for the three clusters with larger sample sizes (i.e., Wabakimi, Geraldton and Cochrane East – Fig. 5) indicate that each cluster contains multiple core use areas. An inspection of the telemetry locations that fall within these core areas indicates that they represent areas that receive relatively intensive use during multiple seasons.

Demographic unit "distinctness"

In the 6-cluster solution depicted in Fig. 5, the 41 caribou collared for multiple years were assigned to the same cluster for each caribou-year included in the anlysis. This general result held true for all of the six-cluster solutions, regardless of which clustering method was applied. This lack of "cross-classification" (Taylor *et al.*, 2001) indicates that no collared caribou emigrated from one cluster to another during the study period.

While hard clustering methods assign each case (i.e., caribou-year) to a single cluster, fuzzy *k*-means clustering assigns "partial membership" coefficients, which sum to 1.00 and quantify the degree of membership that each caribou-year exhibits to all clusters delineated in a given cluster solution. Consequently, general trends in partial membership coefficient values (e.g., whether individuals generally exhibit a high degree of membership for a single cluster or whether they exhibit high coefficient values for multiple clusters) can serve as an indicator of the extent to which clusters can be viewed as distinct demographic units. For the six cluster solution obtained using the fuzzy *k*-means method, all caribou-years exhibited strong membership to a single cluster. The average maximum membership coefficient was 0.97 (standard deviation: 0.06): only 9 caribou-years had dominant membership values < 0.8 and of those, the lowest value was 0.69.

The proximity between the boundaries and core areas associated with adjacent clusters was the other major indicator of whether clusters represented demographically "distinct" groups. In general, there was very little overlap between adjacent boundaries, regardless of whether they were defined using an MCP or a kernel density estimate of range use (Figure 5; Table 1). The proportion of overlap between the boundaries of the two Cochrane ranges was 0.07 using kernel density estimates and 0.12 using MCP boundaries (Table 1). The Lac Seul and Wabakimi ranges overlapped slightly when the kernel density estimates were compared (i.e., 0.01; Table 1), but there was no overlap between the boundaries of any other adjacent range combinations.

The minimum distance between the non-overlapping boundaries of adjacent clusters varied considerably. The distance between the MCP-based boundaries of the Lac Seul and Wabakimi clusters was relatively low (i.e., 18 km; Table 1) and the minimum distance between the Wabakimi and Geraldton ranges was even lower (i.e., 12 km between MCPs and 5 km between kernel density estimates; Table 1). The minimum distance between the Red Lake and Lac Seul clusters was higher at 67 km (Table 1), and both estimates of the minimum distance between the boundaries of the Geraldton and Cochrane West clusters exceeded 300 km (Table 1).

Only one pair of adjacent clusters were considered to have sample sizes large enough to use a KDE to delineate core use areas: Wabakimi and Geraldton (Table 1). While the distance between the adjacent boundaries of these two units was relatively low, there was approximately 32 km between the closest edges of the core use areas delineated for the two ranges. This indicates that the Wabakimi and Geraldton clusters may be more demographically distinct than is suggested by boundary-based distances alone.

Demographic unit reliability

The relationship between cluster size and the number of individuals with locations included in the size estimate is depicted in Fig. 7. Rather than increasing smoothly to a single clear asymptote, the two clusters with the largest sample sizes (i.e., Cochrane East and Wabakimi) reach several prolonged plateaus

Table 1. Proportion of overlap and minimum distances between outer boundaries (100% Minimum Convex Polygon and kernel density estimate-based) and core area boundaries (kernel density estimate-based) of adjacent clusters. For situations where minimum distances between the outer boundaries of adjacent clusters may be exaggerated due to incomplete sampling, the corresponding 'Range combination' and 'Minimum distance' fields are identified by an ' * '. For clusters where available data was determined to be insufficient for obtaining reliable estimates of core use areas (i.e., Red Lake, Lac Seul and Cochrane West), core boundaries were not delineated and distances between cores are listed as 'N/A' in the table.

Range combination	Proportion of overlap		Minimum distance between cluster boundaries (km)		
	100% MCP (outer boundary)	KDE - 95% isopleth (outer boundary)	100% MCP (outer boundary)	KDE - 95% isopleth (outer boundary)	KDE - 50% isopleth (core boundary)
Red Lake & Lac Seul *	0	0	67*	55*	N/A
Lac Seul & Wabakimi	0	0.01	18	0	N/A
Wabakimi & Geraldton	0	0	12	5	32
Geraldton & Cochrane W *	0	0	315*	312*	N/A
Cochrane W & Cochrane E	0.12	0.07	0	0	N/A

when $n \geq 4$ individuals. However, the relatively small increase in cluster size from the second-last to the final plateau for Cochrane East and the prolonged length of the plateau for the Wabakimi population (from $n = 12$ to 21) indicate that sample sizes are likely sufficient for deriving accurate estimates of demographic unit boundaries and cores (EC, 2008: Appendix 6.2). Geraldton was the cluster with the third largest sample size and the relatively prolonged length of the single asymptote that it appears to reach (from $n = 5$ to 11) suggests that the existing sample size for this cluster may also be sufficient for delineating the general extent of the areas used by members of this demographic unit. In contrast, the pattern for the other three support our earlier conclusion that sample sizes are not sufficient to be considered strongly representative of demographic unit cores or boundaries.

While the Red Lake and Lac Seul clusters appear to exhibit very short plateaus when $n \geq 3$, substantial increases in cluster size could occur if more extensive sampling were conducted, as was observed for the Cochrane East and Wabakimi clusters. Additionally, the relationship between the size of the Cochrane West cluster (which has also received limited sampling effort) and number of individuals contributing locations to the estimate does not appear to have reached an asymptote, which suggests that additional sampling is needed to accurately delineate boundaries of this cluster.

Discussion

The results we obtained are significant for two major reasons. First, they demonstrate the challenges associated with delineating demographic structure, particularly when working with historic data that may not have been collected in a manner that is optimal for implementing such analyses. Second, despite the numerous limitations of the dataset, by analyzing it we gained some insight into the demographic structure of woodland caribou in Ontario. Thus, we were able to obtain information that can be used to inform pressing conservation and management decisions until more appropriate and extensive datasets are available.

The dataset: limitations and insights

The reliability of inferences about population structure that are based on spatial proximity and movement data, is dependent on the extent to which sampled individuals can be considered to be representative of the population(s) of interest. This, in turn, is a function of sampling strategy and sample size (Greenwood, 1996), as well as duration of the sampling period (EC, 2008: Appendix 6.2). The dataset analyzed here was not ideal with respect to any of these factors. For example, only the southern portion of the ecotype's range in Ontario was sampled when collecting the historic dataset and even within this region, the intensity of sampling efforts and the spatial distribution of collar deployment locations

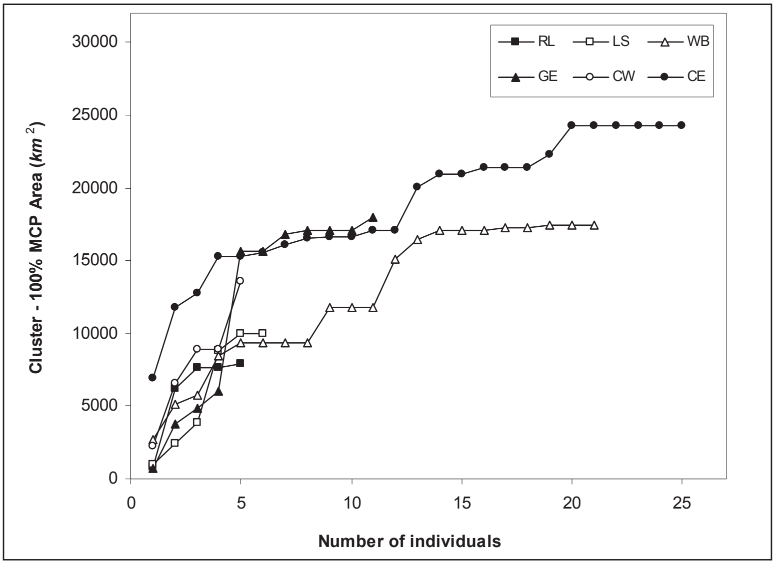

Fig. 7. The relationship between cluster size and the number of classified individuals with locations used to generate the cluster size estimate. Relationships are displayed separately for each identified cluster. The six clusters included are labeled as follows: Red Lake = "RL", Lac Seul = "LS", Wabakimi = "WB", Geraldton = "GE", Cochrane West = "CW", Cochrane East = "CE".

were somewhat uneven. Sample sizes were relatively high in the central and easternmost sections of the sampling region (i.e., Wabakimi = 21, Geraldton = 11 and Cochrane East = 25 individuals) and this, combined with observed asymptotes in the relationship between cluster size and the number of sampled individuals for each of these three clusters, indicates that sufficient data were available to obtain an accurate delineation of the general boundaries and core areas of local populations. In contrast, sample sizes were quite small in the western (i.e., Red Lake and Lac Seul—5 and 6 individuals, respectively) and central-eastern (i.e., Cochrane West—5 individuals) areas of the province, and no lengthy asymptotes were observed in the relationship between cluster size and the number of sampled individuals. Consequently, it was considered inappropriate to delineate cores for these areas and the boundaries delineated for these clusters should be treated as preliminary indicators of the minimum extent of demographic units.

In some regions, spatial gaps in collar deployment locations appear to be representative of patchiness in the distribution of woodland caribou during the aggregative winter season (e.g., between Cochrane East and Cochrane West and in the Geraldton and Wabakimi areas). In others, these gaps reflected a lack of sampling effort (e.g., the intervening area between Cochrane West and Geraldton, and the areas between and surrounding Lac Seul and Red Lake) and they made it impossible to determine whether consequent divisions between adjacent clusters were representative of the distribution of caribou on the landscape or whether they were just artefacts of inadequate sampling. The presence of these gaps affected the cluster structure predicted under the null hypothesis (i.e., panmixia), which demonstrates the importance of identifying and accounting for sampling inadequacies when defining the clustering results expected under alternative hypotheses.

Hastings (1993) found that populations become demographically correlated when between-group migration exceeds 10% and this immigration/emigration threshold has been recommended for delineating demographic units by general (e.g., Palsbøll *et al.*, 2007) and caribou-specific sources (e.g., EC, 2008). While no between-group migration events were documented in this study, small sample sizes and the biased nature of sample composition affected the reliability of assessments of demographic distinctness based on the calculation of immigration/emigration rates. The presence of 41 individuals that were collared for multiple years made it possible to detect emigration/immigration events, but within-group sample sizes of these individuals were insufficient for calculating reliable estimates of immigration/emigration rates between adjacent groups. Additionally, evidence suggests adult female caribou exhibit a high degree of fidelity to calving sites (Fuller & Keith, 1981; Paré & Huot, 1985; Brown *et al.*, 2000; Schaefer *et al.*, 2000; but see Dyke & Manseau, 2009 for contrasting results) and, consequently, individuals in this age/sex group are probably the least likely to move from one demographic group to another. Since most sampled individuals in this study were adult females, any conclusions regarding the frequency of immigration/emigration events may be negatively biased. However, since adult female survival and reproduction are the main determinants of the population dynamics of polygynous, promiscuous species like caribou (Mysterud *et al.*, 2002; Rankin & Kokko,

2007) and their site fidelity is the factor that likely underlies spatial structuring within broader populations (Schaefer *et al.*, 2001), biased sampling in favour of this demographic group is somewhat defensible. In fact, almost all studies of large mammals that have applied similar methodologies to delineate local populations have analyzed datasets that were comprised exclusively (e.g., Bethke *et al.*, 1996; Schaefer *et al.*, 2001; Taylor *et al.*, 2001; Schaefer & Wilson, 2002; Courtois *et al.*, 2007) or predominantly (e.g., Edwards *et al.*, 2008) by adult females. Only McLoughlin *et al.* (2002) analyzed a dataset that contained similar numbers of males and females.

The limitations associated with emigration/immigration-based estimates of demographic distinctness forced us to rely on the spatial proximity of cluster boundaries and core areas as a proxy for the strength of demographic interactions between adjacent groups. Such assessments are not ideal (EC, 2008: Appendix 6.2), especially in western and central-eastern areas of the province, where small sample sizes reduce the reliability of boundary and core area estimates. However, the low degree of boundary overlap and where assessed, the relatively high minimum distances between core areas of adjacent groups, both support the emigration/immigration results and fuzzy membership coefficient results, each of which suggests that the groups delineated in this study may be relatively distinct, from a demographic perspective.

In addition to limitations associated with sample size and composition (i.e., sample dominated by single sex/age class), sampling period duration was another factor that affected the reliability of the results presented here. Environment Canada (2008: Appendix 6.2) recommended that as many as 20 continuous years of observation data be used to delineate local caribou populations, because long sampling periods are more likely to capture inter-annual variability in occupied areas and lagged responses of caribou occupancy to habitat change (e.g., Vors *et al.*, 2007). For each of the demographic units identified here, the associated sampling period was relatively short. The datasets used to delineate the Geraldton and Wabakimi units (Fig. 5) were collected over the longest time period (i.e., approximately 11 years for each area—from 1995 to 2006), but deployed collars were not evenly distributed throughout each demographic unit for the full duration of the sampling period. Sampling periods in other locations were considerably shorter: five years in Lac Seul (1995-2000), three years in Red Lake (1997-2000) and Cochrane East (1998-2001), and two years in Cochrane West (2006-2008). The short duration of sampling in most locations suggests that temporal variability in occupancy may not be well-represented in any of the 6 demographic units identified (Fig. 5). The collection of long-duration datasets (i.e., 20 years) throughout the entire study area will likely improve the ability to detect inter-annual variability and short-term changes in population structure and range boundaries. However, it is important to recognize that caribou population structure is dynamic and that current conditions may not be well-represented by historic patterns, particularly if conditions (e.g., climate, levels of natural or anthropogenic disturbance) have changed over time. For this reason, extant population structure should be re-evaluated and revised (if necessary) on a fairly regular basis (EC, 2008: Appendix 6.2).

Clearly, there is room for improvement in the dataset with respect to sample size, the distribution of sampled individuals and duration of the sampling period. Despite these shortcomings, the analysis presented here is valuable in several respects. First, it highlights the general need for more telemetry data, which can be used to obtain a comprehensive assessment of the number, extent and demographic distinctness of local populations of woodland caribou in Ontario. A formal analysis of telemetry data isn't the only approach available for determining the extent of local populations—alternatives include genetic analyses, the collation of long-term incidental or survey sightings or the use of Traditional Local Knowledge (EC, 2008: Appendix 6.2). Of these, only genetic analyses share the major advantages of telemetry-based analyses. Namely, both approaches can include standardized, objective methodologies for delineating demographic structure and both allow researchers to draw inferences about the level of individual movement between local populations, which is essential for calculating immigration/emigration rates.

Many standard population genetic methods provide genetic divergence estimates that are averaged over recent evolutionary time and may not be indicative of current rates of gene flow (Palsbøll *et al.,* 2007). This can diminish the value of genetic data as a source of information regarding current (vs. historic) demographic structure (Avise, 1992; Cronin, 1993; Moritz, 1994). However, recent developments in molecular ecology allow genetic data to be used to derive dispersal rate estimates that apply to recent generations (Palsbøll *et al.,* 2007). The latter approaches can be applied to determine whether effective dispersal between groups falls above or below the 10% threshold (Palsbøll *et al.,* 2007; EC 2008: Appendix 6.2) and thus, they can be very useful for delineating meaningful demographic units (e.g., Ball *et al.,* 2010). Therefore, genetic analyses can provide insights into demographic structure that complement the information provided by telemetry-based analyses like the one presented here. A combined consideration of individual movements and population genetic data will likely produce a more comprehensive picture of demographic structure than singular reliance on either type of evidence would (e.g., Boulet *et al.*, 2007) and thus, we recommend that further efforts be undertaken to collect and analyze both types of data.

Extensive efforts to collect more caribou telemetry data are currently underway within Ontario (G. Racey, OMNR, pers. comm., 28 May 2010) and the results presented here can provide detailed insight into how and where data collection should proceed. Specifically, more sampling is needed throughout the northern portion of the ecotype's range and in specific sections of the southern portion of the range (i.e., the western and central-eastern sections) to achieve an even distribution of sampling effort throughout the study area (Schaefer *et al.,* 2001) and to ensure that collar deployment locations are representative of the distribution of animals on the landscape. Additionally, longer-term sampling should be considered throughout the entire extent of forest-dwelling woodland caribou range, in order to capture temporal variability in space use. Finally, efforts to increase sampling amongst age/sex classes that have been poorly represented in earlier studies (i.e., adult males and reproductively immature individuals of either sex) should also be considered, as the movements of these individuals may be less constrained by fidelity to specific locations (e.g., calving sites).

The second major contribution of this study is the preliminary insights it provides into the demographic structure of forest-dwelling woodland caribou at the southern edge of their continuous range in Ontario. Specifically, the results presented here support the existence of demographic structuring within the ecotype's continuous range in northern Ontario. The delineation of the Red Lake group and the separation between the Cochrane clusters and the caribou in the central part of the province could just be artefacts of insufficient sampling efforts. However, the cluster results, in combination with an assessment of the representativeness of collar deployment locations, provide support for three additional demographic distinctions: between Cochrane East and Cochrane West, between Geraldton and Wabakimi and between Wabakimi and Lac Seul.

Several lines of evidence suggest that these spatial clusters of caribou represent demographically distinct local populations. These include (1) the high degree of similarity (i.e., in cluster solution size and composition) across cluster methods, (2) the strong membership that each caribou-year exhibited towards a single cluster (as indicated by fuzzy membership coefficient values), (3) the lack of migration between clusters amongst caribou collared for multiple years, (4) the low level of overlap between the boundaries of adjacent clusters and (5) where it was possible to measure, the considerable distance between core use areas associated with adjacent groups. In the end, evidence in favour of multiple demographic units in our study is stronger than that presented by several other studies that claim to delineate population structure, in terms of between-method consistency in results (e.g., Schaefer *et al.,* 2001), the degree of overlap between adjacent clusters (Bethke *et al.,* 1996; Schaefer *et al.,* 2001; Edwards *et al.,* 2008) and immigration/emigration rates (Schaefer *et al.,* 2001; Taylor *et al.,* 2001).

While this evidence does support the presence of demographic structuring, the level of discreteness between adjacent units appears to be relatively low. Short distances between cluster boundaries (relative to home range size), inconsistency in the classification of the Lake Nipigon caribou and the low density of natural and anthropogenic barriers between delineated units indicates that the distribution of caribou throughout the study area may be relatively continuous at a coarse scale. However, the evidence described above is consistent with the existence of geographic clusters of animals with dynamics that are more likely to be influenced by interactions with each other than with members of adjacent groups.

The resources and costs associated with collecting a telemetry dataset that is ideal for population delineation are very high and available funds are often likely to fall short of what is needed. Additionally, even with adequate resources, considerable time would be required to address some of the weaknesses outlined above (e.g., short sampling periods). In the meantime, decisions regarding natural resource extraction and infrastructure development continue to be made in the regions of Ontario that are currently occupied by caribou. As long as the uncertainties associated with the demographic units delineated in this study are explicitly recognized, they can be used to inform land use planning decisions and development and implementation of conservation and recovery strategies for woodland caribou. Relevant policies, plans and guidelines can be adjusted when better data become available.

Levels of organization

The methodological approach that we applied here was based on several earlier studies of various species which analyzed individual locations to identify distinct demographic groups and delineate their boundaries. Most of these focused on large, wide-ranging temperate and arctic-dwelling mammals such as polar bears (*Ursus maritimus*) (e.g., Bethke *et al.*, 1996; Taylor *et al.*, 2001), grizzly bears (*Ursus arctos horribilis*) (e.g., McLoughlin *et al.*, 2002; Edwards *et al.*, 2008) and woodland caribou (e.g., Schaefer *et al.*, 2001; Schaefer & Wilson, 2002; Courtois *et al.*, 2007). Despite the high degree of similarity in methodologies and study organisms, the spatial extent of study areas differed greatly among these studies.

Some studies analyzed datasets that spanned relatively broad areas: 900 km by 350 km (Bethke *et al.*, 1996), 3000 km by 1000 km (Taylor *et al.*, 2001), 1500 km by 1000 km (Schaefer & Wilson, 2002) and 1200 km by 300 km (this study). One study analyzed data collected from more moderately-sized areas (i.e., 450 km by 400 km; McLoughlin *et al.*, 2002), while several others have analyzed data from relatively small study areas: 250 km by 200 km (Schaefer *et al.*, 2001), 300 km by 250 km (Courtois *et al.*, 2007) and 150 km by 250 km (Edwards *et al.*, 2008). Sample sizes amongst these studies ranged from 26 to 131 individuals (average = 69, standard deviation = 36) and there was no apparent relationship between sample size and the size of the study area. Additionally, the number of clusters delineated was similar among studies (average = 4, standard deviation = 1.5), but there was no relationship between the size of study area and cluster number.

Even though there is extensive variation in both study area size and the "sample size-to-study area size" and "study area size-to-cluster number" ratios, all of the studies listed above interpret delineated groups as representing sub-populations that are embedded in larger metapopulations (e.g., Bethke *et al.*, 1996; Schaefer *et al.*, 2001; Courtois *et al.*, 2007; Edwards *et al.*, 2008). However, given that many ecological patterns and processes vary across scales (Wiens, 1989; Schaefer, 2006), it seems likely that the demographic units identified by studies conducted at widely divergent spatial extents represent different levels of spatial organization. The universal application of the "subpopulation" label amongst these studies probably stems from the common characterization of populations as operating at two basic spatial scales: regional and local (i.e., metapopulations and subpopulations) (Schaefer, 2006). This perspective is illustrated in the discussion that Edwards *et al.* (2008) provide regarding the identification of ecologically meaningful scales for conservation and management. However, despite its widespread use, Schaefer (2006) suggests that this two-tier spatial characterization is an oversimplification of population structure and processes, which likely exist at multiple, nested scales.

Allowing for the possibility of more than two levels of population structure seems especially appropriate for forest-dwelling woodland caribou. While they are relatively solitary during and after calving (Bergerud *et al.*, 1990; Schaefer *et al.*, 2001; Ferguson & Elkie, 2004a), they tend to form relatively small groups of individuals during autumn and/or winter (Shoesmith & Storey, 1977; Darby & Pruitt, 1984; Brown *et al.*, 1986; Stuart-Smith *et al.*, 1997; Rettie & Messier, 1998; Brown *et al.*, 2000; Ferguson & Elkie, 2004a). While aggregations of up to 80 individuals have been documented in Ontario during the winter months (Cumming & Beange, 1987), average group sizes have been estimated at less than 10 individuals (Cumming & Beange, 1987; Bergerud *et al.*, 1990). Given the small size of these groups or "bands" (Cumming & Beange, 1987), they are probably best understood as nested subsets of larger subpopulations, which are themselves embedded in broader-scale metapopulations. Cumming and Beange (1987) even suggest that the large aggregations that are occasionally observed are comprised of multiple bands and thus represent an additional level of organization, intermediate between autumn/winter "bands" and subpopulations.

Most of the studies that document group formation during autumn note the association between aggregation and rutting activities (e.g., Bergerud, 1973; Shoesmith & Storey, 1977; Fuller & Keith, 1981; Paré & Huot, 1985; Rettie & Messier, 1998). There is little evidence regarding the rigidity of caribou "band" membership across years and seasons, but that which exists indicates that there may be considerable fluidity in group membership over the autumn-winter period (Bergerud, 1973; Brown *et al.*, 2000) or between years (Paré & Huot, 1985). However, if these groups are at least partially comprised of inter-breeding pairs or closely related individuals (parent-offspring) and/or they share similar experiences (e.g., shared resources or conditions) that cause their vital rates to differ from those of other groups in the subpopulation, then even this finest level of organization may be significant from a demographic perspective.

Since it seems likely that caribou population structure exists at multiple spatio-temporal scales, with spatial and demographic affinities that decline at higher hierarchical levels, some consideration should be given to determining what level of organization is represented by the groups delineated in this study. An inspection of the 100% MCPs generated for each individual (not shown here) reveals that with the exception of Cochrane East, each demographic unit is comprised of multiple groups of individuals (i.e., with highly overlapping home ranges) that are spatially distinct (exhibiting little to no overlap) from other groups. These patterns of individual space use, in combination with the large cluster size (i.e., average = 14 684 km^2, standard deviation = 5699 km^2, for 100% MCPs for each cluster), suggests that the demographic units delineated here correspond with subpopulations that are nested within a broader metapopulation which, in some cases may be comprised of multiple, smaller spatially distinct groups (e.g., the "Wabakimi" cluster and the "Geraldton" cluster – Figure 6). This finest level of organization may occur if significant natural or man-made disturbances temporarily restrict caribou movements (G. Racey, OMNR, pers.comm., 29 Nov. 2010) or if space use is bounded by strong individual selection for static geographic features (e.g., large lakes or peatland complexes).

Management implications

The range retractions and population declines exhibited by the boreal population of forest-dwelling woodland caribou have resulted in its designation as a conservation priority at national and provincial/territorial levels (Thomas & Gray, 2002; EC, 2008; OMNR, 2009). Consequently, in the jurisdictions that overlap the organism's extant range, there have been several recent efforts to develop woodland caribou conservation and recovery strategies (e.g., MC, 2005; MRNFQ, 2008; OWCRT, 2008; OMNR, 2009).

Efforts to incorporate habitat-based considerations when delineating "units of analysis" can aid in designing conservation strategies that avoid fragmenting continuous areas of caribou range (EC, 2008: Appendix 6.2). However, conducting status assessments using data collected over broad geographic areas could mask local variation within the larger range, which could result in unexpected local extirpations and range loss (EC, 2008: Appendix 6.2). Thus, consideration of existing population structure is also critical for delineating meaningful "units of analysis" for the boreal population of woodland caribou. One option for effectively integrating both types of information (i.e., habitat and population structure) would be to prioritize large, habitat-based ranges when developing and implementing recovery strategies, while local populations (defined based on caribou space use and movement) could be used as the primary units of analysis for calculating vital rates and assessing population viability (e.g., Arsenault *et al.* 2003) or the cumulative impacts of anthropogenic disturbance (e.g., Sorensen *et al.* 2008). While implementing the second component (i.e., local population delineation) of this option, it is important to remember both the dynamic nature of caribou population structure and that major changes in caribou occupancy patterns and demographic connections may occur over relatively long time periods (i.e., multiple decades). Consequently, results like those presented here can only provide insight into caribou population structure and occupancy over a discrete period of time. As such, they should be viewed as one of several "snapshots" of population structure that will likely be produced over the course of a long-term adaptive management cycle (EC, 2008: Appendix 6.2; OMNR, 2009).

We did not conduct a formal assessment of the spatial distribution of caribou habitat. However, because the study area is located at the northern limits of commercial logging in Ontario and there are no large communities, extensive permanent developments, or impenetrable geographic boundaries located between the demographic units delineated here, it seems likely that caribou currently occur within relatively continuous habitat. Subsequently, the boundaries of demographic units identified by the methods we have described should be considered when assessing population or range status.

The same general approach for incorporating the information obtained from a telemetry-based analysis of population structure into management can also be used to determine how to deal with the two locations where the determination of demographic unit boundaries was uncertain. The caribou in the Lake Nipigon area were the only individuals with cluster assignments that differed between methods. An evaluation of additional evidence supported grouping them with individuals to the west when delineating population boundaries and core areas. However, the discrepancies between cluster results and the lack of overlap in space use between Lake Nipigon caribou and individuals to the east and west, suggests that considerable uncertainty remains regarding the appropriate classification of these individuals.

A management strategy that explicitly accounts for this uncertainty would assess population viability based on the area of occupancy associated with the Lake Nipigon individuals, while recovery efforts could focus on maintaining or restoring habitat in the intervening landscape between Lake Nipigon and caribou in the Wabakimi and Geraldton areas. With respect to the recovery effort component, such an approach is supported by historic evidence for the movements and seasonal occupancy patterns of Lake Nipigon caribou, which supports demographic connections with groups to the west (Cumming & Beange, 1987; Bergerud *et al.*, 1990) and east (R. Hartley, OMNR, pers. comm., 2 Dec. 2010).

Additionally, more recent evidence of caribou occurrences in the inland areas adjacent to Lake Nipigon (obtained using other survey methods), suggests that these connections may still persist to some degree (G. Racey, OMNR, pers. comm., 29 Nov. 2010). Finally, until further data are available that enables the relationship between the two groups in the Cochrane West and Cochrane East areas to be defined with greater certainty, a similar management approach could be applied in this area of the province. Namely, population viability assessments could be based on the boundaries of the Cochrane East and Cochrane West units and recovery efforts could account for the potential connections between these adjacent groups.

Delineation of "critical" habitat for woodland caribou in Ontario and elsewhere should be based primarily on analyses that identify the resources and conditions associated with occupancy (e.g., by applying Resource Selection Functions - Manly *et al.*, 2002). Undertaking such analyses was beyond the scope of this paper. However, the results of the kernel density estimation analysis provided some insight into areas that could be important from a caribou conservation and management perspective.

There was distinct variation in the intensity of caribou use in each of the three clusters that had sufficient data to generate 50% isopleths (i.e., Wabakimi, Geraldton and Cochrane East). Each cluster contained one or more "core" areas of intensive use, with evidence of some level of occupancy throughout the year.

Resource Selection Functions (RSFs) or other formal analyses of habitat selection would be required to test alternative hypotheses regarding the mechanistic basis for variation in the intensity of use in each cluster and to enable comprehensive mapping of probability of caribou use across the sampled portions of the study area. However, for a variety of reasons (e.g., inadequate characterizations of explanatory variables, metapopulation dynamics – Hanski & Simberloff, 1997), RSF-based probabilities of use may not always correspond with existing patterns of occupancy. Consequently, the geographic areas with high levels of historic caribou use identified here should be considered in conjunction with RSFs to delineate locations that may play an important role in the persistence of local caribou populations. Managers might consider prioritizing these areas for short or long-term conservation efforts, depending on how temporally dynamic the associated resources, conditions or processes that promote caribou occupancy are likely to be.

An evaluation of the characteristics associated with relatively low and high levels of use could also provide insights into which resources and conditions might be producing caribou occupancy and consequently, which environmental correlates may need to be included or improved when generating RSF-based definitions of critical habitat. Finally, the spatial discreteness of core areas within and between clusters and the existence of several areas that are characterized by relatively low probabilities of occupancy, suggests that while caribou are present across much of the sampled portion of the study area, the intensity of caribou use across this broad region may vary considerably. This variation in caribou occupancy should be taken into account when estimating effective range sizes or deriving coarse population estimates.

Until additional data are available for analysis, only provisional conclusions can be drawn about the population structure of woodland caribou at the southern margins of their continuous range in Ontario. While this information can and should be considered when making imminent management decisions, the limitations of the historic dataset and the preliminary nature of the results presented here should not be forgotten. Any future initiatives designed to obtain further information on the demographic structure of caribou in Ontario or elsewhere, should include concerted efforts to ensure that (1) sampling efforts are uniform, (2) collar deployments are representative of the distribution of caribou throughout the study area and (3) the spatio-temporal resolution and extent of the telemetry data are appropriate for capturing spatial population structure and temporal variation in caribou movements. Definitive telemetry-based assessments of population structure are not possible without such datasets.

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Climate and management interact to explain the decline of woodland caribou (*Rangifer tarandus caribou*) in Jasper National Park

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Abstract: Woodland caribou in the southern portion of Jasper National Park have declined from an estimated 435 in the mid 1970s to a population estimate of 87 in the fall of 2009. We examined the available historical information to determine why caribou have declined. We compared three main hypotheses for caribou decline in JNP: human disturbance, climate change, and wildlife management. We used historical human use statistics, climate data, and animal abundance information to weigh the evidence for these competing hypotheses over two time scales. Caribou decline could not be attributed to changes in climate over the long-term, or an increase in human use (our proxy for disturbance). Caribou decline was attributed to a combination of climate and wildlife management. Recovery of caribou in Jasper National Park will likely be contingent on managing the interaction between the predator/prey dynamic and climate change.

Key words: climate; elk; Jasper National Park; wolves; woodland caribou.

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Introduction

Woodland caribou (*Rangifer tarandus caribou*) are declining across Canada. The prevailing theory behind the decline is that industrial development of formerly intact caribou range has altered predator/prey interactions to the detriment of caribou (Bergerud & Ballard, 1988; Stuart-Smith *et al.*, 1997; Rettie & Messier, 1998; Mcloughlin *et al.*, 2003; Mcloughlin *et al.*, 2004; Wittmer *et al.*, 2005b). The altered interactions have been described as apparent competition, identified by Holt (1977), in which the decline of one prey species (e.g. caribou) is caused by higher-than-normal predator densities (e.g. wolf) that are influenced by the abundance of a second prey species (e.g. elk).

Southern mountain caribou (a population of woodland caribou federally designated as Threatened) are among the most vulnerable of Canada's woodland caribou. In 2005, 14 of 16 monitored southern mountain herds were in decline in British Columbia (Wittmer *et al.*, 2005a), while in 2008-09 all but one southern mountain herd were declining in Alberta (Alberta Sustainable Resource Development and Alberta Conservation Association, 2010). Furthermore, the southern-most caribou herds were thought to be in imminent danger of extirpation (Thomas & Gray, 2002). Unfortunately, these dire predictions were fulfilled by the extirpation of caribou in Banff National Park (Hebblewhite *et al.*, 2010b), as well as the extirpation of two herds in British Columbia (Hatter, 2006). As with woodland caribou across Canada, the primary reason for declines in the southern mountain population is attributed to apparent competition driven by human alteration of the landscape for industrial purposes and resulting increases in wolf-caribou encounters and predation (Wittmer *et al.*, 2005a; Wittmer *et al.*, 2005b).

But why have caribou in Jasper National Park also declined? Caribou in the southern part of Jasper National Park numbered approximately 435 animals in the mid-1970s (Stelfox, 1974) but today only 87 remain (90% confidence limits 87 to 96, unpublished Parks Canada data). Compared to the industrial landscape, human alteration of the landscape in Jasper National Park has been modest, and the decline of the park's caribou cannot be explained solely by the industrial landuse/apparent competition hypothesis. Recent monitoring (2001 to 2009) has shown wolf predation to also be important to Jasper caribou population dynamics. A study of collared adult female caribou in Jasper found that wolf predation (cumulative incidence function or CIF = 0.045) and unknown predation (CIF = 0.054) were the most important causes of mortality; however, unknown causes of mortality were also important (CIF = 0.055) (Decesare *et al.*, 2010).

We used the historical record of elk, wolf, and caribou abundance, wildlife management, human use, and weather to examine the decline of caribou in Jasper National Park. In particular, we weighed the evidence to discriminate among three general hypotheses of caribou decline in Jasper National Park: climate change, human disturbance, and wildlife management. The hypothesis of caribou decline due to climate change is that warmer temperatures and shallower snow should favour elk (Creel & Creel, 2009, Hebblewhite et al., 2002) to the detriment of caribou via apparent competition. The hypothesis of caribou decline due to human disturbance is that large numbers of people using wilderness areas can displace caribou from important habitat, thus causing population decline. The hypothesis of caribou decline due to wildlife management is that people have influenced the abundance of elk and wolves, which has in turn affected caribou numbers via apparent competition.

Study area

Caribou inhabit two disjunct areas of Jasper National Park (hereafter referred to as Jasper), one in the north and the other in the south (Fig. 1). The northern caribou, the A La Peche herd, have traditionally migrated between the protected mountain environments of Jasper and Willmore Wilderness Park in the summer to the adjacent industrial landscapes of the Alberta foothills in the winter. The management of the A La Peche caribou has been primarily the jurisdiction of the Alberta provincial government, and will not be considered further in this paper. Jasper's southern caribou live largely within the bounds of Jasper, but their range also extends into British Columbia's Mount Robson Provincial Park, and Alberta's White Goat Wilderness Area. We focused our analyses on the caribou of south Jasper.

The Jasper landscape can be classified into montane, subalpine, and alpine ecoregions (Holland *et al.*, 1983). The low elevation montane ecoregion is primarly lodgepole pine (*Pinus contorta*), with some Douglas fir (*Pseudotsuga menziesii*), willow (*Salix* spp.), aspen (*Populus tremuloides*), and riparian white spruce (*Picea glauca*) areas, interspersed with small grasslands. The mid-elevation subalpine ecoregion consists mainly of subalpine fir (*Abies lasiocarpa*) – Engelmann spruce (*Picea engelmanii*) - lodgepole pine forests with limited grasslands. The alpine ecoregion is largely open shrub-forb meadows. Both alpine and subalpine ecoregions can have avalanche terrain, relatively nonvegetated ridgetops, and areas of rock and ice.

In addition to caribou, the ungulate community consists of elk (*Cervus elaphus*), moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*). Wolves (*Canis lupus*) prey on all of these ungulates, but elk abundance has been considered to be a primary driver of wolf density in the Rocky Mountains (Huggard, 1993; Hebblewhite, 2000). Other predators of large mammals in Jasper include cougar (*Felis concolor*), coyote (*Canis latrans*), wolverine (*Gulo gulo*), black bear (*Ursus americanus*) and grizzly bear (*Ursus arctos*).

Because we were interested in predation impacts on caribou populations in south Jasper, our study area encompassed caribou range, plus the ranges of wolf packs that overlapped with caribou based on current habitat use as determined by current VHF and GPS radio-telemetry (Fig. 2).

Methods

Wildlife abundance data

We examined available records of animal abundance from 1811 (the arrival of the first Europeans) to the present. Data on historical wildlife and wildlife management come from the published literature, Parks Canada's unpublished literature, and from our search of the Parks Canada archives in the Town of Jasper's Yellowhead Museum. Recent wildlife data were from Parks Canada's ongoing research and monitoring efforts. Only wildlife abundance within our study area was considered. Weather variables were obtained from Environment Canada.

Caribou abundance has been estimated in several ways over the years. The 1973 estimate was a subjective combination of aerial and ground-based counts (Stelfox, 1974). The estimate from 1988 was an aerial count adjusted for sightability based on expert opinion (Brown *et al.*, 1994). The estimates for 1993, 1998, and 2000 were aerial counts adjusted for sightability using the average sightability from 2003 to 2009. Estimates from 2003 to 2009 were calculated using a joint hypergeometric mark-recapture procedure, based on a sample of radio-collared females (White, 1996; Neufeld & Bradley, 2009). Caribou population estimates for 2006 to 2008 were corroborated using genotyping data and capture-mark-recapture techniques described by Hettinga *et al.* (2011).

We used historical accounts to estimate elk abundance for years when count data were not available. Otherwise, elk estimates were based on counts conducted from roadsides each winter when a large proportion of the total elk population was observable. The number of elk killed by humans (primarily by highway/railway mortality) was obtained from park records. Park records also informed human use data (number of user nights for backcountry camping) and wolf abundance data.

Data quality

Relying on historical data for long-term abundance was challenging, as meth-

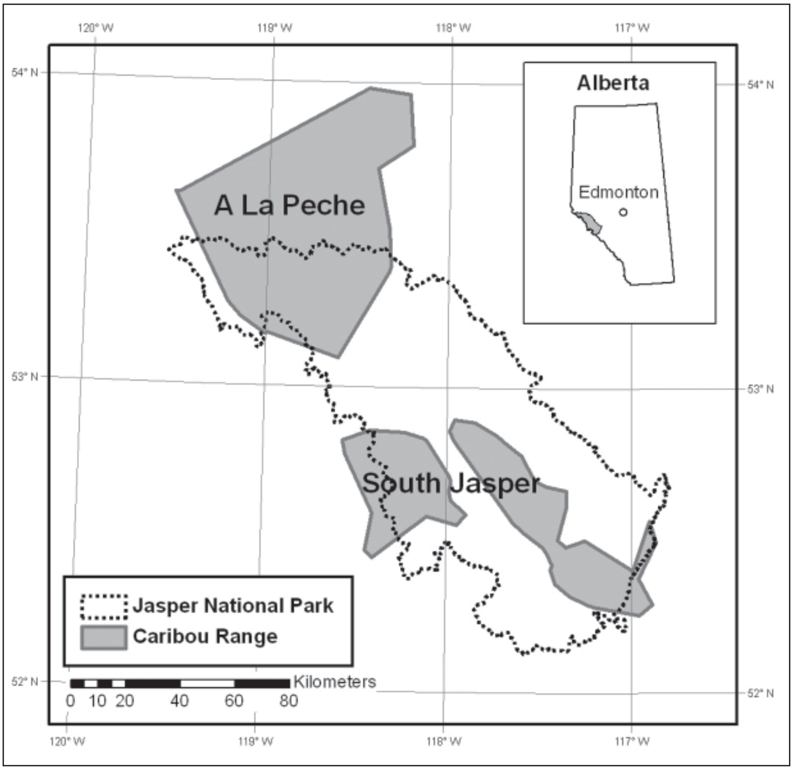

Fig. 1. Caribou ranges in Jasper National Park and surrounding areas.

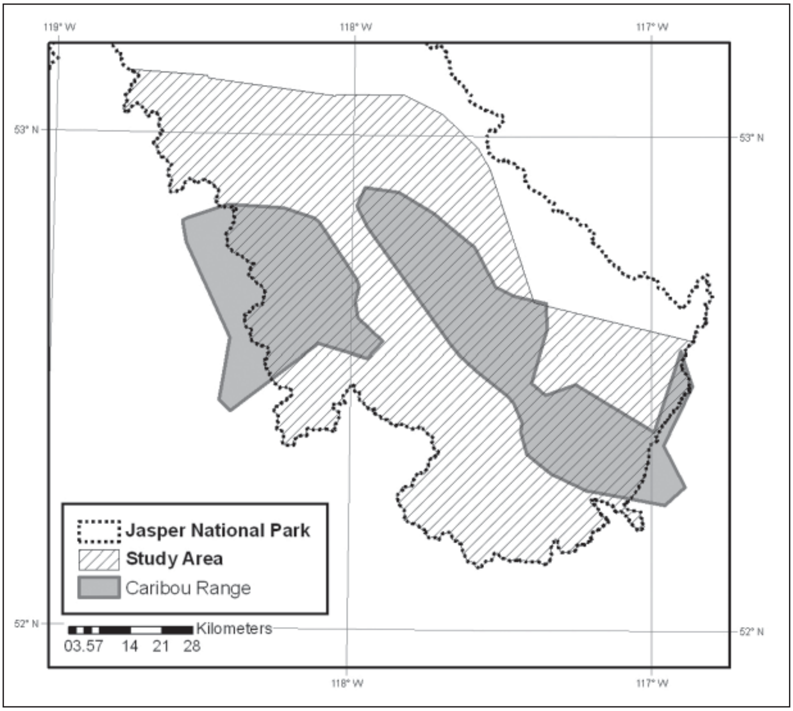

Fig. 2. Caribou and wolf research study area in Jasper National Park as defined by caribou range and associated wolf pack territories.

ods and effort have changed over time. For elk, abundance was mainly derived from expert opinion until 1975, when infrequent aerial counts began. Annual roadside elk counts began in 1997. Historical wolf and caribou data are of lesser quality than historical elk data, because unlike elk, wolves and caribou are difficult to survey without intensive effort.

Despite these shortcomings, major trends in elk abundance can be reliably summarized because elk gather in large groups in open areas, and casual observation can result in the observation of a high proportion of the elk population. For wolves and caribou, year-to-year historical data should be interpreted with caution, but we feel that the general trends are likely representative of changes over time.

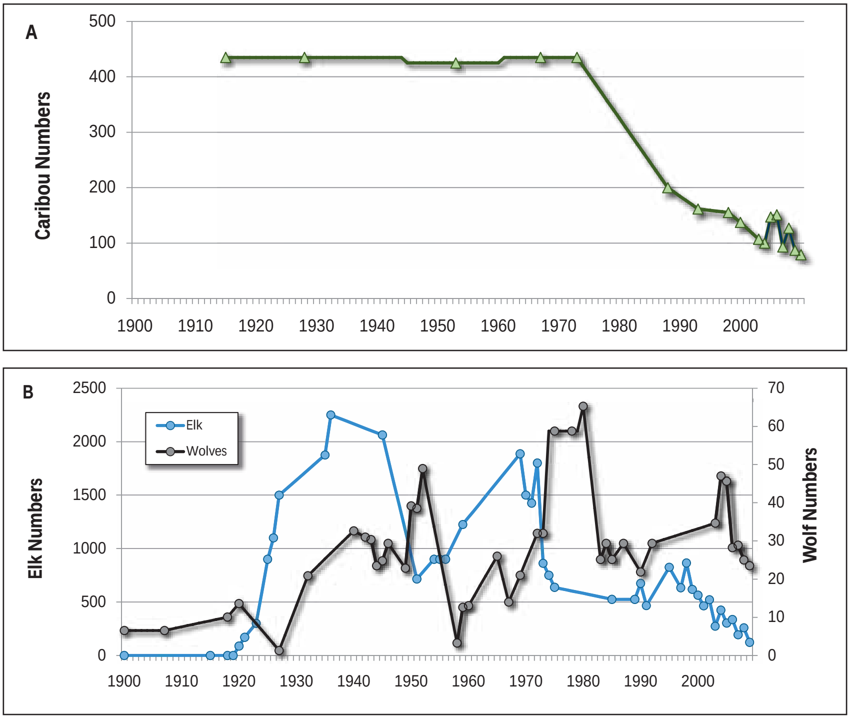

Fig. 3. Trends in approximate abundance of caribou (A), elk (B), and wolves (B), in Jasper National Park from 1900 to 2009. Elk were reintroduced in 1920 while predator control was ongoing (1900-1959). Severe winters affected the elk population in the late 1940s and early 1970s.

Analyses

Because techniques and data collection intervals varied widely throughout the years, we present the data mainly as a description of the wildlife abundance timelines. We also identify some unique turning points in Jasper's wildlife management history that are not amenable to analysis, but offer insight for interpreting trends.

For the long-term time-scale (1900 to 2009), we were not confident in the historical record's capacity to detect annual changes in wildlife abundance and therefore identified two multi-year eras of relatively consistent wildlife trends and management practices. We compared climatic variables between the two eras, using univariate parametric statistical testing (t-tests). Human use data were not available for the early era and therefore were not comparable between the two eras.

For the short-term time scale, from 1973 to 2009, there were more frequent and more objective surveys for all three species (elk, wolf, and caribou), unfortunately, there were still considerable gaps in the data. Moreover, these gaps were not synchronized among the species, so a statistical analysis of the annual changes in all three species in this shorter time-scale was not possible.

Results

Wildlife abundance and wildlife management context

Caribou prior to 1973 were considered relatively abundant in south Jasper - approximately 435 (range 275 to 550; Fig. 3A, (Stelfox, 1974)). The first aerial count of caribou in 1988 was 158, and the authors speculated that there were probably 200 caribou in total (Brown *et al.*, 1994). The 2009 population estimate was 87 caribou (90% confidence limits of 87 to 96).

Seven key events in the elk time series should be noted (Fig. 3B): 1) no or very few elk until the re-introduction of 88 elk in 1920; 2) a population increase to over 2000 elk by 1936; 3) a winter die-off in 1948 and 1949; 4) the subsequent population rebound to approximately pre-1948 numbers by 1969; 5) a second winter die-off in 1972; 6) population stability from 1972 to 1995 (i.e. no population rebound from the winter die-off); and, 7) a linear decrease in elk from 1995 to approximately 200 elk near caribou habitat in 2009 (Lloyd, 1927; Mctaggart-Cowan, 1946; Robinson et al., 2009; Stelfox, 1971a; Stelfox, 1974; Dekker *et al.*, 1995; Parks Canada records). It is worth noting that the number of elk killed by humans probably influenced wolf abundance in Jasper because the practice of disposing of elk carcasses in gravel pits contributed substantial additional food to wolves. Carcass dumping ended in 2006.

As with elk, wolves were rare in the early 1900s (Fig. 3B) (Stelfox, 1971b; Dekker *et al.*, 1995). Wolf control in Jasper, ongoing at the turn of the century, intensified in 1920 in an attempt to aid elk recovery. Following the elk increase, wolves increased from 1930 to 1950, prompting a more aggressive poisoning campaign in 1952 in an attempt to eradicate rabies, and to augment ungulate numbers (this time sheep were the major concern). By 1958 wolves had been reduced to very low numbers before wolf control officially ended in 1959. The end of wolf control marked the beginning of a 20 year increase in wolf numbers. In 1983, wolves experienced a rapid decline attributed, at the time, to the decline of elk. Recovery in wolf numbers occurred between 1990 and 2003, but since 2004, wolves have again declined, this time concurrent with recent elk declines and also with the cessation of leaving road-killed ungulate carcasses in gravel pits for wolf consumption (Mctaggart-Cowan, 1946; Carbyn, 1975; Kaye & Roulet, 1980; Dekker *et al.*, 1995, Parks Canada records).

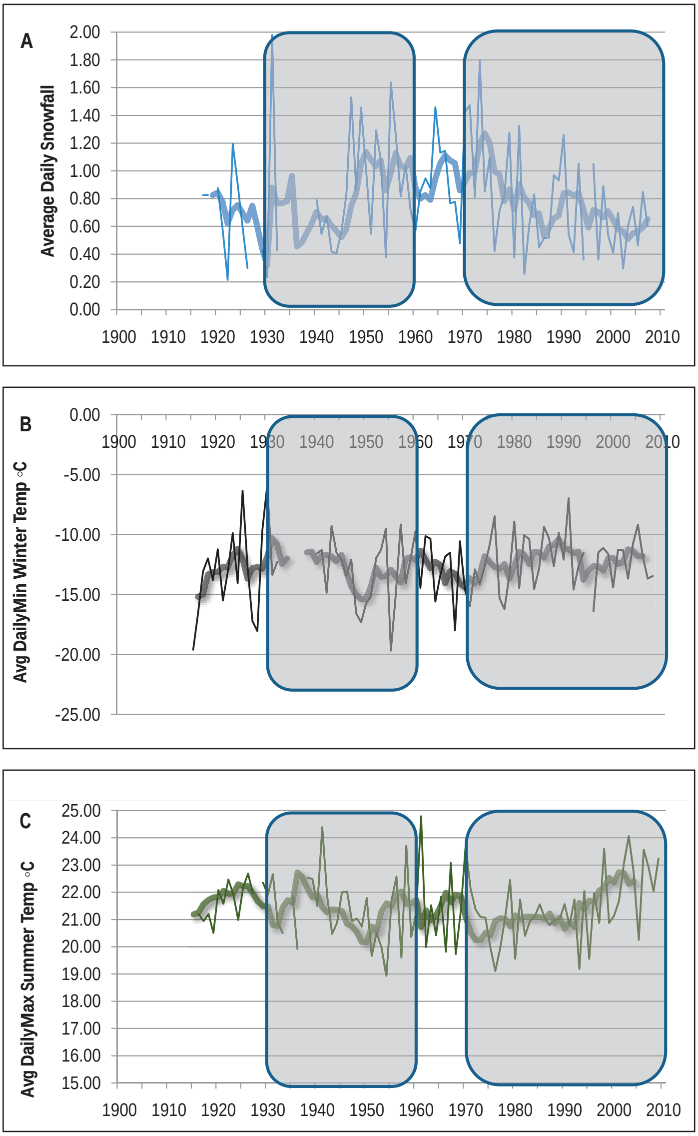

Fig. 4. A) Snowfall, B) average daily minimum winter temperature, and C) average daily maximum summer temperature for Jasper National Park 1900-2009. Grey polygons represent eras within which wildlife abundance trends were consistent. Thick lines depict five year running averages.

The long-term time scale: comparing two eras

We defined two eras of consistent wildlife abundance and management trends based on the historical context: *1930 to 1960:* high elk numbers, high caribou numbers, low wolf numbers, wolf control. *1970 to 2009:* declining elk numbers, declining caribou numbers, higher wolf numbers, no wolf control.

None of the climate variables (average daily winter snowfall (Fig. 4A), average daily minimum winter temperatures (Fig. 4B), and average daily maximum summer temperatures (Fig. 4C)) were significantly different between the two eras (winter temperature $P = 0.6$, winter snowfall $P = 0.6$, summer maximum temperature $P = 0.5$). Multi-year averages can mask trends however, so we also examined weather data within each era. Snowfall tended to increase during the first era (Fig. 4A, P = 0.02), and decrease during the second era (Fig 4A, P < 0.01). Winter minimum temperatures and summer maximum temperatures showed no trends within either era (Fig 4B and 4C, P > 0.05) although later in the second era there is a positive slope for summer maximum temperature.

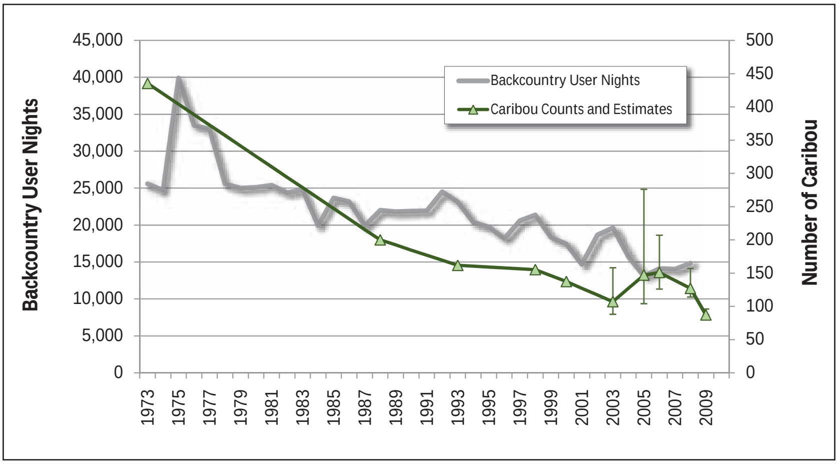

Fig. 5. Number of caribou and number of backcountry user nights in Jasper National Park from 1973-2009.

The Recent Era: 1970 to 2009

Since 1970, elk (Fig. 3), caribou, and human use have all declined (Fig. 5).

While number of elk were declining between 1970 and 2009, for much of that period the number of elk killed (mostly by vehicles), was increasing (Fig. 6). Although the number of elk killed has been stable since 2004, at about 45 animals, carcasses are now disposed in a fenced transfer station away from carnivores.

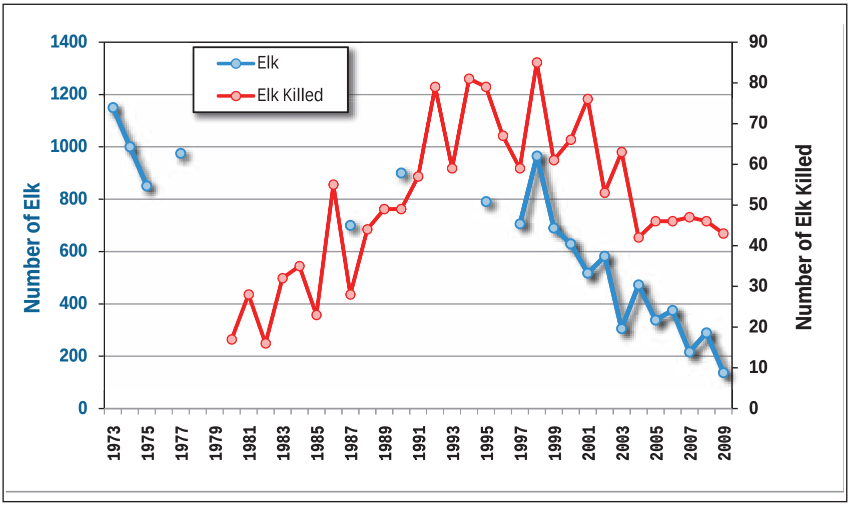

Fig. 6. Number of elk and number of elk killed by humans (vehicles, railway, aggressive elk) in Jasper National Park from 1973 to 2009.

Discussion

We set out to examine three general hypotheses of caribou decline: disturbance by humans, climate, and wildlife management. First, we concluded that the history of human use of Jasper's wilderness areas does not support the idea that disturbance by humans has caused caribou decline. Since 1970, human use of Jasper wilderness areas has declined concurrently with the decline in caribou abundance – i.e. if disturbance were important, we would have expected an increase in human use as caribou declined.

Our conclusion was to some extent unexpected, given that Stelfox (1974) judged human use of Jasper's wilderness areas to be a detriment to caribou in the 1970s, and that a recent behavioural study in Jasper has shown that people can cause a flight response in individual caribou (McKay, 2007). Human use however is currently only a fraction of what it was in the 1970s, so the potential for population level disturbance effects is less. Therefore, while individual caribou may react strongly to encounters with humans, our basic observation of concurrent declines in both human use and caribou leads us to believe that negative consequences to individual caribou have not accumulated into population level effects.

Climate change also did not appear to be solely responsible for the historical decline in caribou abundance. The long-term trend in caribou abundance did not correlate with climate variables. In general, caribou are assumed to use snow to avoid predation (Telfer & Kelsall, 1984; Courbin *et al.*, 2009), and indeed the recent era of caribou decline has also been a time of declining snowfall. However, there have been similar periods of declining snowfall in the past (e.g. 1930 to 1940) that did not result in detectable caribou decline. The difference was that during the early era of milder winters, suppression of predation was occurring through poisoning campaigns. Since excessive predation during shallow snow years will not occur if there are few predators, this interaction between climate and predation is probably important.

Elk cope poorly with deep snow and severe winter weather (Creel & Creel, 2009, Hebblewhite *et al.*, 2002), and in Jasper, severe winter weather did cause two elk population crashes. The crash of the late 1940s occurred during an era of intense predator control, and the elk population subsequently recovered. The crash of the early 1970s however, occurred after predator control had ended and, in the presence of predation, elk populations were not able to fully recover despite declining snowfall since 1973. Thus, for both caribou and elk, we propose that the historical record demonstrates the importance of the interaction between human management practices, predation, and climate.

There has been an intricate connection between elk and wolf populations elsewhere in the Rocky Mountains (Huggard, 1993; Hebblewhite *et al.*, 2002). The trends in Jasper elk and wolf numbers, although imprecisely measured, can at least notionally be attributed to a strong interaction between the two species: at the time of European settlement there were very few elk and few wolves; the re-introduction of elk and concurrent poisoning of wolves resulted in a prolonged period of high elk numbers in an ecosystem; the decline of wolves in the late 1940s occurred after a winter elk die-off; the subsequent rise in elk numbers during the 1960s was mirrored (with a lag) by a rise in wolves; the decline of elk numbers since 1970 has been roughly mirrored (with a lag) by another decline in wolf numbers.

Today, elk abundance is almost an order of magnitude lower than it has been in the past, and it is possible that Jasper is in the process of transitioning away from an elk/wolf driven system. Our current research focus is, in part, addressing questions around predator/prey dynamics in Jasper (Hebblewhite *et al.*, 2010a).

An additional historical management factor is elk highway mortality. The post-1970 data suggest that the number of elk killed by humans (highway and railway deaths) may be as influential as elk abundance alone. The number of elk has declined steadily since 1970, so one might have expected apparent competition to wane, and caribou to increase. The number of elk killed by humans (almost all by vehicles on the highways) however, rose dramatically between 1979 and 1998 (Fig. 6). Prior to 2006, many of these road-killed elk were left in gravel pits for wolves (and other animals) to scavenge, almost certainly contributing to larger pack sizes and subsequent dispersal of young wolves, which could have prevented apparent competition effects on caribou from decreasing. Although it is impossible to be precise, the annual quantity of elk biomass left for wolves would have been almost 10 000 kilograms at its peak in the late 1990s. The origins of elk carcasses being left for wolves was not well recorded, but we found references to the practice as far back as 1980 (Kaye & Roulet, 1980). Since the practise of dumping carcasses was halted, wolf abundance has been halved (Fig. 3b) – we will continue monitoring to see if these lower numbers endure.

What do our results mean for the future of caribou management in Jasper? Parks Canada's first priority is the maintenance or enhancement of ecological integrity as described in the Canada National Parks Act (2000). Maintaining biodiversity is an important component of ecological integrity, and preventing the extirpation of a large mammal is important for preserving biodiversity. Current caribou population trends suggest that they are the large mammal species most likely to disappear from both Jasper and the greater ecosystem. Maintaining ecological processes is another imperative for achieving ecological integrity as identified in the Canada National Parks Act (2000). We believe that Jasper's history has illustrated the negative effect humans have had on predator/prey processes, so in promoting the persistence of caribou, Parks Canada will strive to remove negative or "unnatural" human influences from ecological processes, rather than directly manipulate predator and prey numbers. Excluding elk from the Jasper town site, and restricting unnatural predator access to winter caribou habitat via packed snow trails will be two of our top priorities. We believe that Jasper's history has shown us that predator control promotes hyper-abundance of wolves' primary prey (e.g., Jasper elk in the middle of last century), with disastrous consequences for caribou via apparent competition once predator control ends.

Given Parks Canada's mandate and principles, which human influences are most important to mitigate in order to reverse caribou declines? Our conclusion that climate change is not solely responsible for caribou decline has implications for caribou management. Previous efforts to conserve caribou in Jasper have been criticized because of the belief that climate change would render our efforts fruitless. While we cannot meaningfully reverse climate change directly, Jasper's history suggests that it is the *interaction* of climate and predation that is important. Thus, we can continue to promote caribou recovery by mitigating negative human influences on predation variables. The historical record suggests that past wildlife management practises in Jasper have heavily influenced the relationship between predators and their prey, therefore mitigating human influences and returning the ecosystem to a self regulating condition with minimal human subsidies has a good chance of positively affecting caribou persistence.

We also found no support for the hypothesis that high backcountry human use is directly related to the caribou decline. This is also important, because it allows us to concentrate our efforts on management efforts that have a higher probability of recovering caribou. For example, it is probably more important to devise ways to help caribou avoid unnaturally high predation than it is to attempt to keep hikers and campers away from caribou.

Even with very long-term, extremely detailed predator/prey data, explaining past population trends has been far easier that accurately foretelling the future (Vucetich, 2010). Our examination of historical data of limited quality is therefore unlikely to give us a precise prescription for restoring caribou in Jasper National Park. We believe however, that Jasper's history helps us to better understand the origins of our current situation, and provides broad direction for research and management that will promote caribou persistence.

Acknowledgements

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Methods

Population surveys, home range sizes, remote sensing

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A guide to developing resource selection functions from telemetry data using generalized estimating equations and generalized linear mixed models

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Abstract: Resource selection functions (RSF) are often developed using satellite (ARGOS) or Global Positioning System (GPS) telemetry datasets, which provide a large amount of highly correlated data. We discuss and compare the use of generalized linear mixed-effects models (GLMM) and generalized estimating equations (GEE) for using this type of data to develop RSFs. GLMMs directly model differences among caribou, while GEEs depend on an adjustment of the standard error to compensate for correlation of data points within individuals. Empirical standard errors, rather than model-based standard errors, must be used with either GLMMs or GEEs when developing RSFs. There are several important differences between these approaches; in particular, GLMMs are best for producing parameter estimates that predict how management might influence individuals, while GEEs are best for predicting how management might influence populations. As the interpretation, value, and statistical significance of both types of parameter estimates differ, it is important that users select the appropriate analytical method. We also outline the use of *k*-fold cross validation to assess fit of these models. Both GLMMs and GEEs hold promise for developing RSFs as long as they are used appropriately.

Key words: autocorrelation; conditional models; empirical standard errors; GEE; generalized estimating equations; generalized linear mixed-effects models; GLMM; *k*-fold cross validation; marginal models.

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Introduction and rationale

This document provides a practical guide for developing resource selection functions from telemetry data, using generalized estimating equations and generalized linear mixed models, and outlines how to validate these models using *k*-fold cross validation. For more detailed explanations and to better understand the theory and mathematics behind these methods, readers should refer to Koper & Manseau (2009), in which we cover most of the topics within the present manuscript in more detail; Gillies *et al.* (2006) and Bolker *et al.* (2009) regarding GLMMs; and Boyce *et al.* (2002) regarding *k*-fold cross validation, as well as numerous excellent sources and textbooks referred to in those works. Fieberg *et al.* (2010) provides a useful and detailed comparison among various approaches to analyzing habitat selection, including GEEs and GLMMs. We also note that this paper discusses the development of resource selection functions (RSF), which estimate the *relative* probability of use of different habitat types (suitable vegetation), rather than resource selection probability functions (RSPF), which estimate the *actual* probability of a habitat being used; for more information on the additional assumptions and issues associated with RSPFs, see Lele & Keim (2006).

To facilitate the use of this paper as a guide, we outline a number of components important to RSF development below, and in most cases divide each section into *What*, *Why* and *How* subsections. Statistical codes are provided to conduct GEEs and GLMMs in SAS and to conduct GEEs in R. GLMM code is not provided for R because at the moment, there are no GLMM libraries that allow the user to request empirical standard errors.

Resource selection functions

What are resource selection functions?

Resource selection functions are models used to compare the amount of used habitat with the amount of available habitat (Manly *et al.*, 2002). If a habitat type, such as jack pine stand, is used by animals more than expected relative to the proportion of that habitat across the landscape, the habitat is assumed to be selected; if it is used less often than expected relative to the proportion of that habitat across the landscape, the habitat type is assumed to be avoided. For example, if 10% of the landscape is made up of jack pine stands, but the animals spend 25% in jack pine stands, then the assumption is that jack pine stands are selected.

Why are resource selection functions important?

Resource selection functions are used to quantify the relative importance of different vegetation or habitat types, or different components of the landscape, given the availability of those habitat types on the landscape. This helps define the realized niche of caribou or the species of interest.

How are resource selection functions developed?

When using telemetry data, there are different ways to estimate the resource use including a determination of the resource type associated with each telemetry point, the amount of different resources within a buffer around each telemetry point, the distance to different resource types from each point or the spatial characteristics of resource patches associated with each point. To quantify this, animal locations are imported from the satellite (ARGOS) or GPS telemetry data into a geographic information system (GIS) that also includes a land cover layer and then, the attributes are derived for each landscape parameters of interest and for each location point. To quantify availability, points are randomly generated within the individual's or herd's home range or within a certain distance of the telemetry points, and similarly the attributes are derived for the landscape parameters of interest. The total number of randomly generated points varies with each study; usually, the same number of telemetry points and random points are used, or the number of random points is a multiple (usually between 2 and 10) of the number of telemetry points.

The telemetry points from animal locations ("used" locations) are then compared with these randomly located points ("available" locations), to determine whether there is more or less use of each habitat type than expected given how much of each habitat type is available (Manly *et al.*, 2002). Selection can only be evaluated if availability can also be quantified. For example, if 60% of the caribou locations are in treed muskeg, but that habitat type makes up 75% of the landscape (or 75% of the random points), the results would indicate an avoidance of treed muskeg, even though more than half of the locations are in treed muskeg, because the proportion of telemetry points in treed muskeg is less than the proportion of random points in that habitat on the landscape.

Autocorrelation in telemetry data

What is autocorrelation in telemetry data?

Locations from satellite or GPS collars have provided us with a large amount of data which can be used to infer how animals use the landscape. In particular, once animals are collared, thousands or tens of thousands of locations for that animal are recorded, and by overlaying those locations on a land cover map using a GIS, the way that animal uses its landscape can be determined to a high degree of precision and accuracy.

These data points are, however, not independent of one another. There are two important sources of correlation in telemetry data. The first is that there are many data points from just a few caribou. Data points from a single individual are not independent of one another, and as such do not each provide us with a unique piece of information. For a comprehensive review of this issue, see Gillies *et al.* (2006).

The second source of correlation arises from the fact that animal locations are recorded sequentially. Locations can be recorded as often as every half hour, or less than once a day, as desired. Determining the optimal length of time between locations can be an important question, as more frequent locations result in shorter battery life. If locations are recorded too frequently, each location provides little new information about resource use; presumably, the current location of the animal is highly influenced by the previous location of the animal, or even a number of previous locations. Such data are serially autocorrelated. On the other hand, if locations are too infrequent, there may be insufficient data to evaluate habitat use relative to habitat availability, particularly when estimating the use of uncommon habitat types (see discussion in Fortin *et al.*, 2005).

While locations taken few minutes apart are probably highly correlated, and locations taken 5 days apart are much less correlated, the interval at which points become uncorrelated is not known. Indeed, Cushman *et al.* (2005) argued that locations may be correlated at intervals of a month apart. As such, there is no interval between data locations at which telemetry locations are known to be independent of one another.

Why care about serial autocorrelation in telemetry data?
Autocorrelation between data points might be of interest to the researcher (Boyce *et al.*, 2010). For example, this might help the researcher understand how likely an animal is to stay in a particular habitat type if it is already there. However, in some cases this correlation among data points is not of interest and becomes a statistical nuisance. While generally serial autocorrelation has relatively little effect on the parameter estimates that are derived from statistical models, they can affect any associated statistical comparisons, or any analysis that uses standard errors or confidence intervals. For example, if this correlation is ignored, it might be possible to estimate how much more or less animals use different habitat types in relation to what is available to them, but it would not be possible to determine whether this is a *statistically significant* habitat selection or avoidance.

This is because a key component of calculating statistical significance is knowing how much information is available to go towards comparisons of resource use. More information provides the user with more confidence that estimates of habitat selection or avoidance are trustworthy. However, when there is a lot of information from just a few animals, it can be hard to quantify how much information there really is. If the amount of information available is overestimated, the likelihood of making Type I errors (assuming that there is a statistically significant effect of a variable when in fact there is no effect; Clifford *et al.*, 1989) is increased. To avoid this, we must take correlation among data points within animals into account.

How can serial autocorrelation in telemetry data be controlled for?
Gillies *et al.* (2006) recommended that random variables (also referred to as random effects in the literature) be included in RSFs to account for the fact that data points come from different animals, and that data points from individual animals are not independent from each other. In these models, a variable that represents the individual animal becomes the random variable (see section on *how GLMM work* for more information on random variables). One example of models that include random effects is generalized linear mixed models (GLMM). The "generalized" term refers to the fact that the error term associated with response variables need not follow a normal distribution; as resource selection functions compare used habitats (represented by "1" in the response variable) with available habitats (represented by "0" in the response variable), the response variables follow a binary (binomial) rather than a normal distribution. The "mixed" term in GLMM refers to the fact that both random effects and fixed variables (independent variables such as habitat type) are included in the model.

We believe that the recommendations by Gillies *et al.* (2006) initiated important progress in the trend towards using advanced statistical techniques for developing resource selection functions. However, they made an error by implicitly assuming that individual data points within animals were independent from one another. This is not correct, and GLMM are not robust to deviations from this assumption (Overall & Tonidandel, 2004, and see empirical analysis in Koper & Manseau, 2009); this means that statistical inferences made from models that ignore correlations among data points are likely to be incorrect, leading to increased rates of Type I errors. However, the correlation among telemetry points can be compensated by using empirical, rather than model-based standard errors (e.g., Hardin & Hilbe, 2003).

Empirical standard errors

What are empirical standard errors?
Empirical standard errors are also sometimes called robust standard errors, as they are robust to the lack of independence among data points (i.e., lack of independence among data points does not lead to incorrect empirical standard errors), or Huber-White sandwich standard errors (as applied by Gillies *et al.* 2006). The empirical standard error is generally larger than the model-based standard error, and the closer the modeled correlation structure to the true correlation structure, the closer together the model-based and empirical standard errors will be (Bishop *et al.*, 2000). As such, the correlation should be modeled to reduce the size of standard errors and therefore, increase the power of the analyses. However, this is not possible when telemetry data are compared with random data points. The empirical standard errors are therefore required to correct for the correlation among data points.

Why should empirical standard errors be used for RSFs developed from telemetry data?
It is critical to use empirical standard errors if these are appropriate and necessary. There is often a very large difference between empirical and model-based standard errors, and this directly leads to differences in statistical inference. We found that model-based standard errors could be 1/10 the size of empiri-

cal standard errors (Koper & Manseau, 2009); not surprisingly, this has a dramatic effect on the apparent significance of independent variables. Empirical standard errors must be used to evaluate statistical significance of habitat selection behaviours when resource selection functions are developed using telemetry data.

How are empirical standard errors included in RSFs?
The variance function differs between empirical and model-based standard errors. This is accounted for by the selected statistical computer program when empirical standard errors are selected by the user.

In this paper, we cover two statistical approaches that can both be used with empirical standard errors: generalized linear mixed models (GLMM), and generalized linear models with generalized estimating equations (GEE). There are important practical and conceptual differences between these approaches that must be considered in determining which approach is appropriate. Below, we introduce GLMM and GEE, and follow with a comparison between the two. We then address validation of each type of model using *k*-fold cross validation (Boyce *et al.*, 2002).

Generalized linear mixed-effects models (GLMM)

What are GLMM?
GLMM are sometimes also called generalized linear mixed models (GLME) or hierarchical models, and are referred to as longitudinal, clustered, latent-variable, or multilevel models. They are parametric, and are estimated using maximum likelihood theory or associated methods (see Quinn & Keough, 2002 for a clear explanation of maximum likelihood estimation). Mixed models include fixed and random independent variables. Fixed variables are differentiated from random variables in two ways: all levels of interest for the factor are included in the design, and inference is restricted to these levels. Random variables, in contrast, include randomly selected levels, and allow one to generalize inference over all possible levels of the random variable.

Why are GLMM useful?
Usually a random sample of caribou is monitored to allow the manager to infer habitat selection of all (or at least, other) caribou in a defined population. Differences in habitat selection among individual caribou should therefore be modeled using a random variable, because not all levels of interest are included in the design (i.e., all caribou in the population of interest), and the inference should be relevant to all possible levels of the random variable (i.e., all caribou in the population of interest).

Another benefit of mixed models is that they can be used to analyze hierarchical study designs. This means that one can use a single model to evaluate effects of local-scale variables nested within broad-scale variables. For example, there might be interest in evaluating effects of vegetation structure (e.g., canopy cover), which will be different at every location recorded, nested within caribou-scale variables (e.g., animal age), which will be the same for every data point within an animal. If the hierarchical nature of this design is ignored, there may be two unintended consequences: (1) if the caribou is considered the unit of replication, all local scale variables would have to be collapsed into a single value per caribou, thus losing an enormous amount of data and, therefore, statistical power; and (2) if the local data points are considered as the unit of replication, the degrees of freedom would be artificially increased at the caribou scale, introducing pseudoreplication into the design, and increasing the likelihood of making Type I errors. Mixed models allow us to analyze variables at both of these scales by using the random effect to indicate that local-scale variables are not completely independent of one another, because they are clustered within the broad-scale variables.

How do GLMM work?
Differences among caribou, represented by the random variable, are modeled by allowing the *intercept* of the relationship between each independent fixed variable and the dependent variable to be different for each caribou. It is, in fact, possible to assume that both the intercept and the slopes of the relationships vary among caribou (e.g., see Gillies *et al.*, 2006), but this is more complex than allowing only the intercept to vary among caribou (and is usually unnecessary and results in an overparameterized model; L. Lix, University of Saskatchewan, pers. comm.) and will not be discussed here. Allowing the intercept to vary among caribou recognizes that animals differ from one another, but means that habitat or landscape structures are assumed to have a similar effect on different animals.

While mixed models are an important tool for dealing with clustered sampling designs, they are not a panacea. The addition of a random effect tends to increase standard errors of all the fixed variables in the model (Hox, 2002, Quinn & Keough, 2002). The consequence of including a random effect is a reduction of analytical power, but the inference is then correct.

Generalized estimating equations (GEE)

What are GEEs?

Generalized estimating equations are a semi-parametric alternative to GLMMs. They are semi-parametric because the parameter estimates are estimated parametrically and the variances are estimated non-parametrically.

Usually, part of the process of defining the variance structure is to define the correlation structure of the data points within individual caribou; for example, data collected sequentially over time could be modeled differently from data that were clustered spatially, say across a number of different isolated islands. Correlation structures can include, among others, an independent correlation structure (in SAS, corr=ind), which assumes no correlation among data points; a compound symmetric or exchangeable correlation structure (in SAS, corr=CS), which assumes that data from a single animal is correlated within that animal, but all data points within animals are equally correlated; and an autoregressive correlation structure (in SAS, corr=AR(1)), which assumes that data points within animals that are closer together in time are more correlated than data points that are farther away. We remind the reader that the latter structure is a reasonable assumption for the used data points, but not for the random points (Koper & Manseau, 2009).

Why are GEEs useful?

When sample sizes (number of caribou) are sufficiently high, GEEs with empirical standard errors have the enticing property of producing both parameter estimates and standard errors that are trustworthy even when the correct correlation structure cannot be known (Fitzmaurice *et al.*, 2004). This is important when developing RSFs, because the correlation structure between telemetry points and random points cannot be modeled.

How do GEEs work?

GEEs deal with the correlation caused by collecting numerous samples from each individual (e.g., numerous locations from one caribou) by adjusting the standard error to compensate for the lack of independence among samples. This involves using empirical standard errors, rather than model-based standard errors, as discussed above (Hardin & Hilbe, 2003).

Because tests are more powerful if the covariance structure can be modeled, users should still compare model fit between models with different covariance structures, and use the model that fits the data the best. Covariance structures can be compared by taking the ratio of the empirical standard error to the model-based standard error (SE_E/SE_M), and the model with the ratio that is closest to 1 is the model that fits the data the best (Bishop *et al.*, 2000). Although the non-parametric alternative to AIC, the quasi-likelihood under the independence model information criterion, QIC (Pan, 2001), is also theoretically capable of this comparison, our research has demonstrated that this criterion is biased (Barnett *et al.*, 2010). Therefore, we recommend that QIC should not be used for comparisons among models until it is redeveloped, a process that is in progress (J. Hilbe, 2010, pers. comm.). Because the correlation structure among the used data points differs from the correlation structure among random points, this correlation structure cannot be modeled correctly, and there will be some dependence on the fact that empirical standard errors are robust to misspecification of this structure.

Choosing between GLMM and GEE for developing RSFs

What are the main differences between GLMM and GEE?

There are a number of practical and conceptual differences between GLMM and GEE, and these must be considered before determining which method is appropriate for analyzing any data set. These differences are summarized in Table 1, and are discussed in more detail below.

Parametric and semi-parametric modelling

Because GLMMs are parametric, while GEEs are semi-parametric, the analytical process for generating GLMM is more complex, takes longer, and is more likely to fail to converge (Agresti, 2002). Nonetheless, in our experience GLMM can generally be used successfully for developing resource selection functions using telemetry data.

Hierarchical versus non-hierarchical models

GLMMs model differences among animals directly, and this allows for a hierarchical data analysis that directly models effects of independent variables at different spatial or temporal scales. This hierarchical analysis is not possible with GEEs. GEEs do not directly model differences among animals, but instead account for the lack of independence among samples within animals by adjusting the standard error via an altered variance estimate.

Marginal versus conditional parameter estimates

When response variables are binary (or otherwise non-normal), there is an important difference in the meaning of the parameter estimates gener-

Table 1. Comparison between the use of generalized estimating equations (GEEs) and generalized linear mixed models (GLMMs) for developing resource selection functions using telemetry data.

	GEE	GLMM
Analysis	Semi-parametric	Parametric
Method of dealing with correlation	Adjusts standard error to account for correlation of data points within groups (animals)	Models differences among animals directly, usually by allowing intercept to vary among animals
Complexity	Simpler	More complex
Convergence	More likely	Slightly less likely
Robustness	Parameter estimates and standard errors robust to misspecification of the correlation structure when using empirical standard errors	Standard errors robust to misspecification of the correlation structure when using empirical standard errors
Interpretation	Marginal	Conditional
Information theory	Use with QIC is not recommended	Can use with AIC
Treatment of hierarchical data	All nested levels treated equally – better if clustering is a nuisance, not the focus of the study	Explicitly models hierarchical or nested sampling design
Sensitivity to sample sizes	More robust to differences in sample sizes within groups	Sample sizes within groups should be approximately equal

ated between GEEs and GLMMs (Fitzmaurice *et al.*, 2004: 364), and this can result in large differences in parameter estimates and standard errors between the two approaches (Fitzmaurice *et al.*, 2004; Koper & Manseau, 2009). This is primarily because GLMMs produce conditional (subject-specific) parameter estimates (see Agresti, 2002 for reasons why marginal estimates derived from GLMMs should be avoided), while GEEs produce marginal (population-specific) parameter estimates. Conditional parameter estimates model how a typical *individual* might respond to independent variables. Marginal parameter estimates evaluate effects of independent variables on the *population*.

Two examples may help clarify the difference in interpreting marginal and conditional parameter estimates. First, we will consider an example derived from epidemiology. A marginal question might be, “what is the effect of this drug on cancer rates across a population?” This type of study would be designed to compare how many people got cancer in populations that received the drug, and how many people got cancer in populations that did not receive the drug. This is a population-specific approach because it addresses how the independent variable, use of a drug, affects a whole population.

An equivalent conditional question would be, “what is the likelihood of a typical patient recovering if we give them this drug?” This type of study would be designed to compare whether people who received the drug were more likely to get cancer than people who did not receive the drug. This is a subject-specific approach because it addresses how the independent variable, use of a drug, affects the likelihood of a typical individual getting cancer.

The difference between these two approaches may seem like semantics until one reflects on the position of a patient. Most individuals will care much more about what the effect of the drug might have on their own probability of getting cancer, compared with the effect of the drug on cancer rates across a population. This results in a very real difference in the interpretation of marginal and conditional population estimates.

The difference is also important from a wildlife management perspective. An example of a marginal question might be, “what is the difference in habitat use of caribou between landscapes with high or low jack pine cover?” This type of study might be designed to compare whether populations of caribou that lived in landscapes with high jack pine cover demonstrated different habitat selection from populations of caribou that lived in landscapes with low jack pine cover. This is a marginal or population-specific approach because it addresses how the independent variable, jack pine cover, affects habitat selection across a population.

An equivalent conditional question would be, "how would a typical caribou change its habitat use if its environment changed from having high jack pine cover to relatively little jack pine cover?" This type of study might be designed to compare whether individuals changed their habitat selection if their landscape changed from one of high jack pine cover to low jack pine cover through forestry activities. This is a conditional or subject-specific approach because it addresses how the independent variable, jack pine cover, affects habitat selection of a typical individual.

Again, these questions are different and address different management issues. The marginal approach might be more appropriate for trying to understand effects of habitat on the population of interest; for example, for the development of population recovery plans. In such cases, the interest is on how an entire population will respond to management. The conditional approach might be more appropriate if there is interest in how future changes in an environment might affect a typical caribou; for example, if evaluating the potential impact of future forestry activities on individuals of a population. Regardless, we emphasize that this decision is important because it will change the interpretation of the parameter estimates, will change the actual parameter estimates, and will change their apparent significance. For further discussion about differences between marginal and conditional parameter estimates, and a useful graphical explanation, see Fitzmaurice *et al.* (2004).

How are GEE and GLMM run on statistics programs?
An example of code that can be used for conducting a GLMM using Proc GLIMMIX in SAS is given in Appendix I. An example of code that can be used for conducting a GEE using Proc GENMOD in SAS is given in Appendix II. An example of code that can be used for conducting a GEE using the library geepack in R is given in Appendix III. Koper & Manseau (2009) provides a case study using GLMM and GEE on woodland caribou GPS relocation data.

Model validation

What is model validation?
Model validation allows us to determine how well a dataset, which is collected from a sample of the population of interest, predicts habitat selection by the population from which the sample is drawn. A common approach for validating resource selection functions is to use *k*-fold cross validation (Boyce *et al.*, 2002). An important benefit of this approach is that it may be used with any resource selection function, regardless of the statistical approach used to develop that function. Therefore, it can be applied to models developed using both GLMMs and GEEs.

Why is model validation important?
It allows us to determine the trustworthiness of models.

How are models validated using k*-fold cross validation?*
k-fold cross validation starts by separating the data set into bins (a number of different groups, say k = 10 for this example). A model is developed using all of the data except data from a single bin. Then the fit of the data from the withheld bin is evaluated to the model developed from the other data. This comparison produces a correlation coefficient, r.

This process is repeated, withholding data from one bin at a time, until each bin has been withheld once. This produces k correlation coefficients which are then averaged. The idea behind this approach is that it gives us the opportunity to evaluate the fit of each model using data that are independent of the data used to develop the model.

How are bins selected for the k*-fold cross validation?*
There are several ways in which data can be separated into bins for these comparisons, each of which produces different results. With marginal population estimates, the interest is in predicting habitat selection of other animals in the population, using data from just a few individuals. Therefore, to evaluate predictive capacity of marginal models, models should be developed by withholding all of the data from one or two individuals at a time, and then evaluating how the models developed using the remaining animals to predict habitat selection by those animals (Koper & Manseau, 2009).

At this point, however, we diverge slightly from the recommendations we provided in Koper & Manseau (2009). Previously, we argued that for conditional models, we should withhold a portion of the data from each animal, develop models using all of the remaining data, and then test model fit using the withheld data (Koper & Manseau, 2009). This is still appropriate if the interest is in predicting habitat selection by the specific individuals surveyed, for example, if managers are interested in predicting effects of future management on these animals. However, conditional models can also be used to predict habitat selection of a *typical* animal; in that case, the interest is still in generalizing results to other animals in the population of interest. We note that this is not the same as predicting the effects of habitat on a population overall, but instead still focuses on the habitat selection of individuals; however, that might include the habitat selection of individuals from outside of the study sample. If that is the purpose of the conditional model, then we recommend that the user should follow the process recommended for marginal models; bins should be developed by withholding all the data from one or two animals, and then evaluating how well the models predict the habitat selection of those animals.

Like any statistical model, *k*-fold cross validation has some drawbacks. It is often misused, most commonly by withholding data from each individual in the data set, instead of withholding all the data from certain individuals. Further, the comparison between model predictions and the binned data gives only a coarse estimate of model fit. Apparent fit can change with number of bins, which is determined arbitrarily. Finally, there are no guidelines to indicate what threshold of *r* represents a "good" fit of the model (Pearce & Boyce, 2006). While *k*-fold cross validation remains an important tool in model validation, improvements are likely to continue with time.

Summary: using GLMMs and GEEs to develop RSFs using telemetry data

Both generalized estimating equations and generalized linear mixed models can be used to develop resource selection functions that are robust to the lack of independence among numerous locations collected from individual animals, if they are used in conjunction with empirical standard errors. The decision of which approach to apply should depend on whether a marginal or conditional approach should be taken, which in turn depends on the research or management goals. Following the development of the RSF, *k*-fold cross validation can be useful for model validation; usually this should be conducted by withholding all data collected from individual animals, developing RSFs with the remaining animals, and then comparing these models against the data from the withheld animals.

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Appendices

Appendix I

SAS script for generalized linear mixed-effects model, annotated. The SAS script uses the procedure, “GLIMMIX”.

```
proc sort data = YOURNAME;
by GROUPINGVARIABLE;
run;

* It is necessary for mixed model data to be ordered first by the grouping variable. As such, it is good practices to include a proc sort script prior to any GLMM, to be sure that data are sorted by group prior to the analysis. For RSFs, grouping variable would usually be caribou ID;

TITLE1 ‘GLIMMIX model’;
proc glimmix data = YOURNAME empirical;

* This ensures that the standard errors provided are empirical standard errors;

class GROUPINGVARIABLE INDEPENDENT1 INDEPENDENT2 INDEPENDENT3;

*Above includes all categorical variables;

model RESPONSE = INDEPENDENT1 INDEPENDENT2 INDEPENDENT3 /solution ddfm = betwithin dist = binomial link = logit CL;

* RESPONSE is the name of the column with the response variables (1s and 0s), other variables are the independent variables of interest. ddfm = changes the way that degrees of freedom are calculated. Betwithin stands for Between – Within, the most intuitive method of calculating standard errors. An alternative sometimes preferred by statisticians is Satterthwaite, ddfm = SATTERTH.
random intercept /subject = GROUPINGVARIABLE TYPE = vc;
nloptions tech = nrridg;

*uses newton-raphson with ridging optimization technique, previous line may not be necessary for many data sets;
Title ‘Glimmix model’;
output out = Glimmixconditional pred = p Pearson = PEARSRESID UCL = UPPER LCL = LOWER;

*creates an output file with residuals, which can be analyzed in SAS or exported to Excel for further examination;
Run;
```

SAS model for generalized linear mixed-effects model, without annotation

```
proc sort data = YOURNAME;
by GROUPINGVARIABLE;
run;

TITLE1 ‘GLIMMIX model’;
proc glimmix data = YOURNAME empirical;
class GROUPINGVARIABLE INDEPENDENT1 INDEPENDENT2 INDEPENDENT3;
model RESPONSE = INDEPENDENT1 INDEPENDENT2 INDEPENDENT3 /solution ddfm = betwithin dist = binomial link = logit CL;
random intercept /subject = GROUPINGVARIABLE TYPE = vc;
Title ‘Glimmix model’;
output out = Glimmixconditional pred = p Pearson = PEARSRESID UCL = UPPER LCL = LOWER;
Run;
```

Appendix II

SAS script for developing generalized linear model with generalized estimating equation, annotated. The SAS code uses the procedure, "GENMOD"

```
proc sort data = YOURNAME;

by GROUPINGVARIABLE;
run;

* It is necessary for mixed model data to be ordered first by the grouping variable. As such, it is good practices to include a proc sort script prior to any GLMM, to be sure that data are sorted by group prior to the analysis. For RSFs, grouping variable would usually be caribou ID;

TITLE1 'GEE model';
proc genmod data = YOURNAME descending;

*descending command ensures that used habitat is compared with available habitat, rather than the reverse. By including "descending", this ensures that positive parameter estimates indicate that habitat is selected, while negative parameter estimates indicate that habitat is avoided;
class GROUPINGVARIABLE INDEPENDENT1 INDEPENDENT2 INDEPENDENT3;
*Above includes all categorical variables;

model RESPONSE = INDEPENDENT1 INDEPENDENT2 INDEPENDENT3 / dist = binomial corrb;

* RESPONSE is the name of the column with the response variables (1s and 0s), other variables are the independent variables of interest;
repeated subject = GROUPINGVARIABLE / corr = CS modelse;

*corr = indicates the correlation structured desired (Independent = IND, Compound Symmetric = CS, Autoregressive = AR(1). Model SE will produce both model and empirical standard errors, so that the ratio of SE_E to SE_M can be compared to evaluate model fit;
output out = RESIDS predicted = inverselogit reschi = pearsresid stdreschi = stpearsresid STDXBETA = stdxbeta xbeta = logit;
Run;
```

SAS script for developing generalized linear model with generalized estimating equation, without annotation

```
proc sort data = YOURNAME;
by GROUPINGVARIABLE;
run;

TITLE1 'GEE model';
proc genmod data = YOURNAME descending;
class GROUPINGVARIABLE INDEPENDENT1 INDEPENDENT2 INDEPENDENT3;
model RESPONSE = INDEPENDENT1 INDEPENDENT2 INDEPENDENT3 INDEPENDENT4 / dist = binomial corrb; [  ]
repeated subject = GROUPINGVARIABLE / corr = CS modelse; [...]
output out = RESIDS predicted = inverselogit reschi = pearsresid stdreschi = stpearsresid STDXBETA = stdxbeta xbeta = logit; [...]
Run;
```

Appendix III

R script for developing generalized linear model with generalized estimating equation, annotated. The R script uses the library "geepack" (R code from Dobson & Barnett 2008).

```
>geeind<-geeglm (RESPONSE ~ INDEPENDENT1 INDEPENDENT2 INDEPENDENT3,

# RESPONSE is the name of the column with the response variables (1s and 0s), other variables are the independent variables of interest;

family = binomial, data = YOURNAME, id = GROUPINGVARIABLE, wave = time, corst ="independence")

#corst = indicates the correlation structured desired (Independent = independence, Compound Symmetric = exchangeable, Autoregressive = AR1)
```

R script for developing generalized linear model with generalized estimating equation, withouth annotation.

```
>geeind<-geeglm (RESPONSE ~ INDEPENDENT1 INDEPENDENT2 INDEPENDENT3, family = binomial,

data = YOURNAME, id = GROUPINGVARIABLE, wave = time, corst ="independence")
```

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Comparative woodland caribou population surveys in Slate Islands Provincial Park, Ontario

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Abstract: We evaluated three methods of estimating population size of woodland caribou (boreal ecotype) on the Slate Islands in northern Ontario. Located on the north shore of Lake Superior, the Slate Islands provide a protected and closed population with very limited predator influence that is ideal for a comparison of survey methods. Our objective was to determine the costs and benefits of three population estimation techniques: (1) forward looking infrared (FLIR) technology to count the number of caribou on regular-spaced transects flown by fixed-wing aircraft; (2) observers to count the number of caribou seen or heard while walking random transects in the spring; and, (3) mark-recapture sampling of caribou pellets using DNA analysis. FLIR and the genetics 3-window approach gave much tighter confidence intervals but similar population estimates were found from all three techniques based on their overlapping confidence intervals. There are various costs and benefits to each technique that are discussed further. Understanding the costs and benefits of different population estimation techniques is necessary to develop cost-effective programs for inventorying and monitoring this threatened species not only on the Slate Islands but for other populations as well.

Key words: forest-dwelling woodland caribou; population size; genetic profiling; forward looking infrared; FLIR; mark-recapture; transects; protected areas; *Rangifer tarandus caribou*; Slate Islands Provincial Park.

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Introduction

The forest-dwelling ecotype of woodland caribou (*Rangifer tarandus caribou*) is listed as a threatened species in Canada. Population size estimates are a basic parameter used to assess and monitor a variety of caribou related programmes (e.g., evaluate the status of woodland caribou, track temporal population changes, assess the effectiveness of various management actions to maintain and/or restore populations). However, accurate and precise population estimates have been notoriously difficult for woodland caribou (Thomas, 1998; Courtois *et al.*, 2003) due to very low densities and small groups dispersed over large areas.

A variety of survey methods are available to estimate population size and trend data for ungulates (Leopold, 1933; Caughley, 1977; Davis & Winstead, 1980; Seber, 1982; Sinclair & Caughley, 1994) but there are a number of problems with their application (Caughley, 1977; Seber, 1982; Sinclair & Caughley, 1994; Vincent *et al.*, 1996). Many of these techniques, particularly aerial surveys, are hampered by the size of areas to be surveyed and difficulties in observing animals due to dense vegetation, as well as logistics and costs (McDonald 2004; Pollock *et al.* 2004). These problems are exacerbated for species such as caribou that are sometimes sparsely distributed and difficult to detect. Recently, non-invasive sampling methods such as genetic analyses of faecal or hair samples and thermal infrared imaging in aerial surveys, have increased in popularity and use for estimating abundance of rare or elusive species (Thompson, 2004).

Slate Islands Provincial Park provides an ideal setting to compare various population size estimation techniques for caribou as this archipelago represents an essentially closed population, with minimal immigration and emigration for the past 75 years and little influence of predation (Bergerud, 2001; Bergerud *et al.* 2007). The objective of this study was to evaluate three different population estimation techniques (four different methods) to assess the caribou population on the Slate Islands and discuss the pros and cons of each.

Study area

Slate Islands Provincial Park

Slate Islands Provincial Park, which is approximately 224 km east of Thunder Bay, came under regulation as a natural environment class provincial park in 1985. The total size of the protected area is 47.3 km^2 (OMNR, 1986). The park is comprised of two proximate groups of islands situated roughly 13 km southeast of the coastal mainland town of Terrace Bay (Fig. 1). The relatively small Leadman Islands group (which includes Leadman, Cape, Spar and Fish Island) is located approximately 2 km northeast of Patterson Island, which, along with Mortimer, McColl, Edmonds, Bowes, Delaute and Dupuis Island, constitutes the major grouping of islands included within park boundaries (Fig. 2). The total area of these islands, which were surveyed or sampled, was 37.2 km^2.

The Slate Islands fall within the southern range limits of Ontario's boreal region and consequently they contain floral species and communities that are generally characteristic of the province's southern boreal, including balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*) and Showy mountain-ash (*Sorbus decora*) (McGregor, 1974). The last major wildfire on the islands was believed to have occurred around the beginning of the 20th century (Cringan, 1956). Two logging operations are thought to have taken place on the islands during the late 19th century (Cringan, 1956), while further logging activities were carried out during the 1930s (Cringan, 1956; Euler *et al.*, 1976). Lacking substantial wildfire or recent logging disturbance, natural succession processes are leading to a reduction of deciduous forest cover on the Slate Islands (W.J. Dalton pers. comm., 2002). Based on long-term observations and the preliminary results from exclosures, Bergerud (2001; Bergerud *et al.* 2007) suggested that several plant species are under threat of being extirpated from the islands as a result of intensive browsing and foraging pressure by caribou.

The first definitive evidence of woodland caribou on the Slate Islands dates back to the winter of 1907, when tracks (crossing both to and from the mainland) were noted along the surface of the ice that had formed between the islands and the mainland (Middleton, 1960 cited in McGregor, 1974). Bergerud (2001) has suggested that from 1907 to the mid 1930s, the caribou population was relatively small, with movements of individuals across the 13 km between the islands and the mainland during the occasional winters when an ice bridge formed between them. No definitive evidence for the consistent year-round presence of caribou on the islands existed prior to the 1940s (Bergerud, 2001). Bergerud (2001) has argued that as a result of the end of selection logging activities on the islands in approximately 1935, combined with a possible increase in predation pressure on the mainland, movements of caribou both to and from the islands ceased and the Slate Islands population became relatively isolated. The last recorded solid ice that occurred between the mainland and the Slate Islands was in the winter of 1993-1994 (Bergerud, 2001; Bergerud *et al.* 2007). Movements of caribou to the mainland were not recorded during that winter but two wolves crossed the ice to the Slate Islands and substantially reduced calf survival and overall population numbers until 1996, after which the wolves were no longer observed (Bergerud *et al.*, 2007). Wolf sign was again observed on the Slate Islands in 2003 and 2004 (Bergerud *et al.*, 2007).

Caribou population surveys on the Slates Islands were completed every year from 1974-2003 using the "King census" strip transect technique (King, 1937) and from 1975-1997 using a mark-recapture Lincoln Index (Lincoln, 1930). During this period, Bergerud (2001; Bergerud *et al.* 2007) suggests that the population began to increase and eventually entered a "boom and bust" cycle that he believes has persisted to the present day, whereby the number of individuals has fluctuated between 100 and 600 animals and major "die-offs" are experienced at five year intervals.

Fig. 1. Regional Context for Slate Islands Provincial Park.

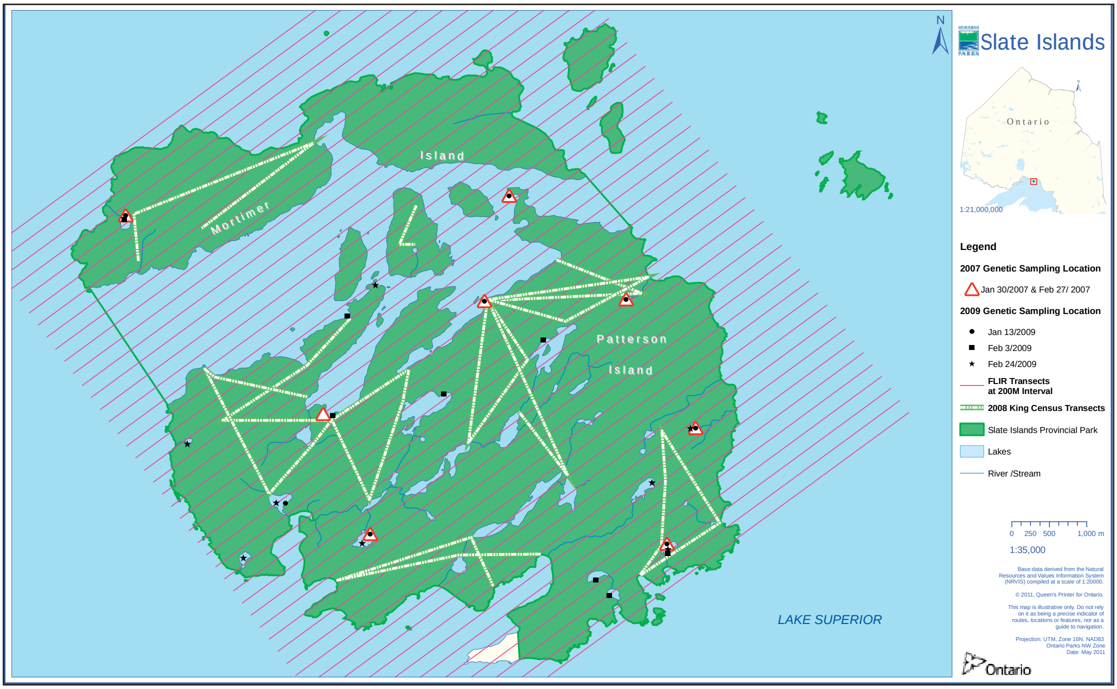

Fig. 2. Locations of faecal pellet collections, ground and FLIR transects surveyed to obtain population estimates of caribou on the Slate Islands, Ontario.

Methods

Distance Sampling Techniques

Forward Looking Infrared (FLIR)

The FLIR surveys of the Slate Islands were conducted by Vision Air Research Inc. (Boise, Idaho) on January 29-30, 2009. They used a PolyTech Kelvin 350 II gimbal (Eskilstuna, Sweden), which included a high resolution Agema Thermovision 1000 (FLIR Systems, Inc., Wilsonville, Oregon) infrared sensor with a spectral range of 8-12 microns and a Sony video camera (Sony Corporation, Minato, Tokyo, Japan), mounted under the left wing of a Cessna 206 "Stationair". The thermal delta of the infrared sensor was less than 1 °C, so it could detect objects with less than 1 °C temperature difference from the background. The sensor gimbal allowed 330° of azimuth and 90° of elevation providing complete coverage except directly behind the airplane. The FLIR system had both a wide (20°) and narrow (5°) field of view (FOV). At 305 m above ground level looking straight down using the wide FOV, the footprint or area covered by the sensor was 110 m in width x 71 m in length, while the narrow FOV provided a footprint of 27 m x 18 m. The sensor operator / wildlife biologist sat in the rear seat of the aircraft and watched a high resolution 38 cm monitor to aim and focus the sensor, which had 800 x 400 pixels resolution. The operator identified animals by their morphology and luminous intensity (Fig. 3). The pilot had >1000 hours of experience flying FLIR surveys and the sensor operator had > 5000 hours experience with FLIR use and interpretation.

Survey flights took place between 1000 and 1400 hrs. Survey transects were oriented to run northeast – southwest to take advantage of the islands' terrain. Transects were spaced 200 m apart to give complete coverage of the area and some overlap to allow more viewing angles of cliffs and steep terrain. Transects were navigated using a Global Positioning System (GPS). For safety reasons, flight altitude was 305 m above ground level of the highest point along each transect flown and the adjacent transect. The sensor look angle was approximately 30° in elevation to nearly straight down. The sensor operator scanned side to side to allow multiple fields of view and additional overlap. Animals were initially sighted using the infrared sensor wide FOV then checked with the narrow FOV and verified using real time video imagery.

The portion of the flight within the study area was recorded on video. The pilot and sensor operator communicated to verify the start and end of each transect to turn the video recorder on and off. The video recorder had slow motion, still image display, and zoom modes. Caribou were located by observing their level of emitted infrared energy versus background levels (Fig. 3). Caribou were mapped at their observed position in relation to physical features (Gill *et al.*, 1997; Bontaites *et al.*, 2000) on an enlarged 1:50 000 topographic map (Energy, Mines and Resources Canada, Ottawa, Ontario, 1986) rather than the position of the airplane. Plotting individual caribou locations allowed identification and omission of duplicate sightings (Haroldson *et al.*, 2003).

Fig. 3. FLIR images of (a) an adult moose near Marathon, Ontario, taken at an altitude of 610 m (2000 ft) a.g.l. and (b) an adult caribou on the west side of Patterson Island taken at an altitude of 305 m (1000 ft) a.g.l. Even at higher altitude, the moose is obviously much larger and has greater luminous intensity than the caribou. Images courtesy of Susan Bernatas, Vision Air Research, Boise, ID, USA.

Analyses

Following the survey, all video recordings were reviewed frame by frame, forward and backward and in slow motion to confirm caribou sightings and locations and to verify the number of individuals that may have occurred in groups. An additional check of the data was performed by sampling the videotape for detection verification and checking for duplicate groups.

Perpendicular distances between caribou locations and transect lines were determined in ArcGIS 9.2 (ESRI, 2006). A caribou population estimate and associated confidence intervals from the FLIR survey were then calculated using Distance 6.0 release 2 (Thomas *et al.*, 2010). The population estimate, assuming 100% sightability along transect lines, was based on a half-normal detection model with simple polynomial adjustment that was chosen by minimisation of Akaike's information criterion (AIC_c) from a variety of hazard rate and half-normal models examined (Buckland *et al.*, 2001). Although caribou could have occurred on ice-covered lakes, no animals were observed more than 100 m from land along any shoreline (i.e., half the distance between transect lines) so density estimates used only those portions of transect lines that occurred on land. The total length of the transect lines that occurred on land was 284.4 km.

Walking transects

The Slate Islands caribou population was estimated using the King census technique described by Bergerud *et al.* (2007). Single persons walked straight line transects by compass over a 30-day period in July 2008 (Fig. 2). Transects were walked on days with little or no wind and with damp ground litter, resulting in good listening conditions. Transects were walked at a normal walking pace, with frequent stops for compass bearings. Noise was kept to moderate levels to limit disturbing or alerting caribou. Transect routes were chosen to cover different habitat classes across the islands (mostly sparse/dense coniferous habitat, taking turning points (topographic features, lakes, bays, etc.) and boat pick-ups and drop offs into consideration. Routes were selected to avoid areas disturbed in recent days by previous transects. Observers estimated the distance to any caribou seen or heard. As indicated previously, no other large mammals are usually present on the Slate Islands other than when wolves are occasionally observed. All transect routes and caribou observations were recorded on a map of the park. The average length of the 11 transect lines that were walked was 4.2 km and the total length was 63.4 km.

Analyses

Caribou density and associated confidence intervals from the ground transect survey were calculated using Distance 6.0 release 2 (Thomas *et al.*, 2010). The population estimate was based on a uniform detection model without adjustment that was chosen by minimisation of Akaike's information criterion (AIC_c) from a variety of uniform models with different adjustment terms that were tried (Buckland *et al.*, 2001).

Mark – Recapture Technique

Genetics

In 2007, faecal pellets were collected on January 30 and February 27 (2-window approach) for mark-recapture analysis. The eight sampling sites were chosen by randomly selecting lakes and/or sheltered bays within the study area that were appropriate for landing a helicopter to collect samples. At each site, four people searched for approximately 20-30 minutes in each of the 4 cardinal compass directions by searching lakes and shorelines. The same random sites were visited on January 30 and February 27. Each faecal sample was placed in a sealable plastic bag to prevent DNA contamination and stored at -20 °C. All samples were shipped frozen to the Natural Resources DNA Profiling and Forensic Centre at Trent University in Peterborough, Ontario for DNA analysis to identify unique individuals.

More sophisticated mark-recapture models, allowing for variation in capture probabilities, can be constructed when 3 or more sampling periods are assessed, so we also estimated caribou population size using a 3-window approach (Otis *et al.*, 1978). In 2009, faecal pellets were collected on January 13, February 3 and February 24 (3-window approach). Sampling sites were again randomly chosen, however, a different random set was chosen for each of the three sampling periods. As with the 2-window approach protocol, all samples were stored in a sealable plastic bag, frozen, and shipped for analysis.

Laboratory analyses

Caribou DNA was extracted from faecal samples using the methods of Ball *et al.* (2007). DNA was amplified using 9 polymorphic, microsatellite markers (Rt6, Rt7, Rt24, Rt30 (Wilson *et al.*, 1997); Map2C, BM848 (Moore *et al.*, 1992); BM888, RT5 (McLoughlin *et al.*, 2004); BMS1788 (Cronin *et al.*, 2005). Each reaction was composed of a 10-µl volume containing: 1x PCR buffer, 2.0 µM $MgCl_2$, 0.2 µg/ml of BSA, 0.4-0.5 µM of each primer (forward primer fluorescently labelled with NED, FAM, or HEX; Applied Biosystems [ABI], Foster City, California, USA); 0.2 µM of each dinucleotide triphosphate; 1 unit of Taq polymerase (Invitrogen Life Technologies, Carlsbad, California, USA) and 2.0 µl of DNA template. The amplification cycle consisted of an initial denaturing of 94 °C for 5 min followed by 30 cycles of 94 °C denaturing for 30 seconds, 56-60 °C annealing for 30 seconds, and 72 °C extension for 30 seconds. The cycling culminated with a final extension of 60 °C for 45 minutes. Thermal cycling was performed in an MJ DNA Engine PTC 200 (MJ Research, Watertown, Massachusetts, USA) configured with a heated lid.

Generally, 0.5 µl of each desalted sample was added to 10 µl of deionized formamide and 0.002 µl of the internal size standard GENESCAN-500 (ROX; ABI). That mixture was subjected to capillary electrophoresis on an ABI 3730 Genetic Analyzer (i.e., automated sequencer) and GENEMARKER AFLP/Genotyping Software (version 1.6; Soft Genetics LLC®, State College, Pennsylvania, USA) was used to score, bin, and output allelic (and genotypic) designations for each caribou sample.

Statistical analyses

We compared genotypes at each of the 9 microsatellite loci to identify the number of unique individuals sampled. We calculated the probability that 2 or more individuals within the population shared the same genotype using the probability of identity for siblings calculations (PI_{sibs}; Evett & Weir, 1998) where caribou genotypes were accepted as unique individuals when $P \leq 0.05$. All calculations were performed in program GENECAP (Wilberg & Dreher, 2004). Information on matching genotypes based on sampling time for 2007 and 2009 was also retained for use in applying mark-recapture models.

Population closure is defined as a population size that remains constant over the period of investigation; that is, where no recruitment (births or immigration) and no losses (death or emigration) occur. Because immigration and emigration of woodland caribou to/from the Slate Islands were unlikely and caribou faecal pellets were collected over relatively short time periods (winter months prior to calving; Pollock *et al.*, 1990), we only considered closed models for population size estimation. Those included the modified Lincoln-Petersen estimator (2-window approach; Seber, 1982) and the multiple mark-recapture models (3-window approach; Otis *et al.*, 1978). Based on guidelines given by Otis *et al.* (1978) and White *et al.* (1982), estimates for all models were produced with the objective to obtain a coefficient of variation (CV) of ≤20% and capture probabilities ≥20%. The examination of woodland caribou population parameters in the application of genetically-based mark-recapture estimates has been applied in other caribou populations (Hettinga, 2010).

The modified Lincoln-Petersen model (Chapman, 1951) was used to estimate caribou abundance based on individual genotypes collected from 2 sampling occasions in 2007. That estimator is based on the ratio of marked and unmarked individuals captured within 2 sampling periods (i.e., 2-window approach; Seber, 1982) and relies on the following assumptions: the population is closed to additions (births or immigrants) and deletions (deaths or emigrants), all animals are equally likely to be captured in each sample, and marks are not lost and are not overlooked by the observer (Pollock *et al.*, 1990). Ninety-five percent confidence intervals for calculated Lincoln-Petersen estimates were estimated using the inverse cube root method (Arnason *et al.*, 1991).

It is widely recognized that the assumption of equal catchability is not met in most mark-recapture studies conducted on natural populations (White *et al.*, 1982). Consequently, the use of multiple mark-recaptures using the 3-window approach (i.e., individual genotypes sampled in 2009) allowed the application of multiple models to assess sampling covariates in the estimation of population size (Otis *et al.*, 1978; White *et al.*, 1982). Following closed population modeling assumptions in acquiring mark-recapture data over multiple sampling intervals, animal capture histories can be used to model variability in estimated capture probability rates and increase the precision and accuracy of calculated estimates (Otis *et al.*, 1978). Models often used in examining variation in capture probability include those assessing time effects, behavioural capture effects, individual heterogeneity or interactions between any and all sampling factors present. The utility of using alternate models to assess variation in capture probability based on sampling covariates is limited by the quality of data available, where increasing sampling times and recapture rates can be important in increasing estimator accuracy and precision (White *et al.*, 1982).

Models run in the interpretation of capture history information from the 3-window approach included the Mo, null model, Mt, time effects models, and Mh, the heterogeneity jackknife model. The Mh estimator is a model derived to look at individual differences in capture probability and has relatively widespread use (Chao & Huggins, 2005). The Mh model is ideal with non-invasive genetic sampling where variability in sampling frequency for identified individuals is often apparent (Mills *et al.*, 2000; Frantz *et al.*, 2003; Hansen *et al.*, 2008) and has been used previously in the estimation of population size for woodland caribou populations (Hettinga, 2010).

Estimation of the Mo, Mt and Mh model was done using the CAPTURE (White *et al.*, 1982) application within program MARK (White & Burnham, 1999). Model ranking was done in CAPTURE where likelihood ratio tests were used to determine if models used could serve as accurate indicators for calculated capture probability values when compared to the null, Mo model, or other imbedded models (Otis *et al.*, 1978). Where a model ranking was given to a model that was unusable (due to the limited number of sampling times or sparseness in sampling data) the next highest ranking model was selected as the candidate model for use in estimating population size.

Results

Forward looking infrared (FLIR)

The FLIR survey of the Slate Islands was completed in 5.3 hours of flying over two days. Follow-up tape review and analysis took 12 hours. The FLIR survey recorded 58 caribou at 46 locations on the Slate Islands; two groups of three individuals, eight groups of two and the remainder were singles. Individuals were not classified by age or sex but most groups of two were cow-calf pairs. The estimated density was 1.56 ± 0.50 caribou/km^2 with a CV of 19.4%, producing a population estimate of 58 caribou (95% CI 40-85) (Table 1).

The costs of the FLIR survey included the actual flight time of 5.3 hrs over two days at CDN$ 750 per hr, 12 hrs of videotape review and analysis at CDN$ 100 per hr, and daily crew support (i.e., food, accommodations, etc.) of CDN$ 310 per day. So, the total cost of the FLIR survey of the Slate Islands was about CDN$ 5800. The ferry costs of bringing the crew and their aircraft to the survey location (CDN$ 370 per hr) have not been included (Table 2).

Walking transects

A total of 11 caribou were observed on transects that were ground surveyed on the Slate Islands. No groups were observed and individuals were not classified by age or sex. The density estimate calculated from the ground survey data was 3.62 ± 0.17 caribou/km^2 with a CV of 29.3%, producing a population estimate of 134 caribou (95% CI 71-255) (Table 1).

The costs of the ground transect survey were minimal and, excluding wages, only included the costs of transportation by boat to the Slate Islands and provisions (i.e., food, camping equipment) for the field crew. We estimated the total cost of the ground transect survey to be < CDN$1000 (Table 2).

Genetics

One hundred faecal samples were analyzed from the 2007 field season and 49 unique individual genotypes were identified. The PI_{sibs} calculated for individuals captured during 2007 (2-window approach) was 4.32 x 10^{-4}. That probability corresponded to a 1 in 2315 chance that 2 individuals had the same genotype at the loci examined. The Lincoln-Petersen model calculated for the 2-window approach in 2007 produced a population estimate of 151 caribou or 4.1 caribou/km^2 (Tables 1 and 4). However, the precision (CV = 37%) and the capture probability of that model was low (10%).

In 2009, 164 faecal samples were analyzed (based on 3 sampling occasions) and 57 unique individual genotypes were identified. The PI_{sibs} was 1.53 x 10^{-3} for the 57 individuals captured during 2009, corresponding to a 1 in 654 chance of encountering identical genotypes. In the use of models examining sampling covariates where three sampling windows were considered, the Mo, Mt and Mh models, alternate population estimates were calculated (Tables 1, 3 and 4). The Mh, heterogeneity jackknife estimator,

Table 1. Estimates of woodland caribou population size on the Slate Islands, Ontario, using three different techniques.

	FLIR	**Walking Transects**	**Genetics (2 sampling periods)**	**Genetics (3 sampling periods)**
Population Estimate	58 (program DISTANCE)	134 (program DISTANCE)	151 (Lincoln-Petersen)	99 (program CAPTURE)
Variability around N (95% Confidence Interval)	40-85 (Thomas *et al.*, 2010)	71-255 (Thomas *et al.*, 2010)	80-349 (Arnason *et al.*, 1991)	85-122 (White *et al.*,1982, Otis *et al.*, 1978)
Confidence in population estimate	High due to narrow confidence intervals	Low due to large confidence intervals	Low due to large confidence intervals	High due to narrow confidence intervals

Table 2. Comparison of potential advantages, disadvantages and costs of three different techniques used to estimate woodland caribou population size on the Slate Islands, Ontario.

	FLIR	**Walking Transects**	**Genetics (2 sampling periods)**	**Genetics (3 sampling periods)**
Correction factor	Possible – marked individuals would provide an estimate of detectability	Possible – marked individuals would provide an estimate of detectability	Inherent in calculation	Inherent in calculation
Male to female ratio	Possible, if image permits	No, few observed individuals can be sexed	Yes, high confidence	Yes, high confidence
Calf ratios	Possible, if image permits and animals are flushed	Unlikely due to few calves observed	Possible, based on size of pellets	Possible, based on size of pellets
Location accuracy	High	Low	High	High
Group sizes estimate	Yes, with high confidence	Yes, with low confidence due to disturbance of individuals by observer	Depends on sampling	Depends on sampling
Time restrictions	Preferably not during leaf out period	Preferably not during leaf out period	Winter	Winter
Additional values of sampling	Census other species		· Contribution to metapopulation research · Collected pellets used for other testing (e.g., pregnancy, diet)	· Contribution to metapopulation research · Collected pellets used for other testing (e.g., pregnancy, diet)
Costs · Does not include air ferrying costs · All costs originate from Terrace Bay · Human hours not included	· 5.3 hrs flying over 2 days@750hr = \$3975 · 12 hrs. videotape review and analysis @100hr = \$1200 · Daily support (food and accommodations) = \$620 · Total **\$5.8K**	· Time of 2 people for approximately 1-2 weeks) · Total **<\$1K** (boat ferry from Terrace Bay plus food)	· 5 hrs flying @1200hr = \$6K · DNA analysis for 100 samples @ \$30 sample = \$3K · 4 people walking transects for 2 days · Total **\$9.0K**	· 7.5 hrs flying @1200hr = \$9K · DNA analysis for 164 samples @ \$30 sample = \$4920 · 4 people walking lines for 3 days · Total **\$13.9K**

was selected as the best fit model for use in estimating population size and an estimate of 99 animals (95% CI 85-122), or 2.7 caribou/km^2 was calculated. Alternately use of the Mo and Mt models yielded estimates of 115 (95% CI 83-185) and 100 (95% CI 75-157) animals, respectively. Those estimates corresponded to densities of 3.1 and 2.7 caribou/km^2, respectively. Calculated coefficient of variation values

Table 3. Estimation of population size, *n*, based on genetic sampling using program CAPTURE (White *et al.,* 1982) with 2009 sampling information from Slate Islands Provincial Park woodland caribou population.

	All animals			Males			Females		
	n	SE	95% CI	*n*	SE	95% CI	*n*	SE	95% CI
Mo	115	23.32	(83,185)	42	8.76	(31,71)	68*	26.91	(38,191)
Mt	100	18.35	(75,157)	38	6.81	(29,63)	58	20.69	(34,158)
Mh	99*	9.41	(85,122)	44*	6.09	(36,60)	47	6.59	(38,64)

* selected as best fit model using Likelihood Ratio Tests in program CAPTURE (White *et al.,* 1982).

Table 4. Sampling information in the collection of woodland caribou faecal pellet samples from the Slate Islands Provincial Park in 2007 and 2009.

	2007		2009		
	Jan 30	Feb 27	Jan 13	Feb 3	Feb 24
Sites Sampled	8	8	8	8	8
Samples Collected	37	63	34	46	84
Genotypes ID`d	18	31	14	16	41
Capture Probability	10%	17%	14%	16%	41%

* Capture probability calculated using time effects (Mt) model.

for the Mh, Mo and Mt models were 10%, 23% and 19%, respectively.

In the estimation of gender-specific population size estimates, the Mh model was again selected as the best fit model, using likelihood ratio tests in CAPTURE (White *et al.*, 1982), in modeling male sampling information, whereas the Mo model was selected in modeling female sampling information. Calculated estimates for sampled males, using the Mh model, was 44 (95% CI 36-60) and for females, using the Mo model, was 68 (95% CI 38,191). In the estimation of females, likelihood ratio tests ranked the Mh model only slightly below (0.80) that of the Mo model (0.83). An estimate of the number of females from the Mh model was 47 (95% CI 38, 64). Calculated CV values for the Mh model were 14% in estimating males and females while, for females alone, the Mo model returned a high CV value of 40%.

The costs of the genetics surveys included the actual flight time of 5.0 hrs over two days at CDN$ 1200 per hr for the 2-sampling period survey in 2007 and 7.5 hrs flight time over three days for the 3-sampling period survey in 2009. DNA analysis for 100 samples at $30 per sample totalled CDN$ 3000 for the two sampling periods and CDN$ 4920 (164 samples) for the three sampling periods. So, the total cost of the genetics survey of the Slate Islands was approximately CDN$ 9000 for the 2-sampling period approach in 2007 and CDN$ 13 920 for the 3-sampling period approach in 2009. Costs do not include aircraft ferrying costs and times are based on flights originating from Terrace Bay (Table 2).

Discussion

All three techniques of estimating the population size of caribou on the Slate Islands gave results with large, overlapping confidence intervals. However, the population estimate based on walking transects and genetic sampling with the 2-window approach had much wider confidence intervals than the FLIR survey or genetic sampling using the 3-window approach. Whereas confidence in population estimates from genetic sampling can be improved by adding more sampling effort and periods, estimates based on walking transects are greatly influenced by observer bias (i.e., experience) that cannot be readily corrected; increasing the number of transects walked will help but observer bias remains high. The most common source of bias in walking transects is the human error associated with a false observation or failure to record an animal along a transect. Careful consideration must also be given to the dispersion of transects through areas to provide appropriate sampling. Ground-based estimates are also limited in capacity to determine sex ratios, cow-calf ratios and group sizes due to limited visibility and observer disturbance. Nonetheless, ground-based transects were the least expensive of the survey options that we compared on the Slate Islands with boat access. Ground-based surveys work best in small, easily accessible areas, but would lose any cost advantage if required over larger and more remote areas requiring access by aircraft. One must also consider timing restrictions with each survey technique. Both FLIR and ground surveys are best conducted when deciduous vegetation has lost its leaves and DNA extraction for genetic analysis produces better results with winter collections of faecal pellets (Ball *et al.*, 2007).

The caribou population estimate from the FLIR survey represents a minimal value that may have been limited by the rugged landscape of the Slate Islands and possibly dense conifer forest cover; subsequent FLIR surveys for moose and caribou in a conifer-dominated landscape on the mainland north of the Slate Islands, however, indicated this forest type does not severely limit detection (A. Rodgers, unpubl. data). Detection rates using FLIR are greater than those achieved by standard aerial census (Naugle *et al.*, 1996; Havens & Sharp 1998; Gill *et al.*, 1997; Bontaites *et al.*, 2000) and are subject to less observer bias caused by experience, fatigue, air sickness, etc. (Caughley, 1974; LeResche & Rausch, 1974) but the possibility of not detecting all animals and undercounting remains a potential source of error (Thompson, 2004; Drake *et al.*, 2005). As with virtually all wildlife survey methods, double counting can lead to biased population estimates. Because the FLIR survey of the Slate Islands was carried out over two days, we cannot completely eliminate the possibility that caribou were double-counted. Consequently, the caribou population estimate from the FLIR survey may be even lower than reported (Table 1).

Similar to standard aerial census methods, FLIR has the additional advantage of objectively detecting multiple species (e.g., moose, wolves) in the same survey. However, the window of opportunity for FLIR surveys is wider than for aerial surveys that require appropriate snow conditions in winter; an important consideration in a period of climate change that may produce mild winters with less snow. Although FLIR surveys require an experienced sensor operator and specialized equipment, they are usually less expensive (Adams 1995; Bernatas & Nelson, 2004) and require less expertise and special equipment than genetic sampling. Occupancy estimation using FLIR and subsequent modeling may provide a cost-effective approach to broad-scale caribou population monitoring covering much larger geographical extents.

Comparison of the FLIR estimate of caribou population size with genetic sampling in three periods, suggests the detection rate of FLIR on the Slate Islands was about 60%. Thus, combining genetic sampling with other survey methods such as FLIR or aerial surveys can provide a correction factor for detection rate. Alternatively, a correction factor could be determined by marking individuals (e.g., radio collars) in a population prior to a survey (Bernatas & Nelson, 2004).

Genetic sampling can provide population estimates with high confidence in a closed system like the Slate Islands and in populations where population modelling assumptions can be verified in the use of mark-recapture models (Hettinga, 2010). However, in this study, variation in the number of animals sampled at each sampling time may have introduced bias in calculated estimates. In particular, in the sampling of caribou faecal pellets in 2007, low recapture rates (17%) were apparent and likely led to a positive bias in the calculated estimate which was also relatively imprecise (CV = 37%). In the calculation of population size using the 2009 collected samples, the incorporation of three sampling periods, as well as the use of mark-recapture models in program CAPTURE (White *et al.*, 1982), likely reduced the amount of bias in calculated population size estimates; despite variation in the number of animals sampled at each sampling time (Table 3). Regardless, because the two methods were applied in different years, comparisons of population size estimated from the 2-sample and 3-sample approach must assume there was no substantial change in population growth rate (λ) between sampling periods.

Genetic sampling may be an expensive option if a lot of helicopter time is required; however, the collection of faecal samples can be an easy addition to an existing survey (e.g., aerial census by helicopter), thus being very cost effective. Additional benefits provided through the collection of faecal pellets include the potential for other genetics based testing in assessing population bottlenecks (Petersen *et al.*, 2010), metapopulation structure (Ball *et al.*, 2010) and sex-ratios (Vors, 2006) and other faecal-based parameters, including: hormonal information to assess pregnancy and stress indicators (Messier *et al.*, 1990; Vors, 2006), the size of pellets as an indicator of age-range (Ball, 2010), diet information (Boertje, 1990) and parasite load (Gray & Samuel, 1986). In conducting multi-year sampling events there is also the potential for the use of open population models where population demographic parameters including population rate of growth and recruitment rates can be estimated (Hettinga, 2010). Non-invasive genetic sampling for estimating population size has been done for mainland mountain and boreal-dwelling populations (Hettinga, 2010). Isolated populations like the Slate Islands are well suited to meeting the assumptions of closed population modelling; however, mainland populations must work within stricter definitions. Notably, additional attention should be paid to the boundaries of the study area and the timing of sampling periods to minimize chances of individuals moving out of or into the study area.

Ultimately, the best survey method to use will depend on the monitoring/research question(s) asked and resources available. Ground-based surveys may be sufficient if a rough estimate of population size is required, but more expensive surveys may be required if a more accurate and/or precise estimate is needed. FLIR and the 3-window genetic approach of sampling provided the most precise estimates in our comparisons. Given a known detection error for a study area, FLIR may be a cost effective monitoring method, but if the detection error is unknown, the 3-window genetic sampling approach will provide a more accurate and precise estimate. A combination of techniques may also be a productive approach, as the benefits of each technique are unique and convergence of population estimates will provide greater certainty to management plans for caribou recovery.

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Using temporary dye marks to estimate ungulate population abundance in southwest Yukon, Canada

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Abstract: We describe the protocols of two mark-resight abundance surveys, using temporary dye-marks, for the Aishihik woodland caribou (*Rangifer tarandus caribou*) and wood bison (*Bison bison athabascae*) populations (herds) in the southwest Yukon Territory, Canada. We also provide recommendations based on experiences from these surveys for biologists and managers considering this approach. The Aishihik woodland caribou herd was the focus of intensive management in the 1990s aimed at recovering the herd. Following recovery activities, a target size of 2000 animals was determined and the Champagne-Aishihik Traditional Territory Community-Based Wildlife Management Plan recommended an estimate of the herd's size be completed before the year 2013. We used an aerial mark-resight approach to estimate the herd's size in March 2009. Caribou (n = 59) were marked from a helicopter with temporary dye, delivered via a CO_2-powered rifle. Two independent resighting sessions were subsequently carried out via helicopter. The herd was estimated at 2044 animals (90% CI: 1768 – 2420) with an overall resighting rate of 0.47. The mean annual growth rate (λ) of the herd from 1997 – 2009 was 1.05 (SE = 0.01). The Aishihik wood bison herd was estimated at 1151 (90% CI: 998 – 1355). Our study suggests that ungulates temporarily marked with dye can be successfully used to obtain statistically sound population estimates.

Key words: abundance; dye-marks; mark-resight; *Rangifer tarandus caribou*; Yukon Territory.

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Introduction

Population abundance is a key parameter used by managers and other stakeholders for effective and sustainable management and conservation of wildlife populations (Milner-Gulland & Rowcliffe, 2007). This information is used, for example, to ensure harvest is sustainable (Sæther *et al*., 2001), to establish baseline conditions prior to anthropogenic activities on the landscape, and to subsequently assess the impacts of these activities (Sorensen *et al*., 2008). Furthermore, abundance estimates can be used to obtain a greater understanding of ecological processes influencing a single population's (e.g., Jenkins & Barten, 2005) or multiple populations' dynamics (e.g., Vors & Boyce, 2009; Wittmer *et al*., 2010).

Estimating abundance in large and remote areas can be expensive and time consuming. This is made more challenging when surveying animals occurring at low densities. A variety of methods are available to estimate population abundance (e.g., Schwarz

& Seber, 1999), and a number have been used to estimate woodland caribou abundance in the Yukon including total counts (e.g., Hayes *et al.*, 2003), a stratified random quadrat (SRQ) method (Farnell & Gauthier, 1988), and mark-resight surveys using radio-collared animals (Environment Yukon, unpubl. data).

The Aishihik caribou (*Rangifer tarandus caribou*) herd (AH) in the southwest Yukon Territory (Yukon), Canada, is a population of the Northern Mountain ecotype of woodland caribou. These caribou are legally listed in the Canadian *Species at Risk Act* as a species of *Special Concern* (COSEWIC, 2002). Following declines in the 1980s and early 1990s, AH was the focus of an intensive population recovery effort in the 1990s (Hayes *et al.*, 2003) and is one of the better-studied herds in the Yukon (Farnell *et al.*, 1998). Recovery actions for AH included limiting human harvest and reducing wolf (*Canis lupus*) populations through sterilization and lethal control (Hayes *et al.*, 2003). A community-based fish and wildlife management plan for the Champagne & Aishihik First Nation's traditional territory, in which AH is located, recommended the herd's size be estimated by 2013 to determine if the herd had reached a management target of 2000 animals. The most recent estimate of the AH was 1148 animals (90% CI: ± 6.5%; Hayes *et al.*, 2003) in 1997. Additionally, there are local concerns regarding the impact of the reintroduced Aishihik wood bison (*Bison bison athabascae*) population (AWB) on the AH. From 1988 to 1992, 170 bison were released into the wild in the Aishihik area and First Nations have expressed concern over the potential impact of reintroduced wood bison on sympatric caribou (Fischer & Gates, 2005).

We lacked radio-collared animals in the AH to correct for sightability, and were wary of attempting a total count approach given its unreliability (e.g., Caughley & Goddard, 1972). Furthermore, previous applications of an SRQ approach on the AH required greater resources (e.g., financial and personnel) than were available (Environment Yukon, unpubl. data). Thus, we applied a standard mark-resight approach using temporary dye (i.e., paintballs) to mark a subsample of animals in AH to estimate its size. This approach has been used to estimate abundance in other ungulate populations including elk (*Cervus elaphus*; Skalski *et al.*, 2005) and mountain goats (*Oreamnus americanus*; Cichowski *et al.*, 1994; Pauley & Crenshaw, 2006). We also adopted this approach to estimate the size of the AWB which has an overlapping range with that of AH.

The primary objective of this paper is to describe and provide practical recommendations for biologists and managers considering a mark-resight approach using temporary dye marks. These recommendations are based on our experiences estimating abundance of the AH and the AWB. Our purpose for briefly including the AWB in this paper is to develop and strengthen our recommendations based on two separate surveys, and species. A secondary objective of this paper is to discuss our findings with respect to the population dynamics of the AH, which was the initial impetus for us to use this method.

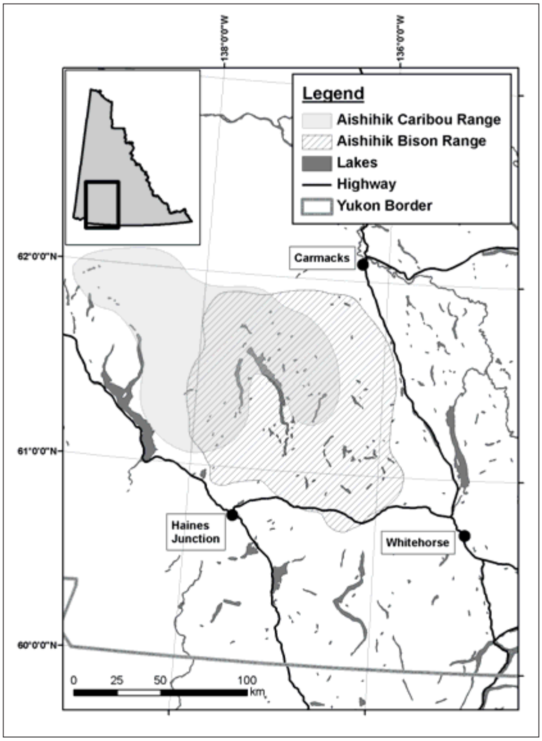

Fig. 1. Generalized range boundaries of the Aishihik caribou and wood bison populations in the southwest Yukon Territory, Canada.

Material and methods

Study area

Both the AH and AWB are located in the southwest Yukon (Fig. 1) within the Boreal Cordillera ecozone (Smith *et al.*, 2004). The area hosts a full complement of native ungulates and large carnivores, including woodland caribou, wood bison, moose (*Alces americanus*), thinhorn sheep (*Ovis dalli*), mule deer (*Odocoileus hemionus*), grizzly bear (*Ursus arctos*), black bear (*Ursus americanus*), wolverine (*Gulo gulo*), and wolves. Topography of the area is mountainous with high plateaus and is characterized by rounded and rolling hills in the east with more rugged terrain in the west. Mean elevation in the area is approximately 1400 m above sea level (asl) and ranges from approximately 800 to 2300 m asl.

The area lies within the St. Elias Mountains rain shadow and is semi-arid, with annual precipitation averaging approximately 250 – 300 mm/year. Mean annual temperature is approximately -3 °C (winter average: -17 °C; summer average: 10 °C). Lower elevation areas below treeline consist primarily of open canopy white spruce (*Picea glauca*) forest. Higher elevations are characterized by shrub (*Betula* spp. and *Salix* spp.) communities in the subalpine. Alpine communities include low lying shrubs, *Dryas* spp., and various graminoids, mosses, and lichens. A detailed description of the area is provided by Smith *et al*. (2004).

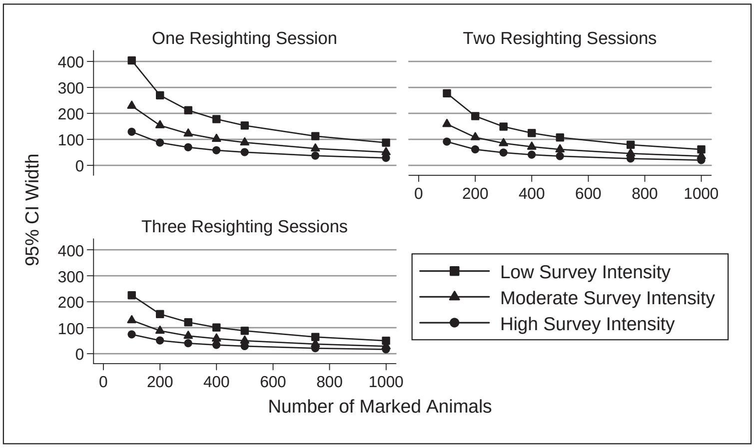

Fig. 2. Simulation results for determining a sampling strategy for the mark-resight survey of the Aishihik caribou herd. Survey intensity is defined by sightability rates and characterized as low (0.50), moderate (0.75), and high (0.90). Simulations were carried out assuming a true population of 2000 individuals. The y-axis represents the width of the 95% confidence interval of the estimate.

Survey protocols

Prior to the caribou study we used a Monte Carlo simulation approach, using the software NOREMARK (White, 1996), to guide our decisions for the survey design. Differing combinations of survey parameters (Fig. 2) were assessed with respect to their effect on precision (i.e., confidence interval width) of the estimate including the number of marked animals, the number of resighting surveys, and resighting rate (i.e., survey intensity). We used 2000 animals as the assumed population size for all simulations. This was based on the minimum number of animals known to be present in the herd from observations during recent fall composition surveys, and projections of a simple population model (Environment Yukon, unpubl. data). We used three resighting rates (0.50, 0.75, and 0.90) representing a range of rates. However, we acknowledge that of the three parameters considered in the simulations, this was the variable we would have the least control over largely due to the effect of environmental conditions (e.g., weather) on sightability.

Based on our computer simulations and financial considerations, our design was to attempt to mark a minimum of 150 animals, followed by two independent resighting sessions. To minimize potential biases associated with marking, and subsequently resighting, animals in different sized groups (Skalski *et al*., 2005) we aimed to mark 20% of the animals in each group. Marking was carried out from a relatively fast and maneuverable helicopter (A-Star 350B1) with a three-member crew: navigator/data recorder, shooter, and a shooter's assistant. The shooter was positioned behind the pilot with the shooter's assistant seated in the adjacent rear seat. The navigator/data recorder occupied the front passenger seat. To mark animals (Skalski *et al.,* 2005; Pauley & Crenshaw, 2006) we used temporary oil-based dye (paint) pellets (Nelson Paint Company of Canada; Sault Ste. Marie, ON) delivered from a compressed CO_2 charged rifle (Tippmann A-5; Tippmann Sports LLC, Fort Wayne, IN). Dyes were non-toxic and of the same type used in the livestock and veterinary fields. Our primary choice of colours was bright orange and bright green as we assumed these colours would be highly visible for subsequent resighting. We also marked a smaller number of animals using yellow, blue, and red dyes, to assess their visibility in the field. To ensure marks were visible for the resighting sessions, we attempted to mark each animal with a minimum of five dye pellets. During marking operations we avoided the animal's head and attempted to place all marks near their hind quarters. Thus, for the purposes of this survey a marked animal was one hit with a minimum of five pellets on its hind quarters (e.g., rump or flank). Calves were not marked.

We used historical late-winter animal locations to guide our aerial search and to increase our efficiency by avoiding those areas where caribou had never been observed during late winter. Additionally, prior to marking we used a fixed-wing aircraft (Cessna 205) to survey the perimeter of the herd's known range to delineate the outer edge of the study area by locating tracks or animals.

During marking, we focused on alpine areas and flew contours along mountain sides and along valleys and alpine plateaus. When a group of animals was located we first tallied its size to determine the number of animals to mark. We then flew towards the group, attempting to move animals uphill if possible, and marked animals from behind at a distance of approximately 5 m (i.e., within the rotor wash of the helicopter). The helicopter was equipped with a sliding door that was opened prior to marking to enable the shooter to mark animals with a wide range of movement. Marking was generally completed within 30 – 45 seconds, after which the helicopter immediately lifted away from the target animal. Marking occurred during 4 – 7 March 2009.

Shortly after marking, we carried out two consecutive and independent aerial resighting sessions. Resighting crews were independent of one another and consisted of three observers and a pilot. Resighting surveys took place using a Bell 206B helicopter. The pilot remained the same for both surveys but was instructed not to impart any information on animal locations to the second resighting crew to ensure independence between the two resighting surveys. During the resighting surveys groups of animals were counted and the number of marked animals was recorded. The first resighting session (14 hours of flying) took place 7 – 9 March 2009 and the second (12.5 hours of flying) occurred on 10, 11, and 15 March 2009.

In July 2009 we conducted a mark-resight population estimate of the AWB. We used the same marking and resighting methodology as for AH described above. Bison were marked with blue dye on 25 July, followed by two independent resighting sessions during 26 – 29 July 2009. During July, this population of wood bison are typically aggregated and found in alpine areas (Environment Yukon, unpubl. data), which facilitates a relatively high resighting rate. Our target was to have 75 marked animals in the population, based on an assumed population size of 1200 wood bison. Blue was selected as the most visible and durable dye colour based on testing on captive bison at the Yukon Wildlife Preserve. Twenty-four bison fitted with radio-collars were also present in the herd during the survey and these animals were also included in the marked sample and were not dye-marked. The survey boundary was delineated based on observations of radio-collared animals located via fixed-wing aircraft 7 days prior to our marking session, and existing radio-telemetry survey data from previous years.

Statistical analysis

We used the program NOREMARK (White, 1996) to estimate abundance, for both the AH and AWB, by fitting the data to a joint hypergeometric distribution (Neal *et al.*, 1993). Given the relatively short time frame between marking and the resighting surveys we assumed the populations were both demographically and geographically closed (i.e., no animals died and no animals left or entered the study area). Confidence intervals were determined using a profile likelihood approach (White, 1996).

The average annual (geometric) growth rate (λ) was estimated for the AH using the equation $N_t = N_0\lambda^t$ (Caughley, 1977), where N_t is the 2009 estimate, N_0 is the 1997 estimate, and t =12 (i.e., the number of years between estimates). The SE of λ was estimated using the Delta method with the 'emdbook' package (version 1.3.1; Bolker, 2008) for the statistical software R (version 2.13.0; R Development Core Team, 2011).

Results

We marked 122 of 793 caribou observed over approximately 14 hours of flying time (approximately 1960 km) during the initial marking session. However, technical problems with the bright orange dye resulted in poorly marked animals and other colours such as yellow were deemed too difficult to observe during the resighting sessions, potentially leading to missed marks. Therefore, for analysis we only considered animals with either blue or bright green dyes to be "marked"; resulting in 59 marked animals. Due to larger than expected group sizes (mean = 27.3, range: 1 – 121) we were unable to mark 20% of the animals in each group, as doing so would have placed too much stress on the animals.

Resighting rates in each of the resight sessions were similar (Table 1) with an overall resighting rate of 0.47. Flight lengths for the first and second resighting sessions were approximately 1460 km and 1580 km, respectively. Based on observed marked and unmarked animals, the AH's size was estimated at 2044 (90% CI: 1768 – 2420). Because of the smaller number of marked animals used in the analysis, the reduced precision in the estimate was expected. The annual population growth rate (λ) of the herd, based on this estimate and the previous SRQ estimate from 1997, was estimated at 1.05 (SE = 0.01).

In July 2009, 59 bison were marked with blue dye during approximately 6 hours of flying and together with the 24 previously radio-collared individuals, 83 bison were "marked" in the population. As with the caribou census, resighting rates of the two resight sessions were also similar (Table 1). The size of the AWB was estimated at 1151 (90% CI: 998 – 1355).

Discussion

Survey recommendations

We obtained acceptable estimates of the AH and AWB, based on the relatively narrow 90% confidence interval coverage. Moreover, the population estimates were consistent with our expectations, based on previous estimates, demographic data, and anecdotal observations (e.g., observed numbers of animals during composition surveys; Environment Yukon, unpublished data). The use of temporary dye marks allowed us to mark more animals than we would have been able to had we relied on using a subsample of radio-collared animals as the marked population, given the resources available. Monte Carlo simulations suggested that an increased proportion of the population being marked would increase the precision of our population estimates. This is not surprising and was reported earlier (Neal *et al.*, 1993) using the same Monte Carlo simulation procedures.

The two mark-resight population estimates we conducted provided us an opportunity to identify those features and aspects of the studies which were useful and effective. We provide our experiences and recommendations in the hope they may be useful for biologists and managers considering this approach in their own work. We acknowledge that our recommendations and opinions are qualitative and generally not based on any formal experimental or comparative approach. Nevertheless, we feel these lessons learned may be useful.

Assuming there is some basic quantitative or qualitative information available for the population of interest, the use of the program NOREMARK (White, 1996) can be a useful tool to guide biologists in allocating marking and resighting efforts. Perhaps the most useful aspect of running a simulation study was the ability to determine how many animals to mark and how many resighting sessions to be flown (e.g., Fig. 2). Given that resighting rates can be influenced by many factors (Caughley *et al.*, 1976; Anderson *et al.*, 1998), some out of the researcher's control, assessing sample size and the number of resighting sessions over a range of differing resighting rates is a valuable approach.

Prior to marking, trials of different colour dyes on live animals can guide the best choice of dye colour to use in the field. In both of our studies, observers noted that blue was the most readily visible colour during the resighting sessions. However, this may not be applicable for all species, seasons, or environments. Because the blue contrasts with many natural environments and terrain, it is a highly recommended colour for increased visibility by search and rescue agencies (National Association for Search and Rescue, 2005).

During animal marking we strongly recommend the use of a fast and maneuverable helicopter. Marking ungulates with temporary dye requires low-level and dangerous flying and a maneuverable helicopter will reduce chase times thus reducing stress on the animals and increasing the safety level for the crew.

Our crews were made up of three members: a navigator/data recorder, a shooter, and a shooter's assis-

Table 1. Resighting summary data from the Aishihik caribou (March 2009) and wood bison (July 2009) mark-resight surveys.

Session	Total Animals Observed	Marked Animals Observed	Resighting Rate (SE)[c]
		Caribou	
Resight 1	1012	29[a]	0.49 (0.07)
Resight 2	928	27[a]	0.46 (0.07)
		Wood bison	
Resight 1	355	33[b]	0.39 (0.05)
Resight 2	512	31[b]	0.37 (0.05)

a: 59 marked animals available; b: 83 marked animals available; c: Resighting rates did not differ between sessions of the caribou (Z = 0.37, P = 0.712, n = 59) and wood bison (Z = 0.31, P = 0.750, n = 83) surveys, respectively.

tant. Fewer crew members would have substantially slowed down the marking operations as personnel would have had too many tasks in the helicopter. In addition to having multiple crew members, backup equipment (e.g., CO_2 rifles and barrels) and cleaning gear is also highly recommended. If one rifle breaks or malfunctions, significant time can be lost if the crew must return to replace it. Additionally, dye pellets can break in the barrel of the rifles and must be cleaned by the shooter's assistant. Having multiple barrels available to be changed rapidly also increases the overall efficiency of the marking operations.

Care and maintenance of the equipment can prove to be critical and greatly increase the likelihood of a successful marking operation. We recommend that dye pellets do not freeze or be exposed to extreme heat as extreme temperatures may damage the outer shell or alter the shape of the pellets. The technical problems with the bright orange pellets which we experienced during the marking of AH during late winter may have been due to these pellets freezing during shipping from the manufacturer in February. Upon closer inspection following the survey we noticed that nearly all pellets had been warped to a more ovoid shape rather than spherical. This change in shape may have lead to pellets prematurely bursting in the barrel of the rifle.

Having a properly tuned rifle is important. Regulators govern the amount of CO_2 entering the rifle and hence influencing the speed and trajectory of the pellets. Adjustments on these can have a significant influence on the effectiveness of the rifles, which is critical when firing at a moving animal from a helicopter. Ensuring rifles are working properly prior to field effort may only require a short amount of time relative to the overall benefits obtained during marking operations.

A limitation of this approach is the potential to violate a key assumption of mark-recapture analyses: that all animals have equal probability of being marked and resighted (Skalski *et al.*, 2005). For animals occurring in groups (e.g., *Rangifer* sp.), detectability is often positively related to group size (Anderson *et al.*, 1998). Thus, animals in larger groups may have a higher probability of being marked, and resighted, than those in smaller groups which may bias abundance estimates. This becomes a greater issue when groups are unequal in size and remain constant in size between marking and resighting sessions, and when individuals exhibit at least partial group fidelity.

The nature of the marking approach used here requires that large amounts of time should not be allowed for between marking and resighting in order to avoid losing marks (another assumption of mark-recapture analyses). To account for the potential biases associated with varying group sizes, Skalski *et al.* (2005) recommend marking a constant proportion of animals within a group, which we attempted here. They also recommend marking animals when they occur in smaller and less stable groups. For populations having varying sized groups and individuals exhibiting partial fidelity to those groups, Skalski *et al.* (2005) provide information on the degree of bias based on the overall variation in group sizes and the degree of fidelity that individuals exhibit. The degree of fidelity may be challenging to estimate however, as it is based on the correlation in group size an individual is associated with over time. The inability to uniquely identify dye-marked animals is one challenge; as is the minimum number of resighting sessions required to adequately estimate this correlation (i.e., fidelity). Prior monitoring of uniquely identifiable marked animals (e.g., through radio-collaring) could provide this information.

In this study we lacked uniquely marked individuals, and therefore could not formally estimate group fidelity. Two factors may have minimized the bias in our abundance estimate for the AH. First, the AH is an alpine-wintering herd (Kuzyk *et al.*, 1999) which may reduce the influence of group size on sightability. That is, large and small groups may have similar detectability in treeless alpine areas under the same surveying route. The Chisana herd in the southwest Yukon (Kuzyk *et al.*, 1999) also occurs in high elevation habitats with low tree cover and a recent mark-resight estimate, using radio-collared individuals, of it found no strong relationship between detection and group size ($\beta_{\text{Group Size}} = 0.77$, SE = 0.64, $P = 0.23$; Environment Yukon, unpublished data).

Second, groups may not have been constant in size in the AH over the marking and resighting sessions. For example, a closer examination of groups observed during the marking and resighting session in one drainage (Raft Creek) of the study area found a range of group sizes with similar numbers of total animals counted. During marking 140 animals were observed in four groups ranging in size from 12 to 62. Subsequently, in one resighting session 140 animals were observed in one group and in the other resighting session 180 animals were observed in five groups (range: 4 – 90).

Aishihik caribou population dynamics

The roughly 5% annual increase in the AH from 1997 to 2009 contrasts the broader pattern of *Rangifer* declines observed globally (Vors & Boyce, 2009) and at the local population level elsewhere (Wittmer *et al.*, 2005). Licensed bull harvest of the herd was stopped prior to recovery efforts in the 1990s and a permit-based hunt began in 2002 with approximately 19 bulls harvested annually (Environment Yukon, unpubl.). Aboriginal subsistence harvest of the herd, not regulated by the Government of Yukon, was voluntarily halted during this time. Thus, cow harvest of the herd has been minimal, if present at all, from the 1990s to the present. Given the strong influence of adult female survival on ungulate population dynamics (Gaillard *et al.*, 2000) the lack of a cow harvest may have contributed to this increase.

The increasing trends in the AH and AWB suggests there is little evidence that interspecific competition between caribou and bison has resulted in a decline of the caribou population. Fischer & Gates (2005) found little basis for competition between AH and AWB based on winter habitat and diet overlap. However, we are unable to assess what the trend in AH would have been in the absence of the AWB.

Conclusion

Overall we deemed the temporary dye mark-resight approach effective in our estimation of abundance of two ungulate populations. A key benefit of this approach is the relative speed in which many animals can be marked, greatly increasing the precision in the population estimate. Dye marks can be the sole marking source or can be used to augment existing marks (e.g., radio-collars) as was the case with the AWB survey. Augmenting existing marks may be useful in situations where, for example, only females are radio-collared and males are unmarked and spatially separated from females. In such situations making inferences on male resighting rates from marked females may be unjustified. Further, the general statistical framework (i.e., numbers of marked and unmarked animals observed during a survey) of this approach is relatively intuitive and may be easier to communicate to the public than more complex quantitative methods. Mark-resight estimators (McClintock & White, in press) have recently been incorporated into the software MARK (White & Burnham, 1999), greatly enhancing the ability to model both abundance and resighting rates, including the specification of temporal, group-level, and individual covariates.

A final recommendation we offer relates to the use of terminology. We use the term dye-marks rather than paintballs when discussing this methodology. We feel this euphemism conveys a more professional attitude towards the survey approach. Indeed, in many areas biologists must be aware of and respect cultural sensitivities surrounding the impact of research or management activities on wildlife (e.g., Wilson & McMahon, 2006). Use of less technical terms such as "paintballs" may convey a message that this survey approach is less rigorous than it actually is, and that in fact marking animals with dye may be less invasive than marking with collars which requires capture and handling.

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The effect of temporal sampling regime on the characterization of home range for female boreal woodland caribou (*Rangifer tarandus caribou*) in Labrador, Canada

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Abstract: Our objective was to determine the influence of temporal sampling regime on the characteristics of individual female caribou home ranges and to explore implications of these findings to the conservation of caribou. The study population was 24 adult female caribou monitored for between 4 and 11 consecutive years between 1986 and 2009 from the Red Wine Mountain (RWM) and Lac Joseph (LJ) herds of boreal caribou in Labrador. We evaluated the influence of length of the monitoring period on the size of home ranges and fidelity of caribou to their ranges by measuring the percent overlap of multi-annual ranges on the total time period a caribou was collared and by calculating displacement between centroids of annual and multi-annual ranges for a given caribou. We found that the size of the range increased with each additional year of monitoring—initially at a rate greater than 20% per year, and then more slowly until an asymptote was reached after 7 years. The distance ratio declined with an increase in the monitoring interval until after approximately 6 years of monitoring. Finally, we evaluated trade-offs between monitoring interval and sample size by measuring the proportion of the total herd range captured by multi-annual ranges for given monitoring interval and sample size combinations. Caribou with the longest monitoring interval inevitably captured the greatest portion of the range at each given sample size. Only monitoring intervals of 4 years or greater captured more than 65% of the herd range even when sample size was doubled for shorter monitoring intervals. Our results suggest that long term monitoring is important when defining the extent of caribou ranges.

Key words: fidelity; home range; monitoring regime; *Rangifer tarandus caribou*; temporal scale.

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Introduction

Boreal caribou *Rangifer tarandus caribou* have experienced range contractions and population declines over the past three decades in North America. Forest-dwelling caribou belong to the sedentary ecotype and are distinguished by their dispersion during calving and because they are distributed as individuals and small groups (rather than large aggregations) throughout their range (Bergerud *et al.*, 2008). The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has assessed boreal caribou as 'threatened', and they are legally listed under the federal Species at Risk Act (SARA) and are afforded protection in several provincial and territorial jurisdictions. A central requirement of recovery planning for Boreal caribou is the identification of critical habitat, or habitat essential to the survival and recovery of the species. A crucial element of the determination of critical habitat is the determination of individual and local population ranges (Environment Canada, 2008). Range size and the tendency of an animal to return to the same range during consecutive years (fidelity) reflect the interaction between an individual and its environment, and have direct ramifications for survival, predation and reproduction. Caribou range use varies over different spatial and temporal scales (Rettie & Messier, 2000; Schaefer *et al.*, 2000; Johnson *et al.*, 2004; Mayor *et al.*, 2009) as foraging strategies, and reducing risk of exposure to parasites and predators occur at fine and coarse scales. Anthropogenic footprints can also influence range use (Nellemann & Cameron, 1998; Nellemann *et al.*, 2003; Dyer *et al.*, 2001, 2002; Banks *et al.*, 2007; Courtois *et al.*, 2007; Faille *et al.*, 2010). Collectively, this suggests that a conceptually simple task (e.g. mapping) is fraught with complexity imbued by the ecology of caribou themselves and the properties of the landscapes they occupy.

Home range is the area used by an animal over a given time interval (White & Garrot, 1990), and is described through the compilation of radio telemetry data over time. There are significant costs associated with radio telemetry of long-lived animals over vast areas and there is little guidance in the literature on how to prioritize sampling effort. The null model of home range area is that a 'true' home range size is reached with increasing sample size. Correspondingly, numerous efforts have been directed at determining the minimum number of fixes (e.g., Seaman *et al.*, 1999) and the methods used to accurately describe a home range (Burgman & Fox, 2003; Laver & Kelley, 2008). However, other studies suggest there may be trade-offs between the number of fixes, the number of individuals sampled, and the sampling interval (Hansteen *et al.* 1997). In their study of moose habitat selection under various sampling regimes, Girard *et al.* (2006) suggested that researchers prioritize the number of individuals studied rather than the number of locations per individual. Similarly, Börger *et al.* (2006) found that inter-animal variation affected home range size, and recommended that more individuals should be sampled over long periods at the expense of sampling rate per individual.

Sampling a representative distribution over time is complicated for boreal caribou as they are long-lived and occur over vast areas in dynamic landscapes. In Labrador, boreal caribou populations exhibit subpopulation structure where the population is comprised of numerous subpopulations, isolated by distance and sometimes by geographic barriers (Schaefer *et al.*, 2001). This poses considerable difficulty in obtaining a representative sample which accurately describes the local population range particularly where subpopulation structure is not known and the allocation of sampling effort is not distributed equally throughout the range. Populations are composed of groups of individuals which are exposed to varying environmental conditions over space and time. Home ranges are the manifestation of interactions between an individual and its environment (Brown *et al.*, 1996). For this reason many resource selection analyses use individuals as the sampling unit (Manly 1993) and measure use at the home range scale (2nd order design of Johnson, 1980). While several studies have characterized caribou home ranges, the potential influence of the monitoring interval on the size of and fidelity of caribou to home ranges for caribou has not yet been reported. In general, studies are restricted to 2-3 years of consecutive monitoring (Rettie & Messier, 2000; Brown *et al.*, 2001; Mosnier *et al.*, 2003). However, caribou use of landscapes is affected by factors such as fire, insect harassment and snow and ice conditions, all of which may vary temporally in terms of their effect on the landscape, and suggest that time itself may be a component of home range expression in caribou, particularly given their longevity. Consequently the interpretation and comparison of existing studies, and any recommendations pertaining to a sampling regime, are constrained.

The objective of this study is to determine the extent to which temporal sampling regime influences the characterization of individual female caribou home ranges. A secondary objective is to evaluate trade-offs between the length of the monitoring interval and sample size in describing herd ranges, and to make recommendations regarding alternatives which allow for an optimal allocation of monitoring effort. The study populations in Labrador, Canada, occur in a relatively pristine landscape and therefore allow consideration of range use under natural conditions.

Methods

Study area

The Red Wine Mountain (RWM) and Lac Joseph (LJ) are boreal caribou herds in central Labrador, Canada (Fig. 1). They are two of three 'threatened' populations that form a continuum across south-central Labrador and northeastern Québec, with respective range sizes of 5900 km^2 and 4600 km^2. Herd ranges overlap to a small degree, and during winter migratory forest-tundra caribou enter northern portions of the RWM (and to a lesser degree, LJ ranges) resulting in intermingling of animals (Schmelzer *et al.*, 2004). The Lac Joseph herd currently numbers approximately 1300 animals (Schmelzer, 2011). Historical surveys suggest this population declined from 1300 caribou in 1977 to less than 500 during the mid 1980s. Between 1986 and 2000 the population grew at 10%/yr to more than 2000 individuals, and since then has undergone a decline of approximately 7%/yr (Schmelzer *et al.*, 2004; Schmelzer, 2011). Declines have been attributed to overharvest and partial loss of a calving area due to hydro-electric development (Bergerud *et al.*, 2008; Schmelzer *et al.*, 2004). The Red Wine Mountain population currently numbers less than 100 individuals, a significant decline from the 600 to 750 individuals surveyed during the 1980s. Between 1989 and 1997 the herd declined by 85%, from 741 to 129. Since 2001, incursion of migratory George River caribou into the winter ranges of this herd has precluded a census. A count (2009) of all caribou associated with radio-collared individuals (conducted while populations were still separate) indicates that there are at least 75 caribou remaining in this population. The cause of the population decline remains unclear, however Bergerud *et al.* (2008) suggest a demographic explanation, specifically low adult female survival and poor calf recruitment during the mid 1990s. Mean survival rates between 1997 and 2009 indicate that these have returned to levels observed prior to the decline. Wolf predation is the primary source of mortality in both populations (Wildlife Division, unpubl. data). Other sources of mortality include incidental and subsistence hunting, which occurs primarily during incursion of migratory caribou.

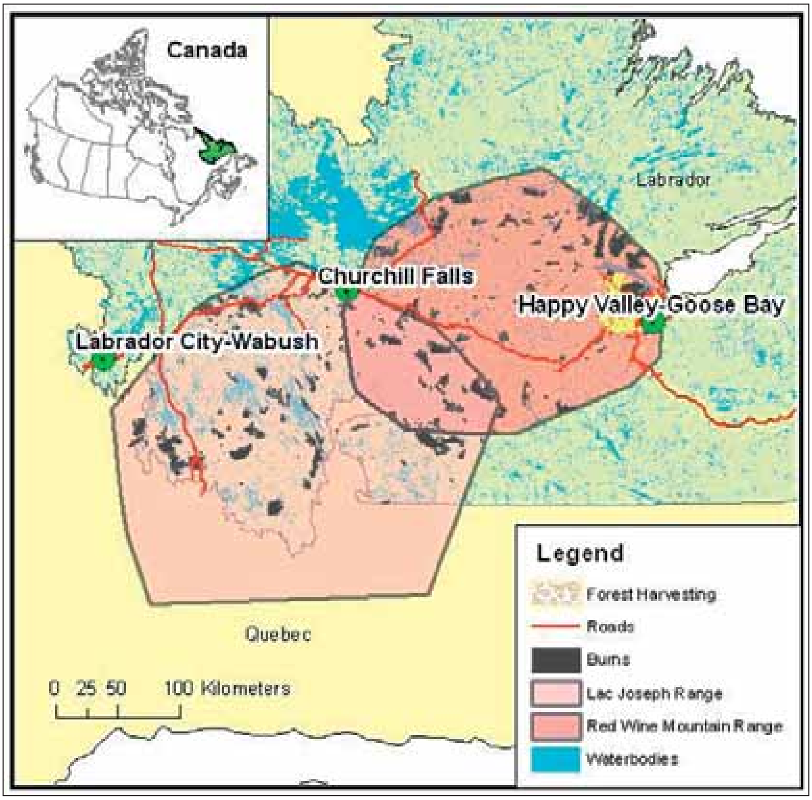

Fig. 1. Range boundaries of the Lac Joseph and Red Wine Mountain caribou populations.

The study populations are located in the Taiga Shield Ecozone (NRCAN, 2007). The landscape includes many glacial features such as eskers and moraines. Lakes, extensive peatlands and open-canopied spruce-lichen woodlands dominate the landscape of the Taiga Shield. Black spruce (*Picea mariana*) is the dominant tree species; however, white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*) and white birch (*Betula papyrifera*) also occur intermittently. Lichens (*Cladonia* and *Cladina* spp) are the primary understory species in lichen woodlands, and often co-occur with ericaceous plants such as northern blueberry (*Vaccinium boreale*) and mountain cranberry (*Vaccinium vitaes-idaea)* (Roberts *et al.*, 2006). Only 5.9% and 10.8% of the population's range for LJ and RWM, respectively, is affected by anthropogenic or natural disturbances (Environment Canada, 2008; Appendix 6.5). Range disturbance is primarily due to fire, but also included industrial disturbance such as linear features (roads, railroads, transmission corridors and skidoo trails) and commercial forestry.

Radio telemetry

We evaluated the effect of the monitoring period on the size and location of home ranges using two methods: by measuring the percent overlap of multi-annual ranges on the total monitored range, and by calculating displacement between centroids of annual ranges for a given caribou. The study population was 24 adult female (> 20 months) caribou monitored for between 4 and 11 consecutive years. Caribou were selected on the basis of having a) at least 4 consecutive years of monitoring and b) at least 12 locations per year distributed among all seasons, and a minimum of 100 locations in total (range 12 – 597 locations/yr). The sample unit is the individual animal. Adult female caribou were captured and fitted with either ARGOS satellite collars or GPS collars between 1986 and 2009 and equipped with satellite-tracked ultra-high frequency Platform Terminal Transmitters (PTTs; Service ARGOS, Landover Maryland, USA) or GPS (2007-2009) receivers. PTTs were programmed to a 4-day transmission cycle, and GPS collars to a daily or twice daily transmission cycle. When possible, collars were replaced prior to battery exhaustion. Annual rates of parturition were obtained by post partum aerial surveys of radio-collared adult females between 1982-88 and 1993-1997 for the RWM population and indicated a parturition rate of 78%, and 71% respectively for these periods. Parturition rates are unknown for LJ caribou; however the mean recruitment rate 1998 to 2009 in this population is 21%, double that of the RWM herd (Wildlife Division, Government of Newfoundland and Labrador, unpubl. data).

In order to identify potentially erroneous locations, we calculated Keatings epsilon (Keating, 1994) and retained locations in the 95th or greater percentile only if they could be corroborated by a second transmission (of class 1-3) from the same time period, or were part of a uni-directional movement such as a movement to a different area. Locations belonging to location quality (NQ) class 3 (error < 150 m, ARGOS User's manual) were retained on the basis of one location per transmission day per collar. The total monitoring period for each individual and the number of ARGOS and GPS locations used in each analysis is given in Table 1.

Table 1. A list individual caribou, their associated population, total number of years monitored, and the corresponding number of ARGOS and/or GPS telemetry data points.

Population	Years	Number of locations
RWM1	4	167
RWM2	4	300
RWM3	4	256
RWM4	5	251
RWM5	6	359
RWM6	6	159
RWM7	6	315
RWM8	7	345
LJ1	7	702
LJ2	7	134
RWM9	8	183
RWM10	8	1023
RWM11	8	244
LJ3	8	217
LJ4	8	303
LJ5	8	187
LJ6	8	1237
RWM12	9	986
RWM13	9	197
RWM14	10	129
LJ7	10	448
LJ8	10	1340
LJ9	10	1176
RWM15	11	332
Total		10990

Data analysis

Each annual range, as well as every possible combination of multi-annual home ranges was calculated for all female caribou included in the study using Hawth's Tools (version 3.27 for ArcGIS 9.3; Beyer, 2004). In all cases, Minimum Convex Polygons (100% MCPs) were used (Mohr, 1947). A 'total range', using all locations from an individual's entire monitoring period, was also calculated. The percent overlap of each annual and multi-annual range on the 'total range' was calculated for each individual. Multi-annual ranges were constructed for every possible combination of consecutive-year values. For example, for an animal monitored for 10 consecutive years, there are 9 combinations of consecutive 2-year combinations, eight combinations of consecutive

3-year monitoring periods, seven 4-year monitoring periods and so on. Areas for each polygon were calculated in km^2. Finally, the mean and standard error of the percent overlap between multi-annual and 'total' ranges was calculated as a function of the length of the monitoring interval for each population. The latter was plotted and fitted with a polynomial trend line summarizing the relationship and its explanatory power via a coefficient of determination (r^2). The difference in mean values in area and percent overlap between populations was explicitly compared using an independent sample *t*-test for each monitoring interval. All tests were set at $\alpha = 0.05/10$ or 0.005 (Bonferonni adjustment for 10 comparisons) and were two-tailed.

Sample size

We created 9 random subsamples of radio locations which incrementally removed between 10 and 90 percent of the data at 10% intervals. This process was repeated five times for each individual. A MCP was generated for each iteration, and the mean area calculated and compared to the MCP generated for that individual using all data over its sampling period. We felt this approach was preferable to the conventional one which plots range size versus sample size given inter-animal variability in range size and differences in the length of monitoring intervals between individuals (e.g. more locations are required to describe a larger range size). The mean proportion and standard error of the 100% MCP captured for a given individual was plotted as a function of the subset of data retained and sample size.

Assessing dispersion

Displacement between annual ranges was determined using a displacement ratio (scaled between 0 and 1) which was a function of the distance between the first and last year for the 'total' or lifetime monitoring interval and the sum of distances between centroids of consecutive years:

$$DR = \frac{\text{Distance between centroïds of first and last year}}{\sum \text{Distance between centroïds of consecutive years}}$$

Centroids were created using the Hawth's Tools (version 3.27 for ArcGIS 9.3; Beyer, 2004). The displacement ratio (DR) was calculated for every possible combination of consecutive years for each animal, as for the prior analysis. A large ratio (close to 1) was indicative of an individual whose 'final' or total range was increasingly distant from its initial range (e.g. a lack of fidelity); while a small value (close to 0) represents an individual whose 'final' range was relatively close to its initial range. For the purpose of this study, fidelity is defined as the tendency to return to the same or similar place (Schaefer *et al.* 2000), here expressed as the DR. The Displacement Ratio was plotted as a function of the difference (in years) between the first and last year, or the monitoring interval between centroids. In order to correct for inter-animal variation, 7 plots were drawn for each sample population—one for each combination of years of data between 4 and 10 years. Each plot was fitted with a best fit trend line and the coefficient of determination (r^2) was calculated for each model. Corresponding distances (and standard deviation) between centroids for every monitoring interval were also calculated in kilometres. Finally, the mean and standard error of the distance ratio as a function of the duration of the monitoring interval was calculated for each population. The latter was plotted and fitted with a polynomial trend line summarizing the relationship and its explanatory power via a coefficient of determination (r^2). The difference in mean values for distance ratios for each monitoring interval was compared between LJ and RWM populations using an independent sample t-test for each monitoring interval. All tests were set at $\alpha = 0.005$ and were two-tailed.

Determining an optimal monitoring regime

We defined an optimal sampling regime as one which captured the greatest proportion of the herd range with the smallest allocation of effort, where effort is a function of the number of years of monitoring and the number of collared animals. We measured the proportion of the total herd range captured by multi-annual ranges for a given monitoring interval and sample size. This analysis was restricted to the RWM population, and to telemetry data collected for caribou monitored 4-11 years as in the prior analyses. To calculate the proportion of the total herd range captured we plotted and calculated total area for MCPs used in each monitoring interval/sample size pairing (using the merge and dissolve feature in ArcGIS 9.3) and compared them to the total range area for each herd. The total herd range was determined by pooling all data excluding emigrations outside the herd range from 1982 to 2010 using a 100% MCP, a region encompassing 42 536.07 km^2.

As with the prior analyses, multi-annual ranges were constructed for every possible combination of consecutive-year values. The number of possible combinations (z) for each monitoring interval and sample size pairing was calculated using the following formula, where n equals the number of possible MCPs to select from, and r equals the number of caribou

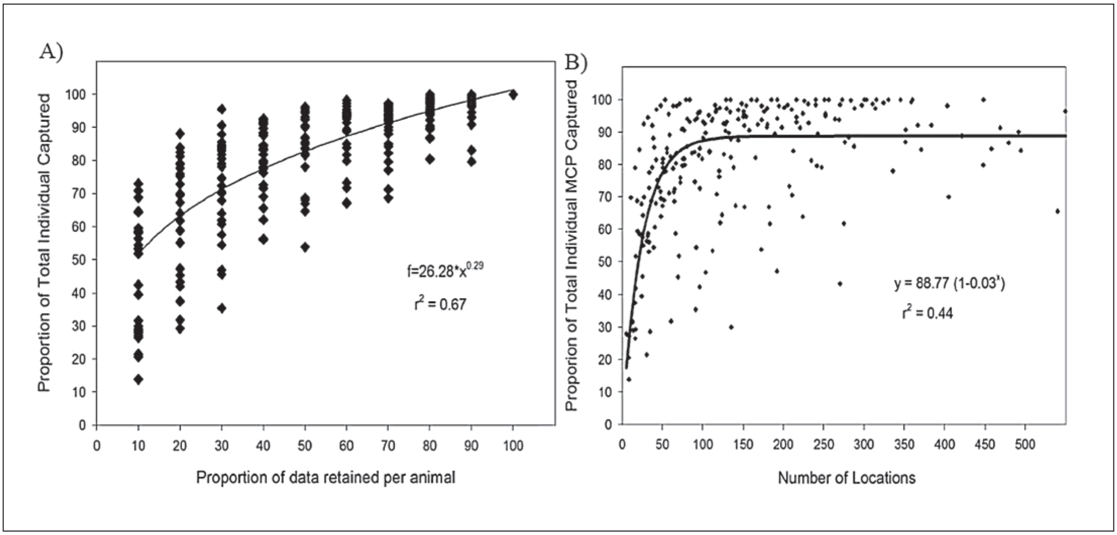

Fig. 2. Relationship between the proportion of individual 100% MCP range captured and a) the proportion of locations used per individual and b) the number of locations used.

included in each selection. The equation assumes that order of combinations is not important, and no repetitions of any combinations:

$$z = \frac{n!}{(n-r)!} \times \frac{1}{r!} = \frac{n!}{r!(n-r)!}$$

For example, there are 18 564 possible combinations of 6 animals monitored for 2 consecutive years. Consequently we included every other monitoring interval from 2 to 8 years, and stepped sample size by an interval of 2 from 2 to 18 animals. We also limited the number of comparisons from each number of animals/monitoring interval combination to twenty random selections. These twenty selections were chosen by assigning a random number between 0 and 1 (the number of decimal places included being determined by the number of possible combinations, i.e., for 18564 combinations, 5 decimal places were used) to each combination, and then choosing the twenty combinations with the lowest random numbers. Within each random grouping of animals, no animal was used more than once. If a combination was generated that included a given animal more than once, it was discounted and the next random combination of animal/monitoring interval was chosen. The mean and standard error of the proportion of total herd range captured as a function of the number of radio-collared animals was calculated and plotted for each interval.

Results

The relationship between the number of locations and the proportion of the total range of a given individual being captured was curvilinear and indicated no improvement after 100 locations irrespective of the size (Fig. 2b). Caribou with fewer than 100 locations in total were removed from the analysis. In contrast, as few as 40 locations described 70% of the total range for a given caribou. A significant portion of an individual animals' data could be removed and still describe the total home range adequately; removing 30% of the data still captured approximately 90% of the total range (Fig. 2a). Note that since these locations were selected randomly from the dataset collected over the lifetime of an individual they cannot be assumed to be equivalent to the first 40 locations collected in a monitoring program.

Caribou in both populations added new areas into their annual ranges with each additional year of monitoring—initially at a rate greater than 20% per year (between the first and second year of monitoring), and then more slowly, at a rate of less than 5% /yr after 7 consecutive years of monitoring, when an asymptote is reached (Fig. 3a). In both populations, mean percent overlap for a single annual home range is less than 20% of the total estimated range. After 3 years of consecutive monitoring, only 50% of the 'total' range for a given animal had been described in either population. Between 4 to 7 years of consecutive years of monitoring, the rate of overlap increased from 59% to 80% (LJ) and 65% to 90%, (RWM). Limited additional area (an increase of less than 2%

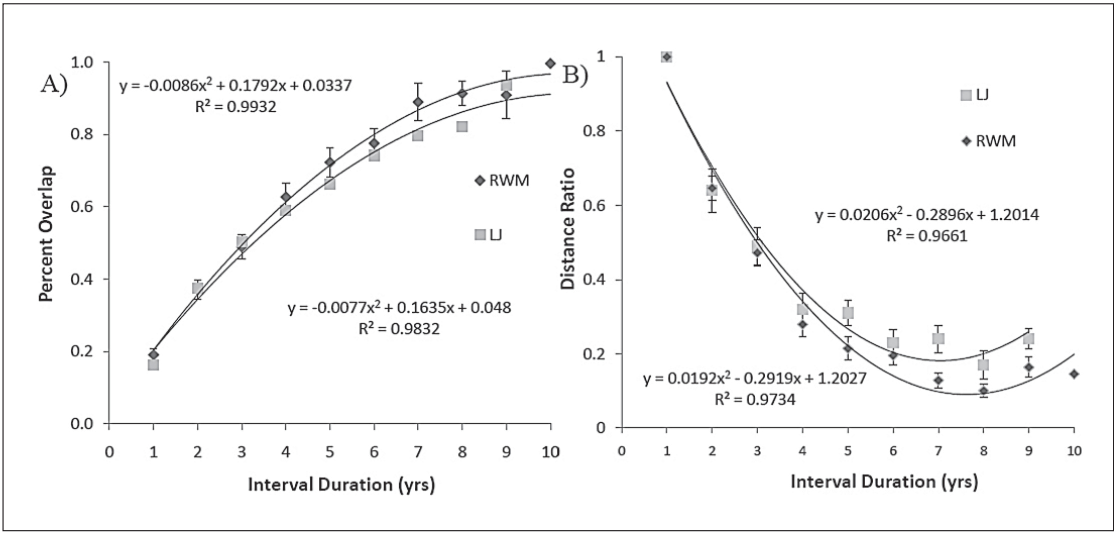

Fig. 3. A) Mean percent overlap (and standard error) between annual and multi-annual ranges on the 'total' range used by each caribou in RWM (r^2=0.993) and LJ (r^2=0.983) populations. Multi-annual ranges were constructed for every possible combination of consecutive-year values for each individual.
B) Mean displacement ratio (and standard errors) shown in relation to the monitoring interval duration (consecutive years). A large ratio (close to 1) indicates an individual's lifetime range was distant from its initial range (e.g. a lack of fidelity) while a small value (close to 0) suggests site fidelity.

Table 2. Mean range area (and standard error) for all calculated ranges, the corresponding duration of the monitoring interval and number of ranges in LJ and RWM populations. There were no significant differences at $P < 0.005$ (Bonferroni adjustment for 10 comparisons) in mean range area for any time interval.

LJ			RWM		
Years	Mean km^2 (SE)	N (# Ranges)	Years	Mean km^2 (SE)	N (# Ranges)
1	2090.44 (251.98)	72	1	1820.58 (221.30)	99
2	3318.05 (350.67)	61	2	3579.10 (394.66)	82
3	4600.54 (491.43)	52	3	4960.21 (559.72)	68
4	5584.29 (644.02)	44	4	6615.25 (731.52)	55
5	6482.66 (826.30)	36	5	8286.15 (941.88)	43
6	7216.9 (1075.53)	29	6	10346.60 (1182.45)	31
7	7658.31 (1358.36)	21	7	12456.84 (1477.95)	22
8	8151.48 (1858.24)	13	8	13304.27 (1768.96)	14
9	10177.76 (3685.64)	6	9	13423.62 (2514.29)	7
10	10561.34 (5770.02)	3	10	11693.77 (412.68)	3
			11	12152	1

per additional monitoring year) was added into the total range after 7 years of monitoring. There were no significant differences in mean percent overlap at any of the time intervals between the two populations.

Mean areas for annual and multi-annual ranges also increased with the length of the monitoring period (Table 2). There was a linear relationship between the overlapping area of multi-annual ranges and range size for both the LJ and RWM populations (r^2 = 0.97 for both). As a whole range sizes were significantly larger for the RWM caribou, at 5650 ± 259 km^2 versus 4866± 256 km^2 for LJ caribou (F

= 5.26, P = 0.02). These sizes were attained after approximately 4 years of consecutive monitoring in both populations (Table 2). After 2 years of monitoring, range sizes were approximately 3300 km^2 for each population. Range sizes were remarkably similar for LJ and RWM caribou for the first 3 years of monitoring (Table 2), but after 4 years of monitoring there was a tendency for larger ranges in each monitoring interval for RWM caribou. Range sizes were marginally significant for RWM caribou after 7 years of monitoring (t = 2.17, P = 0.03), and also for intervals of 6 and 8 years (P < 0.1; Table 2). Fewer than 10 animals were monitored for more than 9 consecutive years so range sizes for intervals of 9 and 10 should be interpreted cautiously.

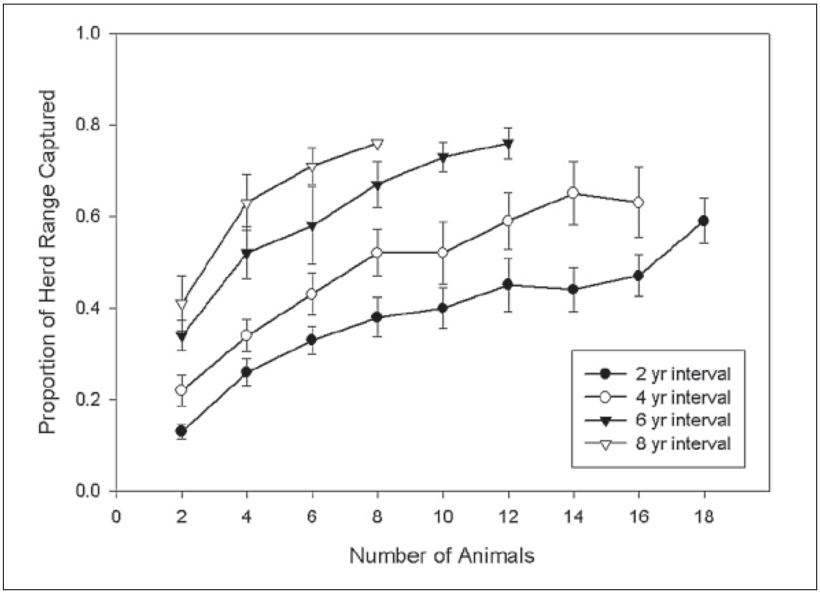

Fig. 4. Trade-offs between length of monitoring interval and number of caribou monitored with description of the population range for the Red Wine Mountain herd, Labrador. Each curve represents a monitoring interval of a different length. Values represent averages calculated from twenty repetitions randomly sampled from potential combinations of sample size/interval length groupings.

Displacement

The distance between centroids of annual or multi-annual ranges declined with an increase in the monitoring interval until it reached a plateau after approximately 5 years of monitoring (Fig. 6). The relationship is well-described by the second order polynomial $y = 0.0206x^2 - 0.2896x + 1.2014$ for LJ and $y = 0.0192x^2 - 0.2919x + 1.2027$ for RWM, respectively (Fig. 3b). For monitoring periods of less than 3 consecutive years, the distance ratio was high (> 0.4), indicating that the centroid of a caribou's 'total range' range was distant from its initial range (e.g., a lack of fidelity). As the length of the monitoring interval increased, the distance between lifetime and monitoring interval centroids also decreased, suggesting fidelity to a particular region (e.g., the center of the range had been captured during the monitoring interval). After 6 years of monitoring, there was little further decline in the distance ratio for the LJ population while RWM continued to decrease the DR for one additional year. Mean distance between centroids ranged from 17.66 km to 39.5 km for LJ caribou and 11.86km and 43.8km for RWM, though distances were quite variable overall. The mean distance between centroids was 22 km for LJ caribou and 28 km for RWM caribou, a result that is consistent with the larger range sizes observed in RWM caribou.

Monitoring regime

Caribou with the longest monitoring interval inevitably captured the greatest portion of the range at each given sample size (Fig. 4). Further, only monitoring intervals of 4 years or more captured greater than 65% of the herd range, a rate that was never achieved even when 18 animals were followed for two years. The proportion of herd range captured also increased with sample size, with the greatest increases occurring between sample sizes of two and four across all monitoring intervals, particularly for monitoring intervals of six or eight years (18% and 22% increase respectively). Increasing the sample size from four to six caribou resulted in an increase of 6-9% across all intervals, a result that was duplicated over the sample sizes six to eight. The rate at which the herd range was captured reached an asymptote after eight animals had been collared across all monitoring intervals, though there was a tendency for longer monitoring intervals to continue to describe the herd range at larger sample sizes. For example, at a monitoring interval of two years, the proportion captured increased by less than 10% even when sample size was doubled from 8 to 16 caribou (0.38 to 0.47; Fig.

4). However, the proportion of the range described increased by 12% between 16 and 18 individuals monitored for two years, (0.47 to 0.59). The herd range was best described (76% of the range captured) by monitoring 8 animals for 8 years (though it was not possible to evaluate a larger sample size for this monitoring interval).

Discussion

Our results demonstrate that duration of monitoring influences the measured size of female caribou home ranges in Labrador. Overall, results were consistent between the analyses and between the two populations; asymptotes occurred at similar sampling intervals. For example, few additional areas were added after 7 years of monitoring, which captured 80 and 90% respectively, of the total range for the LJ and RWM individual caribou studied, and the majority of the lifetime range had been previously defined in both populations after 5 years of consecutive monitoring. Similarly, caribou home ranges exhibited fidelity after 6 years of monitoring (LJ) and 7 (RWM) years respectively.

For cows in the two herds, a monitoring interval of 2 years captured only 38% of the lifetime range and exhibited displacement consistent with a lack of fidelity to the previous year's range. Notably, the degree of inter-annual range fidelity over the 3-year monitoring period (50%) was similar to that reported by Faille *et al.* (2010), and Rettie & Messier (2001), which reported 0.45 and 0.52, respectively, for caribou monitored for the same duration and in relatively undisturbed landscapes. Mean overlap reported in Tracz *et al.* (2010) was 0.76, though caribou in their study were located in a landscape heavily impacted by petroleum development. A sampling framework that would allow the description of 80% of the total range of an individual caribou and a relatively stationary location (DR < 0.25) and 75% of the total area would require six years of consecutive monitoring. The minimum length of the monitoring period should be considered as four years, as this marks the initiation of the asymptote in both Distance Ratio and degree of overlap between lifetime and monitoring interval ranges, and any temporal sampling regime shorter than that would be associated with a high degree of uncertainty in the description of the individual range. Conversely, there is little benefit to a monitoring period of longer than seven years per individual, though it is possible that this is related to reproductive senescence associated with older age (e.g., Rettie & Messier, 2001).

There were several alternative designs for a monitoring program that balanced length of the monitoring interval and sample size for a desired level of herd range description. For example, to capture 40% of the RWM herd range, two caribou could be monitored for eight years (16 animal years), four animals for six years, six animals for four years (24 animal years) or 10 animals for two years (20 animal years). In this case the smallest allocation of effort is given by the first scenario. There were no alternatives with a monitoring interval of less than six years that captured at least 70% of the herd range (six animals for eight years or 10 animals for six years), though this might change if more than 20 caribou were included in a telemetry program at once. These similarities show that in this instance a longer monitoring interval can be used in conjunction with a smaller sample size and yield a comparable result with fewer total monitoring years. An ideal allocation of field effort should attempt to capture lifetime ranges of individual caribou as well as describe the range as a whole. In this study these objectives were mutually supportive; long-term monitoring enhanced description of both the individual and herd range.

One of the strengths of this study is that it does not use simulated data (e.g. Burgman & Fox, 2003). However, field derived data sets are invariably governed by logistical and financial constraints that limit the size and properties of the dataset. As a result, we could not partition the individual effects of fix rate and length of the temporal sampling regime due to the relatively late advent of the use of GPS collars (2007) and the long time frame of the monitoring intervals we evaluated. Accordingly, we cannot explicitly rule out the possibility that our result is an artefact of relatively low sample size per animal per year (e.g. that the length of the monitoring interval required would decline with a larger number of fixes per individual). However our analyses suggest that our findings are robust: we could remove a third of the data for a given caribou and still capture the vast majority (90%) of a total home range. Under ideal circumstances however, each annual range would have 100 telemetry locations distributed equally throughout the seasons, and the increase availability of multi-year datasets from GPS-collared individuals should facilitate meeting this criteria in the future. Finally, we examined the influence of the monitoring period on the description of caribou home ranges in isolation of other factors that may influence range size. For example, fidelity has previously been found to be associated with individual reproductive status or population social structure (Rettie & Messier, 2001; Wittmer *et al.*, 2006). Consequently the relative influence of these or other factors cannot be assessed in conjunction with the temporal sampling regime.

Home range sizes were compiled for 10 different studies throughout Canada which monitored adult female caribou (Table 3). The monitoring intervals of these studies ranged from 10 months to 8 years, and mean annual caribou range sizes varied from 208 km^2 to 4790 km^2. The majority of studies tracked individuals for less than 3 years, and often home ranges sizes were constructed from data pooled over a variety of monitoring intervals.

In this study, caribou occurred in ranges several thousand square kilometres in size (as also seen in Brown *et al.*, 2001), and added new areas with each passing year, a life history strategy consistent with that of a long-lived animal maintaining low densities on the landscape. In Labrador, the density of caribou measured during surveys in the core ranges varies between 0.03-0.05 caribou per km^2 (Schmelzer *et al.*, 2004; WD unpubl. data). Maintaining large home ranges and low densities is a life history strategy that allows caribou to avoid detection and predation by wolves and other predators (Bergerud, 1992), and limit exposure to parasites which influence body condition and fitness (Bordes *et al.*, 2009; Gunn & Irvine, 2003). Fragmentation and direct or effective loss of available habitat as a result of anthropogenic change has been linked to range loss and caribou extirpation (e.g., Schaefer, 2003; Vors *et al.*, 2007). Caribou have been shown to avoid roads and seismic lines (Dyer *et al.*, 2001, 2002), transmission corridors, (Nellemann *et al.*, 2003), forest harvesting (Smith *et al.*, 2000; Schaefer, 2003; Houle *et al.*, 2010) and other types of disturbance. This effective loss of area fragments ranges and likely constrains choice (e.g., to selection of remnants of high value habitats). Given the small anthropogenic footprint within the herd ranges of the two populations we studied, our results suggest that in undisturbed landscapes caribou shift ranges and make use of large areas throughout their lifetime. However, given the relative lack of pristine areas throughout the distribution of boreal caribou in North America (Environment Canada, 2008), the likelihood that caribou movements within more disturbed landscapes would be constrained—and hence that the 'lifetime' range of a caribou might be measured over a shorter timeframe and at a smaller spatial scale—is possible. This phenomenon was recently documented by Faille *et al.* (2010), who found that the degree of anthropogenic disturbance was the mirror image of annual home range size. Similarly, caribou living in ranges with a lower disturbance rate occupied greater areas (Smith *et al.*, 2000; Dyer *et al.* 2002). Several other studies are in agreement with the latter studies: range overlap over time was much higher (0.76) for caribou ranges in Alberta with high levels of petroleum development (Tracz *et al.*, 2010), and home range size and movement rate of adult female caribou decreased as the anthropogenic footprint increased in central Saskatchewan (Arlt & Manseau, 2011). Similarly, home range sizes measured for populations in western Canada (excluding the NWT), which tend to include greater anthropogenic footprints (Environment Canada, 2008) were much smaller as a whole. In Labrador, cows in both study populations had annual range size very comparable to those of other studies of caribou in relatively intact boreal forest of Eastern Canada.

In conclusion, our results highlight the importance of conducting baseline ecological studies of caribou space use and fidelity to interpret, and manage for, spatial and temporal properties of caribou ranges. Sampling regimes that balances length of the monitoring interval with sample size can be an efficient means of fully describing both individual ranges and that of the population as a whole. While it may take six years to capture range use for a given individual female caribou in Labrador, different ecological conditions and higher densities of caribou elsewhere may result in a different optimal sampling regime. Our intent here is less to emphasize the length of the temporal sampling regime required *per se* but rather to underscore the necessity of evaluating the possible influence of the monitoring interval on the description and interpretation of range sizes for caribou in general, particularly over short monitoring intervals and where these are being used in management and landscape planning. Our review of other studies indicates that home range size is most often reported from data pooled over a variety of monitoring intervals, and generally for monitoring programs of less than three years in duration. This precludes direct comparison of the results of this study to others. If monitoring interval were standardized in the reporting of home range sizes in the future, variability of reported range sizes may well decrease, and inter-annual fidelity of caribou to these ranges may increase. Additional long-term studies, perhaps through retrospective analyses of ongoing monitoring programs, would provide insightful comparisons. As technology associated with radio telemetry improves, studies which include more individuals monitored at a higher sampling intensity will allow for explicit comparison of trade-offs between sampling intensity (number of fixes), relocation interval, and study duration for the design of an optimal sampling regime.

Table 3. Summary of studies reporting home range sizes for woodland caribou.

Study	Eco-type	Range size	# individuals	Monitoring length	Estimator
Brown *et al.*, 2001	Boreal woodland (Ontario)	3664	13	1 year	95% MCP
		4790	20	1 year	
		3212	13	1 year	
		4026	46	3 years	
Courtois *et al.*, 2007	Boreal woodland (Québec)	224	30	1-3 years	100% MCP
		607	55		
		558	19		
		1198	7		
		153	9		
Dalerum *et al.*, 2007	Moutain (Alberta)	1450	28	Mean = 3.25 years	95% fixed kernel
		650	33	Mean = 1.9 years	
		400	44	Mean = 3 years	
Faille *et al.*, 2010	Boreal woodland (Québec)	350	20	1-3 years	100% MCP
		700	17		
		1375	10		
Fuller & Kieth, 1981	Woodland (Alberta)	539	1	3 years	MPP
Larter & Allaire, 2005	Boreal (NWT)	900	1	10 months	MCP
Nagy *et al.*, 2005	Woodland (NWT)	1796	1	1 year	MCP
		1914	1		
Rettie & Messier, 2001	Woodland (Saskatchewan)	208	6	1-3 years	100% MCP
		221	3		
		1240	5		
		413	5		
		404	4		
Schindler, 2005	Woodland (Manitoba)	1235	6	1-8 years	MCP
		1651	9		
		705	12		
		461	5		
		1847	2		
Tracz *et al.*, 2010	Boreal woodland (Alberta)	382	45	Mean = 3.87 years	100% MCP

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The 13th North American Caribou Workshop
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Methods

Population Biology / Ecology

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Are warbles and bots related to reproductive status in West Greenland caribou?

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Abstract: In March-April 2008-09, using CARMA protocols, 81 cows and 16 calves were collected in West Greenland from two caribou populations; Akia-Maniitsoq (AM) and Kangerlussuaq-Sisimiut (KS). In both populations, warble larvae numbers were highest in calves and higher in non-pregnant than pregnant cows. Nose bots showed no relationship with pregnancy or lactation; KS calves had higher nose bot loads than cows, a pattern not observed in AM. Pregnant cows had more rump fat than non-pregnant cows. KS cows lacking rump fat entirely had the highest warble burdens. We observed lactating pregnant cows with moderate larval burdens. Projected energy cost of the heaviest observed combined larvae burdens was equivalent to 2-5 days basal metabolic rate (BMR) for a cow, and 7-12 days BMR for a calf. Foregone fattening in adult cows with average burdens was 0.2 to 0.5 kg, but almost doubled with the heaviest infestations to 0.4 and 0.8 kg. Average burdens in calves resulted in forgone fattening of about 0.5 kg, with peak costs equivalent to 0.7 and 1.1 kg fat for AM and KS calves respectively. Although modest, these projected energy costs of hosting larvae for cows support the negative relationship between rump fat and larvae burden. For calves, hosting high burdens of warble larvae could affect winter survival, specifically those weaned normally in October or in early winter. Harmful effects of oestrid larvae burdens may remain subtle but clearly cumulative in relation to seasonal forage availability and incidence of other parasites.

Key words: energetics; nose bot larvae; oestridae; *Rangifer*; reproduction; survival; warble larvae.

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Introduction

Parasites are increasingly considered to play an important role in cycles of host abundance and population dynamics (Hudson *et al.,* 2001; Gunn & Irvine, 2003). In totally or relatively predator-free environments, gastro-intestinal parasites with direct life-cycles, have been shown to have population level consequences in hares (*Lepus timidus*), feral Soay sheep (*Ovis aries*) and Svalbard reindeer (*Rangifer tarandus platyrhynchus*), reducing fecundity and contributing to population instability (Dobson & Hudson, 1992; Gulland *et al*., 1993; Iver *et al*., 2002; Albon *et al*., 2004; Newery & Thirgood, 2004). The parasite–mediated reduction in calf production in Svalbard reindeer was dependent on parasite density in the host, which in turn was a delayed density dependent response to host densities (Albon *et al*., 2004). The effects of other direct life-cycle parasites in predator-free environments are not well understood.

Whereas intestinal parasites exert influence through metabolic effects within the host (Hudson *et al*., 2001; Gunn & Irvine 2003), macro-parasites such as larvae of warble (*Hypoderma tarandi*) and nose bot flies (*Cephenemyia trompe*) of the Oestridae family, that are host-specific endoparasites in reindeer and caribou (*Rangifer tarandus*), as well as having metabolic costs, also cause energetically costly behavioural responses. In summer, the presence of adult oestrid flies can provoke intense behavioural responses in *Rangifer*, disturbing foraging and increasing movement (Kelsall, 1968; White *et al*., 1975, Reimers, 1980; Helle & Tarvainen, 1984; Kojola, 1991; Walsh *et al*., 1992; Russell, *et al*., 1993; Iver *et al*., 2002; Bergerud *et al*., 2008; Witter *et al*., 2011). Adult flies are strong fast fliers (Nilssen & Anderson 1995), which make it easy to locate, track and follow their hosts (Iver, *et al*., 2002). Hot summers increase adult fly activity and thus harassment of caribou (Thomas & Kiliaan, 1990; Folstad *et al*., 1991; Nilssen & Haugerud, 1994; Mörschell, 1999; Witter *et al*., 2011). An extreme example of the influence of oestrid flies was the summer of 1977 in north-west Alaska. High temperatures and exceptionally low precipitation (Haugen & Brown, 1980) resulted in warble fly harassment and overwinter loss of a portion of the 1977 calf cohort. Warble larvae numbered between 1900 and 2000 in one dead calf (Davis *et al*., 1980), in excess of 1000 in others (White, unpubl. data), and upon palpation, hides of these dead calves resembled bubble-wrap in appearance and texture (White, unpubl. observations). In semi-domestic reindeer extreme cases of parasitic larvae infection, which weaken body condition, can cause death (Helle, 1980; Folstad, *et al*., 1989). Scandinavian reindeer husbandry considers warbles the parasite causing the most losses (Josefsen *et al*., 2006). Thus combined effects of adult warble fly disturbance and the energetic cost of harbouring larval stages internally can impact demography. In addition to mortality, a negative relationship between the number of warble larvae and the probability of pregnancy, or of fat reserves in cows in late winter, could also drive demographic outcomes (Thomas & Kiliaan, 1990; Hughes *et al*., 2009).

Oestrid flies have a one year direct life cycle, with no intermediate hosts (Savel'ev, 1961; Anderson & Nilssen, 1990; Nilssen & Haugerud, 1994, 1995; Nilssen, 1997). Adult flies develop and mate in summer, while larvae over-winter inside reindeer/caribou. Over-wintering warble larvae live under the skin, typically on either side of the host's spine, and nose bot larvae live in nasal cavities and pharynx. Warble numbers in caribou vary widely both among populations and years (Kelsall, 1975; Bergerud *et al*., 2008). Mean larvae numbers in North American caribou cows of 38 ± 43 (Thomas & Kiliaan, 1990) and 51 ± 4 have been observed (Bergerud *et al*., 2008), and means of under a 100 larvae are common (Kelsall, 1975). Semi-domestic reindeer cows in Finland had mean warble numbers < 50 larvae (Helle, 1980). However, exceptional maximums of from 300 to 600 warble larvae also were observed in female caribou (Kelsall, 1975).

Caribou are not defenceless against their oestrid parasite predators. In addition to initial avoidance reactions to the presence of adult flies, a caribou's immune system mounts biochemical and inflammatory responses to larvae (Helle, 1980; Solomakha, 1990) and larval mortality has been observed (Kelsall, 1975). There is high mortality among warble larvae in the first larval stage, specifically in hosts of good body condition (Savel'ev, 1961). Although oestrid larvae occur in 97-100% of caribou, calves or juveniles generally have greater warble infections than adults, and bulls more than cows (Helle, 1980; Folstad, *et al*., 1989; Thomas & Kiliaan, 1990; Syroechkovskii 1995; Bergerud *et al*., 2008). Beyond weather and caribou density, individual variation in defence response, e.g., migratory behaviour, avoidance behaviour, immune response and timing of hair moult, may account for observed differences in larvae number by late winter (Thomas & Kiliaan 1990).

We explored the number and weight of warble and nose bot fly larvae parasites in Greenland caribou cows and their calves-at-heel. We also investigated late-winter body condition and reproductive status, which was categorized by whether the cow was pregnant, lactating, recently weaned, had a calf at heel or any combination thereof. Specifically we tested whether: 1) 10-month old calves-at-heel had greater number / weight of larvae than adults, 2) non-pregnant cows had greater number / weight of larvae than pregnant cows, and 3) non-lactating cows had greater number / weight of larvae than lactating cows. Since the energetic cost of larvae loads may not be trivial, we also calculated the approximate energetic cost to the host associated with the cumulative oestrid parasite burden and discuss this cost in relation to the basal metabolic rates of cows and calves, the amount of foregone fattening based on the energy costs, and possible consequences for winter survival.

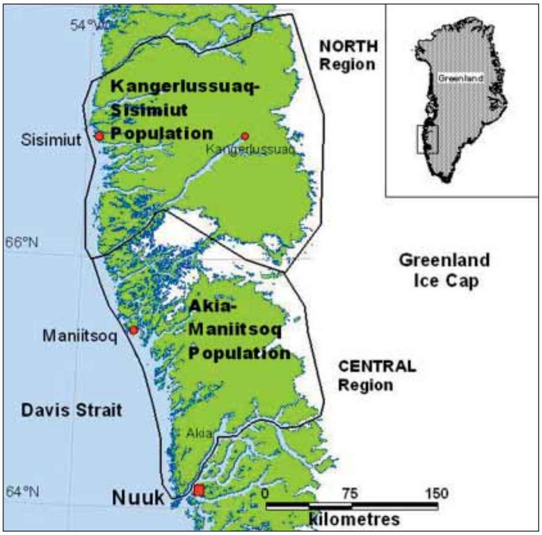

Fig. 1. Regions for the Kangerlussuaq-Sisimiut and Akia-Maniitsoq caribou herds in West Greenland, elevations are not shown.

Study area and populations

We studied the largest, Kangerlussuaq-Sisimiut (KS), and second largest, Akia-Maniitsoq (AM), caribou populations in West Greenland (Fig. 1), as both are commercially important and significant to Greenland culture and traditions (Cuyler *et al*., 2005). KS caribou were from the North region in close proximity to the Greenland Ice Cap, 67°03'N, 50°59'W, in an area characterised by dry continental desert steppe climate and lacking the macro-lichens favoured by caribou. The winter diet of KS caribou is dependent on dwarf shrubs, grasses and sedges, which regenerate each year (Lund *et al*., 2000). Winter snow cover often arrives late, is incomplete (patchy), light (< 15 cm deep), often absent, and can disappear early. The terrain is rugged and largely under 500 m elevation. AM caribou were from the Central region's Akia-Nordland area north of the Godthåbfjord system, 64°34'N, 51°44'W, where although rugged, elevations are largely < 100 metres. The area is characterised by a wet maritime climate and presence of macro-lichens that are showing signs of overgrazing. The AM winter diet is dependent on lichens (Lund *et al*., 2000), which may take decades to regenerate and about a century to achieve climax status (Kumpula *et al*., 2000). Similar to KS, AM winter snow cover is incomplete; however it can be ca. 70 cm deep, arrive early and remain late. In summer many AM cows migrate to the inland near the Greenland Ice Cap where elevations are generally 500-800 m. Throughout their range, AM caribou have access to elevations >500 m. Local knowledge, which is neither confirmed or refuted, states that warbles and bots arrived in Greenland with the introduction of semi-domesticated reindeer from Norway to the inner fjord system east of Nuuk in 1952.

In March 2010 the KS and AM populations numbered approximately 98 000 and 32 000 respectively (Cuyler, *et al*., 2011). The KS and AM herds have been at high abundance for at least the last decade, with current densities on preferred winter range of about seven and two caribou per square kilometre respectively (Cuyler *et al*., 2005, 2011). While the KS herd has remained stable in number, the AM herd abundance has declined slowly (Cuyler *et al*., 2011). Both herds are predator free. Spring migration distances are short and on a generally east-west gradient for both the KS and AM caribou, with maximums of about 60 and 170 km respectively (Cuyler & Linnell, 2004).

Methods

From 29 March to 13 April 2008, we shot 41 cows and 6 calves-at-heel (age ca. 10-months) from the AM caribou population. Similarly, 40 cows and 10 calves-at-heel (age ca. 10-months) were collected from the KS caribou population from 3 to 17 March 2009. Animals were shot in the neck. We conducted thorough post-mortem examinations as detailed in CARMA (CircumArctic Rangifer Monitoring & Assessment) protocols (http://www.carmanetwork.com). For each caribou these included measuring total and dressed carcass weight (i.e., carcass minus hide, head, all thoracic and abdominal organs, and the metacarpals / metatarsals with hooves), rump fat depth, the presence or absence of pregnancy, lactation status (white/milky-lactating, or clear liquid-recently weaned (R.G. White & W.E. Hauer, unpubl. observations; White *et al*., 2000)), and presence of calf-at-heel. We counted the number of warble larvae manually, and weighed 10. This weight with the total number was used to calculate total warble larvae weight. Bot larvae were measured similarly.

We used weather data from the CARMA MERRA files (Russell *et al*., in press), for the period 15 June to 15 August for the preceding summers to the AM and KS collections, i.e., 2007 and 2008 respectively, to calculate an oestrid fly activity index (OFI). The index employed daily mean temperature (T, °C) and wind (W, m/s). Thus OFI = T_1 x W_1, where, T_1=1 if (daily mean temperature >18 °C) else if (daily mean temperature <13 °C) = 0 else = 1-((18- daily mean temperature)/10), and W_1= 0 if (wind at 10 m/s > 9) else = (9-wind 10 m/s)/9 (Russell *et al*., 1993).

We used caribou body weights from adult cows, to estimate basal metabolic rate ($BMR_{kcal} = 70 \times weight^{0.75}$, weight given in kg) in kcal (Kleiber, 1975), and converted to kJ by multiplying by the factor 4.187. Metabolic rate of individual larvae was estimated from its weight assuming a BMR of 5% of interspecies coefficient (Glazier, 2005). Thus oestrid daily BMR = $(0.05*70*4.187*$ (individual larvae weight, kg)$)^{0.75}$. Larvae weights during the growing period were estimated from observed mean weights in March-April, and an emergent weight of 2.25 g. The metabolic cost of BMR, i.e., maintenance cost of an individual larva, was determined as the integral of daily BMR of an individual larva assuming an efficiency of use of the host's metabolizable energy of 0.85. To estimate net energy deposited in the larvae (NE, kJ) we assumed a larva was composed of 60% water and 40% dry matter that was composed of 50% fat at 39.54 kJ/g, 40% protein at 23.7 kJ/g, and 10% carbohydrate at 17.5 kJ/g (Standard energy contents - White, *et al*., 2010). We assumed metabolizable energy absorbed from the host was deposited as NE in larvae fat, protein and carbohydrate with 98% efficiency. Cost to the host for NE was the individual larval NE/0.98 multiplied by the number of larvae. Costs of BMR to the host were assessed as the accumulated daily BMR/0.85 to a shedding weight of 2.25 g for warbles and 0.5 g for bots on or about 1 June. Total energy cost to the host was (NE/0.98) + (cumulative BMR/0.85). Average and maximum cumulative energy costs of the oestrid larvae burden were calculated for calves-at-heel and for adult cows stratified by pregnancy status. In calculating the energy cost of larvae burden we ignored the energy costs of mounting an immune response and that due to increased heat loss that would result from a disrupted fur surface. Specific cow age was obtained from incisor cementum rings (McEwan, 1963; Reimers & Nordby, 1968). Alternately we used two age categories in analyses, 10-month old calves or adults (age > 3 years). Adult cows were classified by reproductive status into four categories; pregnant and non-lactating (P+NL), pregnant and lactating (P+L), non-pregnant and non-lactating (NP+NL) and non-pregnant and lactating (NP+L).

We used the Student's *t*-test to compare dressed carcass weights and rump fat depths of pregnant and non-pregnant adult cows. We used ANOVA's to describe differences in parasite burden with the four reproductive categories and age. Herds were analysed separately because collections were made in separate years. In all cases assumptions of the model were met or violation of an assumption was insubstantial to the result of the test. If the original ANOVA was significant, we conducted three planned comparisons (i.e. 1-tailed contrasts) to further test our hypotheses that larval numbers and weights vary by age and reproductive status (Crawley 2007). All analyses were conducted in R (R Development Core Team, 2009). We used regressions to examine cow age against their rump fat depth or pregnancy.

Results

Pregnancy and age of sampled caribou

The 41 cows shot in March/April 2008 from the AM herd included 34 adults of age > 3-years (Fig. 2) and seven sub-adults. The latter were 2.83 years old, not pregnant and had no calf-at-heel. Similarly, among the 40 cows shot in March 2009 from the KS herd, 36 were adults of age > 3-years (Fig. 3) and four sub-adults aged 2.83 years. One of the latter was pregnant, and none had a calf-at-heel. The pregnancy rates among sampled adult cows were 82% for the AM herd and 53% for the KS. Six female calves-at-heel were sampled from the AM herd and six females and four male calves from the KS herd. There was no relationship between cow age and pregnancy ($P > 0.05$) in KS and AM caribou.

Rump fat and lactation

Four mature AM cows (Fig. 2), aged ca. 7.85 to 9.85 years, possessed rump fat while being pregnant and with a ca. 10-month old calf-at-heel. Their rump fat depths were a mean 0.7 cm with a range of 0.5 to 1.0 cm. Based on expressible mammary fluid two of these cows were producing white milk and still nursing their calf. Two of the four cows had recently weaned, based on clear expressible liquid, and a further cow had recently weaned and had no visible calf-at-heel. All non-pregnant adult cows with a calf-at-heel were producing white milk. There was no relationship between cow age and rump fat depth or lactation ($P > 0.05$) in KS and AM caribou.

Of the 19 pregnant adult KS cows (Fig. 3), three aged ca. 4.83, 7.83 and 8.83 years, were pregnant, had their 10-month old calf-at-heel, which they were nursing, and still possessed some remaining rump fat. The youngest had a fat depth of 1.5 cm remaining, while the two older cows had 0.8 and 0.1 respectively (n=3, mean 0.8 cm). For the pregnant cows, three that had a calf-at heel had recently weaned. A further five pregnant cows had probably weaned as they showed a clear mammary fluid, but had no visible calf-at-heel. Of the 17 non-pregnant adult KS cows, 15 had their calf-at-heel and 14 of these were producing white milk.

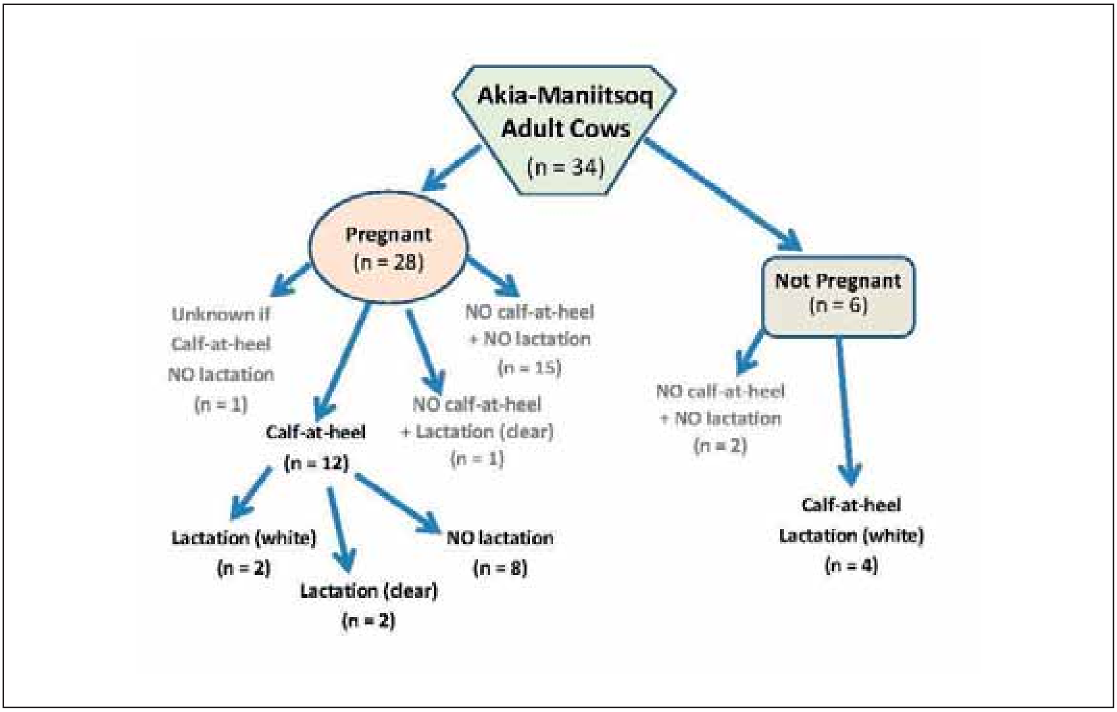

Fig. 2. Reproductive status among the adult cows from the Akia-Maniitsoq caribou herd of West Greenland collected from 29 March to 13 April 2008.

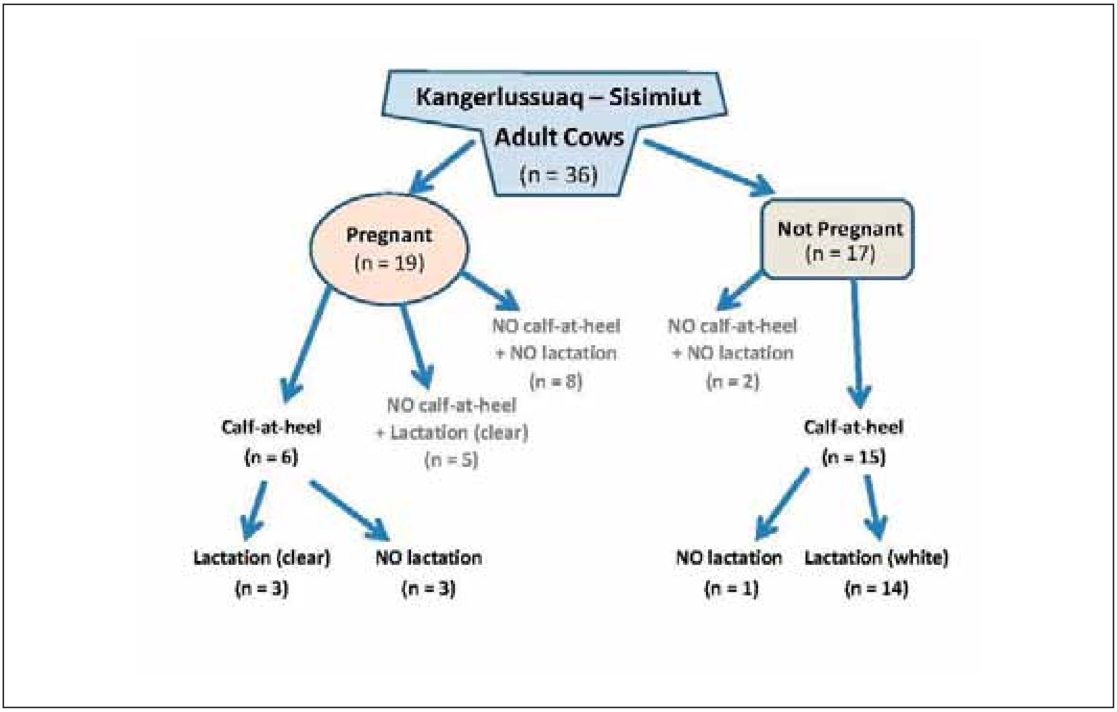

Fig. 3. Reproductive status among the adult cows from the Kangerlussuaq-Sisimiut caribou herd of West Greenland collected from 3 to 17 March 2009.

Table 1. Akia-Maniitsoq caribou of West Greenland: data from adult cows (age > 3-years) and calves-at-heel (age 10-months) collected 29 March – 13 April 2008, mean ± SD or maximum.

	Akia-Maniitsoq 2008		
	Pregnant	Non-pregnant	Calf-at-heel
Number collected (n)	28	6	6
Mean age (yr)	6.2 ± 2.3	8.3 ± 1.4	10-months
Mean total body weight (kg)	60.5 ± 3.2	52.8 ± 7.1	30.8 ± 4.2
Mean dressed carcass weight (kg)	29.0 ± 2.1	27.1 ± 4.0	15.3 ± 3.1
Mean BMR1 caribou (kJ/day)	6361 ± 251	5735 ± 579	3821 ± 385
Mean rump fat depth (cm)	0.8 ± 0.7	0.05 ± 0.08	0
Mean warble number	119 ± 77	205 ± 186	318 ± 160
Max warble number	294	537	517
Mean weight ONE warble larva (g)	1.35 ± 0.18	1.28 ± 0.16	1.54 ± 0.13
Mean warbles total weight (g)	160 ± 107	260 ± 246	478 ± 218
Mean energy cost warbles (kJ)	6240	10 749	16 674
Mean fat equivalent warbles (g)	158	271	421
Maximum[1] energy cost warbles (kJ)	15 416	28 158	27 109
Maximum fat equivalent warbles (g)	389	711	685
Mean nose bot number	70 ± 63	67 ± 63	53 ± 50
Max nose bot number	180	178	125
Mean weight ONE nose bot larva (g)	0.22 ± 0.13	0.18 ± 0.14	0.18 ± 0.06
Mean nose bot total weight (g)	21 ± 25	19 ± 28	10 ± 11
Mean energy cost nose bots (kJ)	667	639	505
Mean fat equivalent nose bots (g)	17	16	13
Maximum energy cost nose bots (kJ)	1716	1697	1192
Maximum fat equivalent nose bots (g)	43	43	30
Warbles & bots combined			
Mean energy cost (kJ)	6907	11 388	17 180
Mean fat equivalent (g)	174	288	434
Maximum energy cost (kJ)	17 132	29 855	28 301
Maximum fat equivalent (g)	433	754	715
Mean equivalent days of caribou BMR	1.1	2	4.5
Maximum equivalent days of caribou BMR	2.7	5.2	7.4

[1] Maximums were the heaviest infestations observed.

Within herds, pregnant adult cows (age > 3-years) possessed significantly greater rump fat than non-pregnant (AM $P < 0.0001$, df = 32, t = 5.929; KS $P = 0.0005$, df = 34, t = 3.849) (Table 1, 2). Fat depth did not differ between herds for either pregnant or non-pregnant adult cows. All 10-month old calves-at-heel had zero rump fat regardless of herd. Zero rump fat on adult cows was observed on 22 KS and 9 AM cows. All seven AM sub-adult cows and two of the four KS sub-adults had zero rump fat and were not pregnant. The remaining two KS sub-adult cows had rump fat depths of 0.1 and 0.4 cm, and the latter sub-adult was pregnant. Although mean rump fat depths were 1.2 ± 0.7 cm for the 14 KS adult cows possessing rump fat and 0.9 ± 0.6 for the 25 AM adult cows, the difference was not significant ($P = 0.12$, df = 37, t = 1.570). Within the KS herd adult cows with zero rump fat had significantly higher larvae burdens than cows possessing rump fat ($P = 0.0005$, df = 34, t = 3.857). In contrast, no significant difference was found among AM adult cows ($P = 0.17$, df = 32, t = 1.401).

Table 2. Kangerlussuaq-Sisimiut caribou of West Greenland: data from adult cows (age > 3-years) and calves-at-heel (age 10-months) collected 3 – 17 March 2009, mean ± SD or maximum.

	Kangerlussuaq-Sisimiut 2009		
	Pregnant	Non-pregnant	Calf-at-heel
Number collected (n)	19	17	10
Mean age (yr)	8.0 ± 2.5	8.1 ± 2.9	10-months
Mean total body weight (kg)	68.3 ± 3.7	61.8 ± 3.6	32.8 ± 4.4
Mean dressed carcass weight (kg)	32.8 ± 2.3	29.5 ± 2.0	15.5 ± 2.7
Mean BMR1 caribou (kJ/day)	6961 ± 279	6458 ± 282	4006 ± 401
Mean rump fat depth (cm)	0.8 ± 0.8	0.1 ± 0.2	0
Mean warble number	138 ± 64	311 ± 189	457 ± 284
Max warble number	287	722	1008
Mean weight ONE warble larva (g)	0.87 ± 0.23	0.99 ± 0.13	1.12 ± 0.11
Mean warbles total weight (g)	127 ± 82	298 ± 165	498 ± 299
Mean energy cost warbles (kJ)	6494	14 636	21 507
Mean fat equivalent warbles (g)	164	370	543
Maximum[1] energy cost warbles (kJ)	13 506	33 978	47 437
Maximum fat equivalent warbles (g)	341	858	1198
Mean nose bot number	18 ± 28	37 ± 49	0.3 ± 0.7
Max nose bot number	112	119	2
Mean weight ONE nose bot larva (g)	0.28 ± 0.11	0.3 ± 0.1	0.23 ± 0.25
Mean nose bot total weight (g)	6 ± 10	13 ± 17	0.2 ± 0.2
Mean energy cost nose bots (kJ)	154	317	3
Mean fat equivalent nose bots (g)	4	8	0,1
Maximum energy cost nose bots (kJ)	958	1018	17
Maximum fat equivalent nose bots (g)	24	26	0,4
Warbles & bots combined			
Mean energy cost (kJ)	6648	14 952	21 509
Mean fat equivalent (g)	168	378	543
Maximum energy cost (kJ)	14 465	34 996	47 454
Maximum fat equivalent (g)	365	884	1198
Mean equivalent days of caribou BMR	1	2.3	5.4
Maximum equivalent days of caribou BMR	2.1	5.4	11.8

[1] Maximums were the heaviest infestations observed.

Larvae abundance and weight

Abundance and weight of warble larvae exceeded nose bot larvae in both herds ($P < 0.0001$, df = 80, t = 4.108 AM; $p < 0.00001$, df = 78, t = 7. 088 KS) (Figs. 4, 5). Adult KS cows carried fewer nose bots ($P = 0.0007$, df = 79, t = 3.533) and more warbles ($P = 0.006$, df = 79, t = 2. 828) than AM cows; warble number in AM and KS calves were not significantly different ($P = 0.234$, df = 14, t = 1.244), and KS calves had marginally fewer nose bots than AM calves ($P = 0.0481$, df = 14, t = 1.166).

Akia-Maniitsoq caribou and warble larvae

Number of warbles differed among reproductive categories ($F_{4,41} = 5.104$, $P = 0.002$) (Figure 4). 10-month old calves-at-heel had significantly higher numbers of warbles than adults (t = 2.907, $P = 0.003$). Pregnant cows had fewer warbles than non-pregnant (t = 1.734, $P = 0.045$); although the sample size was small and the *P*-value was close to 0.05. The number of warbles was not influenced by whether a cow was lactating or not (t = 0.814, $P = 0.2$). Similarly, weight of warbles differed among the categories ($F_{4,41} = 6.045$, $P = 0.0006$). 10-month old calves-at-heel

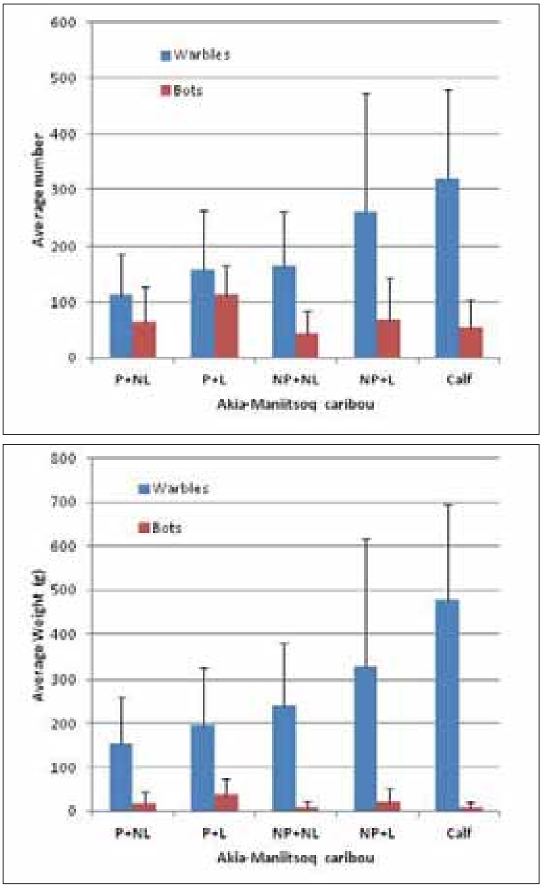

Fig. 4. Average number and weight of warble and nose bot larvae in Akia-Maniitsoq caribou collected in March/April 2008 in West Greenland: pregnant & not-lactating (P+NL) *n* = 23; pregnant & lactating (P+L) *n* = 4; not-pregnant & not-lactating (NP+NL) *n* = 9; not-pregnant & lactating (NP+L) *n* = 4; calf *n* = 6.

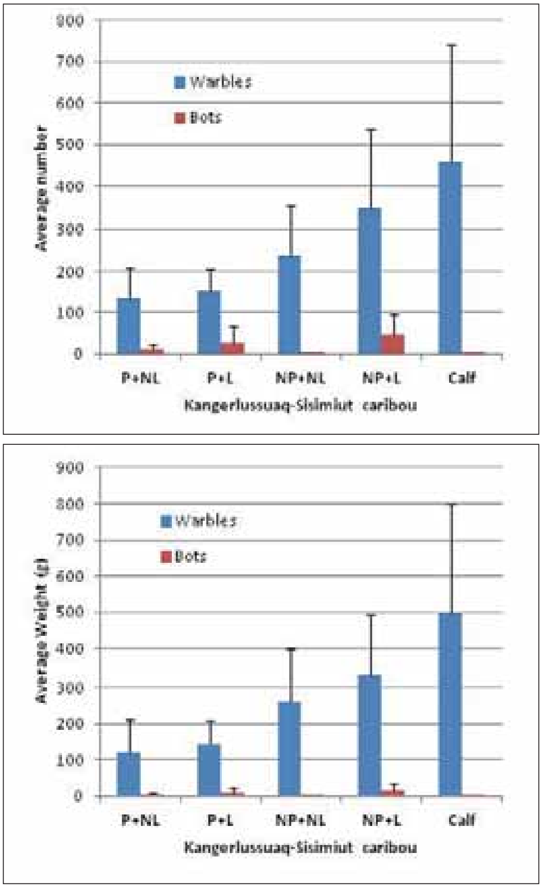

Fig. 5. Average number and weight of warble and nose bot larvae in Kangerlussuaq-Sisimiut caribou, March 2009 in West Greenland: pregnant & not-lactating (P+NL) *n* = 12; pregnant & lactating (P+L) *n* = 8; not-pregnant & not-lactating (NP+NL) *n* = 6; not-pregnant & lactating (NP+L) *n* = 14; calf *n* = 10.

had significantly higher warble weights than adults (t = 3.611, P = 0.0004). Pregnant cows had lower warble weights than non-pregnant cows (t = 1.834, *P* = 0.03). Weight of warbles was not influenced by lactation (t =0.496, *P* = 0.3).

Akia-Maniitsoq caribou and nose bot larvae

The number and weight of nose bot larvae did not differ among categories (Number: $F_{4,41}$ = 0.9996, *P* = 0.4188; Weight: $F_{4,41}$ = 1.267, *P* = 0.2985). All hypotheses were rejected. Nose bots were not significantly related to age, pregnancy, or lactation in the AM herd.

Kangerlussuaq-Sisimiut caribou and warble larvae

Number of warbles differed between categories ($F_{4,45}$ = 6.409, *P* = 0.00036) (Figure 5). 10-month old calves-at-heel had significantly higher numbers of warbles than adults (t = 3.873, *P* = 0.0002). Pregnant cows had fewer warbles than non-pregnant cows (t = 2.569, *P* = 0.007). Number of warbles did not appear influenced by whether a cow was lactating or not (t = 0.21, *P* = 0.4).

The weight of warbles differed among categories ($F_{4,41}$ = 4.168, *P* = 0.00589). 10-month old calves-at-heel had significantly (t = 4.545, *P* = 0.00002) higher warble weight than adults. Pregnant cows had less warble weight than non-pregnant (t = 2.825, *P* = 0.0035). Lactation was not related to the weight of warbles (t = 0.27, *P* = 0.4).

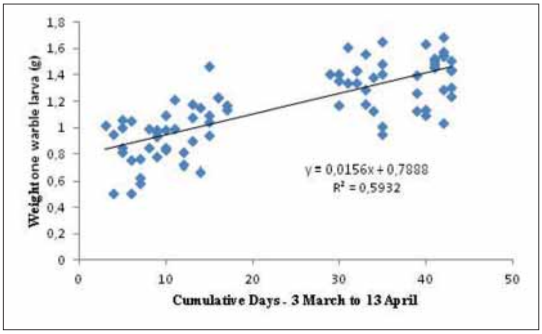

Fig. 6. Individual weight of warble larvae in relation to date from 3 March to 13 April during two sampling years (2008, 2009). Regression slope was significant (*P* < 0.0001).

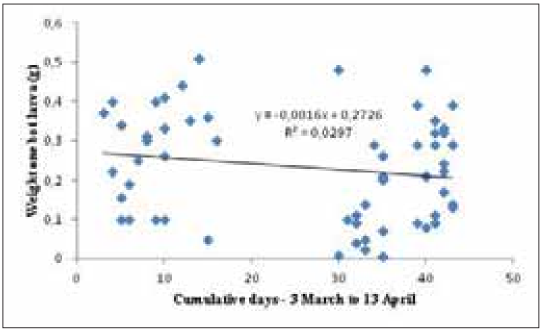

Fig. 7. Individual weight of bot larvae in relation to date from 3 March to 13 April during two sampling years (2008, 2009). Regression slope was not significant (*P* = 0.19).

Kangerlussuaq-Sisimiut caribou and nose bot larvae

Many KS caribou lacked the presence of nose bot larvae (Fig. 5). Number of nose bot larvae was significantly and inversely related to age category ($F_{4,41}$ = 4.168, *P* = 0.006). 10-month old calves-at-heel had significantly (t = -1.822, *P* = 0.037) fewer nose bots than adults. Pregnancy and lactation were not related to the number of nose bots (t = 0.341, *P* = 0.35 and t = 1.237, *P* = 0.11 respectively), and nose bot weight was not significant ($F_{4,20}$ = 2.174, *P* = 0.1090). Sample size for this data set is small and given the number of animals without nose bot larvae, all hypotheses were rejected.

Warble larvae grow during early spring (Fig. 6), while bot larvae do not (Fig. 7). These data were used to assess minimal average warble and bot larvae of 2.25 g and 0.5 g at shedding for modeling energy costs and a mean growth of warble larvae of 0.016 g/day was assumed. Bot larvae were assumed to make minor growth between sampling and dates of shedding in June.

Metabolic costs of larval growth and metabolism

Basal metabolism of cows and calves-at-heel

Adult KS cows were larger bodied than AM (Tables 1, 2). Mean total body weight of the AM adult cows (age > 3-years) was significantly less than the KS cows, e.g., for pregnant adult cows *P* < 0.0001, df = 46, and for non-pregnant cows *P* = 0.01, df = 22. Dressed carcass weight for adult pregnant KS cows was also greater than AM (*P* < 0.0001). Within herds, non-pregnant cows weighed significantly less than those pregnant (AM *P* = 0.02, df = 33; KS *P* < 0.0001, df = 35). For calves-at-heel we found no significant difference in mean total body weight (*P* = 0.21, df = 15) between the AM and KS herds. Basal metabolic rate (BMR) of adult cows was 6250 ± 400 kJ/day for AM and 6723 ± 376 kJ/day for KS, while calves-at-heel were 3936 ± 418 kJ/day (Tables 1, 2).

Warbles and nose bots

Important to estimating a metabolic cost to the host of warble burdens is knowledge of the larval growth functions and the approximate weight of larvae at shedding. Within herds pregnant and non-pregnant adult cows had mean individual warble weight that did not differ significantly, AM (*P* = 0.3, df = 33) and KS (*P* = 0.06, df = 35). Given the almost one month difference in collection periods between herds, mean individual warble weight in adult pregnant cows at 1.35 g for AM (April) and 0.87 g for KS (March) were different (*P* < 0.0001, df = 46). Similarly, mean warble weights in adult non-pregnant cows were 1.28 g for AM and 0.99 g for KS (*P* = 0.006, df = 22) (Table 1, 2). Within both herds individual warble weight in calves exceeded that of the adult cows (1.5 g and 1.1 g for AM and KS respectively (*P* < 0.02)). Mean individual nose bot weight in adult cows showed no significant differences (*P* > 0.05), whether within or between herds or between pregnant and non-pregnant. The situation was similar for mean individual nose bot weight in calves versus adults (*P* > 0.8).

Due to differences in sampling date, we used a mature larvae weight of 2.25 g in early June. Expected weight gains between sampling and emergence were similar at approximately 0.016 g/day for warble larvae from both herds (Fig. 6). Estimated peak weight of individual bot larvae at 1 March was approximately 0.5 g (Fig. 7), and we assumed all bot larvae reached this weight at shedding. At shedding, the estimate cost of hosting an individual larva was 17-19 kJ/g of which 54-60% was attributable to NE and 40-46% to the summated support metabolism. Absolute costs to caribou were then assessed from larvae burdens as reported above. Among AM caribou the approximate energy cost associated with larvae burden was a mean 7000 to 11 000 kJ for adult pregnant and non-pregnant cows respectively. Heavily infested cows had energy costs of 17 000 to 30 000 kJ (Table 1). Of these costs only 10-15% were due to bot fly larvae. The energy cost to the most heavily infected cows was equivalent to about 3-5 days BMR. Similarly for the KS caribou (Table 2), larvae burden cost a mean 7000 to 15 000 kJ for adult pregnant and non-pregnant cows respectively, while heavily infested cows had burdens costing 14 000 to 35 000 kJ, which were equivalent to about 2-5 days BMR. Because of the low infestation by bot fly larvae only approximately 2% of this cost was attributable to them. For calves-at-heel larvae burdens were greater and energy costs for mean burdens were 17 000 and 21 000 kJ for AM and KS calves respectively. In the most heavily infested calves, energy costs were about 28 000 kJ and 47 000 kJ for AM and KS respectively. These latter costs were equivalent to about 7-12 days BMR of a calf-at-heel. Again, due to low infestation by bot larvae, the cost for AM calves was only 3% while that for KM calves was less than 0.1%. An alternate expression of the energy cost is to express that cost in terms of forgone fattening. Lowest levels in forgone fattening were for pregnant cows at about 0.1-0.4 kg for the mean and highest infestation rates in both AM and KS females (Table 1, 2). Greatest levels of foregone fattening were estimated in non-pregnant cows at 0.7 and 0.8 kg for respectively the AM and KS herds (Table 1, 2). Foregone fattening was even higher in calves-at-heal at 0.7 kg for the AM and 1.2 kg for the KS animals.

Discussion

Our results were similar to other studies that have found a relationship between warble infection, fat reserves and pregnancy (Thomas & Kiliaan, 1990; Hughes *et al.*, 2009). Further, a recent experimental approach employing removal of warble larvae observed that warbles have a significant negative impact on cow body mass, despite relatively low numbers of larvae (Ballesteros *et al.*, 2011). Our results are also interpreted in relation to a theoretical analysis of energetic costs of hosting variable burdens of warble and bot larvae. For the two herds we examined in West Greenland age was not associated with reproductive status of cows in March-April, however, warble larvae burden was. Pregnant cows had fewer warbles and greater rump fat than non-pregnant cows, and lower energy cost associated with hosting larvae. Cow age was not associated with rump fat reserves. Adult cows that we examined had rump fat reserves with a mean < 1 cm, compared to pregnant cows, non-pregnant cows had significantly greater number of warbles, and less rump fat, specifically notable in non-pregnant KS cows. Again these findings are consistent with the higher host energy costs and the predicted fat draw-down necessary to meet the oestrid cost when all nutrients are obtained from the host's reserves. Sampled adult KS cows had high warble burdens and a low pregnancy rate of 53%. Relative to KS, the AM cows had lower warble burdens and a pregnancy rate of 82%. Calves-at-heel had zero rump fat and exhibited the highest mean larvae numbers observed. Our findings support those by Hughes *et al.* (2009), who observed that warble abundance was higher in animals with less back fat and that the difference was most apparent in non-pregnant cows, even at lower abundance of warble larvae. Hughes *et al.* (2009) concluded that a negative relationship exists between abundance of warbles and probability of being pregnant. They proposed that high infestations have a cost to the host, reflected in reduced weight gain owing to harassment and reduced time feeding the previous summer. Further, that poor condition or social status of an animal may increase susceptibility to adult fly attack.

Warble load in winter may be influenced by the timing of summer hair shedding among caribou, which occurs in warble fly season (Thomas & Kiliaan, 1990; Syroechkovski, 1995; Bergerud *et al.*, 2008). The successful implant of warble larvae under the hide may be related to the stage of hair loss at the time of peak adult fly harassment, i.e., mid-July to mid-August (Syroechkovski, 1995, p. 162; Josefsen *et al.*, 2006). Lactating cows are actively shedding their winter coat during the height of warble fly season. We suggest that eggs deposited on the winter coat of cows may be lost with shed hair before being able to burrow under the skin. In contrast, calves, juveniles and bulls are well advanced in their hair shedding at peak fly season (Fig. 8), and thus may be more susceptible to successful adherence of eggs to newly growing hair and implantation by warble fly larvae. The warble eggs have a flexible stem which is glued to the hair (Cogley *et al.*, 1981). Thus the eggs lie flat along the hair shaft and would be resistant to grooming but not to loss of the hair shaft. The variation in warble counts may then be related to the timing of hair loss relative to the time adult flies are laying eggs.

Mean numbers of warble larvae in the adult KS cows were 138 ± 64 SD for pregnant and 311 ± 189 SD for non-pregnant, while means in the AM cows were 119 ± 77 SD and 205 ± 186 SD respectively.

Fig. 8. Differential timing of hair moult among caribou during July (Photo, Leslie Witter).

Table 3. Temperature, precipitation and cumulative oestrid (adult warble & bot fly) index for the period 15 June to 15 August 2007 for Akia-Maniitsoq and 2008 for Kangerlussuaq-Sisimiut.

	Daily Temperature (°C)[1]				
Population	Mean	Max	Min	Mean daily total surface precipitation (kg/m2)	Warble & Bot Fly Cumulative Index
AM	10.2	20.2	0.1	4.1	5.52
KS	12.9	23.6	1.2	0.8	16.4

[1] *Two metres above ground surface.*

These means range from roughly double to eight times greater than the 38 ± 43, 51 ± 4 or median 76 observed in North American caribou (respectively: Thomas & Kiliaan, 1990; Bergerud *et al.*, 2008 Hughes *et al.*, 2009). Even higher were the mean warble larvae number in calves, 457 ± 284 KS, and 318 ± 160 AM. The high larval burdens in Greenland caribou, relative to observations from other CircumArctic herds, may be connected to their short spring migrations (<200 km). Migration can minimize re-infestation by warble and bot flies in wild reindeer and caribou (Thomas & Kiliaan 1990; Folstad *et al.*, 1991) and timing of movement between ranges is recommended as a means of minimizing infestation in domestic reindeer herds (Folstad *et al.*, 1991). The short spring migration distances of the AM and KS herds would not separate them from the areas where the larvae were dropped to pupate, which would put the caribou in close proximity to adult flies when these emerged, promoting high infestations of larvae the following winter.

KS caribou showed a higher average warble to nose bot ratio by number of larvae than the AM (KS, 3.75-7.5 : 1; AM, 1.42-2.85 : 1). This regional difference suggests that parasite prevalence differs between these two West Greenland populations or differed substantially between the years in which the collections were made. Explanations for the high number of warble larvae in KS relative to AM might include the dissimilarities in topography, weather and caribou density. The sampled KS cows inhabit an area lacking high elevations, while AM habitat includes elevations > 700 metres, which provide options for caribou to reduce the risk of exposure to the adult flies. Recent KS densities are ca. 7 caribou per km^2 relative to AM's ca. 2 caribou per km^2 (Cuyler *et al.*, 2011) and spring migration distances are about ½ those of the AM caribou. Both would allow adult flies to easily locate KS caribou. Local weather in the summer preceding the March collections can also explain some of the difference in AM and KS larval burdens. Hot dry summers benefit adult fly activity (Thomas & Kiliaan, 1990) and also could control phenology of shedding or pupation (Nilssen & Haugerud, 1994). The dryer warmer calmer weather at KS resulted in a summer oestrid index of 16.4, in contrast to 5.5 at AM (Table 3).

In adult cows, nose bot larvae were far outnumbered by warble larvae. We do not know why nose bot larvae occurred in lower numbers than warble larvae. Syroechkovski (1995) also found fewer bot larvae in Russian reindeer. At the prevalence and intensity of infection that we recorded, nose bot larvae were not related to reproductive status, although detecting an effect was difficult due to low number or absence of nose bots, which reduced already low sample sizes for some categories in particular. Alternately, these tests may have suffered from low statistical power. Nose bot presence should not yet be rejected as influencing fitness of the host.

In the most heavily infested cows, the energy cost of 'growing' the combined warble and nose bot burdens was equivalent to 2-5 days of the host cow's BMR and foregone body fat reserves of 0.4-0.9 kg. Although these results are modest, any increases in energy expenditure in the three month period prior to parturition, when warble larvae are growing and cows are heavily pregnant, could be critical to fetal development (Roffe, 1993). Maternal condition during late pregnancy influences calf survival (Cameron *et al.*, 1993) and calf birth weight (Russell *et al.*, 2002). Our calculated energy costs for the larvae burden during this period may be a minimum, because we did not account for increased heat loss as the fur surface becomes increasingly disrupted by larger warbles, and increasingly larger "breathing-hole" sizes, or the protein costs of both a heightened immune and inflammatory response by the host to the larvae. Further, calving, specifically 10-days post calving with lactation, is the most energetically demanding period for cows (White & Luick, 1984; Oftedal, 1985; Clutton-Brock *et al.*, 1989; Russell, *et al.*, 1993). This period coincides with peak larvae growth and energy requirements prior to exiting their host (Josefsen *et al.*, 2006). Adverse severe weather events in late winter / spring causing further energy expenditures beyond the already present parasite loads, could negatively affect survival, specifically in malnourished cows (Bergerud *et al.*, 2008). The unusually high warble loads occurring in Greenland cows could intensify the effects of negative weather events on caribou populations in West Greenland. The situation was worse for 10-month old calves-at-heel than for their dams, because calves in addition to being small and having zero rump fat, averaged 320 to 460 warble larvae in AM and KS herds respectively. Calves-at-heel had higher burdens than cows and heavy infestations were over 1000 warbles. Energy costs of the heaviest larvae burdens were equivalent to ca. 7-12 days BMR, and foregone body fat reserves of 0.7 to 1.2 kg. This puts into perspective the minimum energy cost associated with heavy warble infestations in calves, as 1.2 kg fat would raise their body fat by about 3-4%. Although this oestrid fly model addresses an assessment of both the retained energy (NE) and the summated costs of support metabolism, many assumptions are made. We recommend that larvae counts and weights be made throughout the winter to accurately predict growth curves, and to make extensive measurements of nutrient contents (water/dry matter, energy, fat, protein, carbohydrate and ash) be made on larvae from these collections. In addition a more robust measure of the metabolic rate of the growing larva needs to be made. We consider our current estimates to be minimal. Our finding that the overall cost to the host is almost equally distributed between NE and summated metabolism is novel and requires verification because the balance is dependent on larvae composition, growth rate and date of shedding. Thus we have not attempted to relate energy costs on an individual host basis, but have reserved the analysis to gross mean.

The survival to March-April of heavily infested calves-at-heel in this study could be attributed to the high level of extended lactation exhibited by their dams. Given high mean warble numbers, and the March-April timing for our collections we were surprised that several pregnant cows were also nursing their ca. 10-month old calf-at-heel. Sometimes these pregnant lactating cows possessed rump fat greater than average for those sampled. Lactation extending into spring among Greenland cows was rare in a similar 1997 study (C. Cuyler unpubl. data). Extended lactation occurs sporadically in caribou (Bergerud *et al.*, 2008), but is considered a rare event. A four year study of the Porcupine herd showed that extended lactation was associated with infertility, however the authors did not report a weaning time for these cows (Gerhart *et al.*, 1997). Currently, West Greenland caribou are exceptional, since both pregnant and non-pregnant females display extended lactation. Based on the greater incidence of clear liquid in the mammary glands of pregnant KS cows (8 of 19, Fig. 3) collected almost one month earlier than the AM cows (3 of 28, Fig. 2), we suggest weaning following extended lactation had begun in early March for pregnant cows. For non-pregnant cows, however, lactation may be extended beyond mid-April. The likely increased fitness of cows exhibiting extended lactation suggests that they, and their calves-at-heel, would be resilient to survive the energy cost to parturition plus any subsequent restricted forage availability caused by weather. Bergerud *et al.* (2008) argue that overwinter-fat reserves are retained for energy costs of spring migration. However, this is not the case for Greenland caribou because of the short distances. Alternately, White & Luick (1975) suggest that body fat reserves stimulate early post parturient milk secretion. Although our findings are not in conflict with this hypothesis, we suggest that presence of fat reserve in lactating and pregnant cows emphasizes the role of individual variation in caribou populations, possibly driven by responses to parasitism. Individual quality is considered to affect survival and reproduction in semi-domestic reindeer (Weladji *et al.*, 2008) and red deer (Moyes *et al.*, 2011). To capture and measure this variation and to test these hypotheses, we need to increase sample sizes and to consider more targeted and stratified sampling in order to measure differential effect of parasites on their hosts.

Despite the apparent high level of maternal investment, extended lactation still may not satisfy the energy demands of the most heavily infected calves. Normal autumn weaning or in early winter, or an inability of females to maintain extended lactation, plus unfavourable events creating additional energy expenditures in late winter / spring, separately or in combination, could negatively affect survival of calves with poor body condition and large numbers of warble larvae. This may be a factor behind the observed decreasing trend in late-winter calf-recruitment over the last decade (Cuyler *et al.,* 2005, 2011).

Greenland caribou cows are smaller bodied than other CircumArctic herds, which typically range about 80-90 kg in March-April (Adamczewski *et al.*, 1987; Gerhart *et al.*, 1996; Bergerud *et al.*, 2008). Greenland cow weights are even below Bergerud *et al.*'s (2008) June cows in Ungava, Canada, which were at their lowest annual weight. Pregnancy rates in relation to body weight of Ungava caribou in April (Fig. 9.15, Bergerud *et al.*, 2008) would predict a pregnancy rate of 20-45% based on body weights for AM and KS cows (Table 1, 2). These predictions for light weight cows are low compared with the 53-82% observed for the KS and AM herds. Although these body weight results partially explain the level of fecundity, we cannot discount a bias in sampling and errors associated with small sample sizes. Body size differences between the small AM and KS caribou are best reflected by dressed carcass weight, because KS ingest copious amounts of graminoids (Lund *et al.*, 2000), which cause higher rumen volume and weight (C. Cuyler unpubl.). A comparison of AM and KS calf body and carcass weights clearly confirms a larger alimentary fill in the KS calves compared to AM calves. While pregnant KS cows were larger than AM, their amount of rump fat was the same, making their percentage of fat less than for AM. KS also had greater warble burdens with accompanying greater winter energy costs, and a low pregnancy rate, i.e., 53%. The latter may be another factor behind the decreasing trend in calf-recruitment mentioned above. Regardless, despite their small body size and high warble loads relative to other herds, Greenland cows may maintain extended lactation to their calf-at-heel in addition to being pregnant. Thus to date, it appears that both KS and AM have been able to compensate with adequate winter energy intake. For KS the abundance of readily available graminoids may be the key, while for AM it may be the presence of macro-lichens (albeit reduced in abundance this past decade, C. Cuyler pers. observation). Until the occurrence of a regional negative stochastic weather event, e.g., severe thaw-refreeze icing restricting forage availability, warbles will not appear detrimental to their hosts, as their effects are subtle. Further analysis for other parasite species will reveal the extent that high oestrid larvae burdens described coincide with elevated levels of gastro-intestinal nematodes that have been implicated in affecting reproduction in Svalbard reindeer (Albon *et al.*, 2004).

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A conceptual model for migratory tundra caribou to explain and predict why shifts in spatial fidelity of breeding cows to their calving grounds are infrequent

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Abstract: Calving grounds of migratory tundra caribou (*Rangifer tarandus)* have two prominent characteristics. Firstly, the cows are gregarious, and secondly, the annual calving grounds spatially overlap in consecutive years (spatial fidelity). The location of consecutive annual calving grounds can gradually shift (either rotationally or un-directional) or more rarely, abruptly (non-overlapping). We propose a mechanism to interpret and predict changes in spatial fidelity. We propose that fidelity is linked to gregariousness with its advantages for individual fitness (positive density-dependence). Our argument is based on a curvilinear relationship between the density of cows on the calving ground (which we use to index gregariousness) and spatial fidelity. Extremely high or low densities are two different mechanisms which can lead to reduced spatial fidelity to annual calving grounds and reflect the caribou's adaptive use of its calving ranges.

Key words: calving grounds; gregariousness; spatial fidelity; mechanisms; *Rangifer tarandus*.

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Introduction

Bergerud *et al.* (2008) reminds us about caribou's (*Rangifer tarandus)* adaptable use of space. Our paper is to consider the adaptable use of calving grounds by migratory tundra caribou. The starting point is that calving grounds have two conspicuous characteristics. Firstly, the cows are highly gregarious and correspondingly, animal densities on the calving grounds can be high (e.g., Skoog, 1968; Bergerud *et al.,* 2008). As an example, density on the calving ground of the Bathurst herd in northern Canada in 1984 was 203 caribou/km^2 (photographic estimate) (Sutherland & Gunn, 1996).

The second characteristic is that there is a high degree of geographic overlap between annual calving grounds, as most information supports the return of breeding cows to the calving ground where they previously calved (for example, Skoog, 1968; Cameron *et al.,* 1986; Gunn & Miller, 1986; Schaefer et al., 2000; Bergerud *et al.,* 2008). For the Bathurst herd, Gunn *et al.* (2008) reported that the spatial overlap for the 24 calving distributions mapped during the 42 years of monitoring averaged 43% (± 3.8% SE). To emphasise that the cow's annual return to a calving ground is not just a return to a specific geographic place, in this paper we refer to spatial fidelity as the tendency of the cows to return to the general area that they previously used rather than a specific site.

Information on the geographic locations of calving grounds has increased since the 1960s and 1970s through the cumulative number of aerial surveys. As a result, changes in the geographic locations of area used for calving were documented, which led to questioning the concept of fidelity to these areas (e.g., Davis *et al.,* 1986; Valkenburg & Davis, 1986; Hinkes *et al.,* 2005). The amount of overlap between annual calving grounds varies and the annual differences in overlap of consecutive calving distributions can show a consistent direction (Gunn *et al.,* 2007, 2008). For example, Bergerud *et al.* (2008) describe directional shifts and their reversal for the Leaf and George River herds between 1973 and 1993 relative to changes in herd size. Without a strongly directional shift in most years, annual calving grounds tend to have a cumulative clumped distribution. For example, the Qamanirjuaq calving grounds between 1979 and 2004 mostly overlapped with no consistent directional shifts, which is a similar pattern to the Beverly herd for 1978-1994 (Gunn *et al.,* 2007). The Bathurst herd also had periods (1966-1984 and 1996-2007) when the annual calving grounds were relatively clumped. However, the herd also had a period of directional shift between 1984 and 1996 (Gunn *et al.,* 2008).

Although infrequent, directional shifts in spatial fidelity have resulted in one herd's calving ground overlapping neighbouring herd's calving grounds (which is different in degree from individual cows switching geographically discrete calving grounds). The two reported instances are from the Alaskan mountains, where the calving grounds of two large caribou herds shifted <25 km and engulfed the dispersed calving sites of two small herds (Davis *et al.,* 1986; Valkenburg *et al.,* 2003; Hinkes *et al.,* 2005).

The widespread use of telemetry is producing an increasing amount of information at both the herd and individual levels. The proportion of individual cows switching to neighbouring calving grounds vary between herds from the documented 0.5% over 9 years for the Mentasta and Nelchina herds in Alaska (Lieb *et al.,* 1994), to annual rates of 6.6% and 0.9% for the George River and Leaf River herds, respectively, between 1986 and 2003 (Boulet *et al.,* 2007). Proportions of cows switching to neighbouring calving grounds vary within a herd, which appears to be the case for the switching of individual cows between the Beverly and neighbouring Ahiak herd (this paper; Nagy *et al.*, 2011).

Our point is not, however, to simply catalogue historical variations in the use of calving grounds, but to search for underlying mechanisms to describe the adaptable use of space by barren-ground or migratory tundra caribou. As we learn more about the use of space relative to increasing and decreasing phases of population abundance (Bergerud *et al.,* 2008), we now have the opportunity to explore underlying mechanisms and concepts so we can have predictive insights into changes in calving ground use.

Davis *et al.* (1986) commented on the lack of a conceptual model of caribou socio-ecology to explain fidelity to calving grounds, among other aspects of caribou spatial dynamics. However, they offered no suggestions and there have been no concerted efforts to examine the relationship between the two characteristics of calving grounds (gregariousness and spatial fidelity) and how they relate to changes in spatial fidelity. In this paper, we propose a conceptual model based on a relationship between gregarious calving and spatial fidelity relative to the individual fitness of breeding caribou cows in raising a calf.

Proposed conceptual model

Our conceptual model is about the relationship between animal density on the calving grounds and the animal's fidelity to these areas. We consider density of breeding females on an annual calving ground to be an index of gregariousness. Density is usually measured through aerial transect surveys during calving. We define spatial fidelity as the distance between the centroids of the annual calving ground delineated at the peak of calving (based on definitions in Russell *et al.,* 2002) between any two consecutive years.

We propose a curvilinear relationship between density of caribou at calving and annual spatial fidelity to a herd's calving ground (Fig. 1). We propose that extremely high or low densities are two different mechanisms that trigger a change in spatial fidelity. We also propose that the underlying mechanism for the relationship depends on the advantages and disadvantages of gregarious behaviour to individual fitness of breeding females and their calves.

We used average density (numbers of caribou/km^2) of successive annual calving grounds as an index to gregariousness (based on estimated density measured during calving ground surveys). We are not using density-dependence in the sense of population dynamics – the relationship between density and rate of population increase (sensu Krebs, 2002). Individual fitness initially increases with density (positive density-dependence, also termed inverse density-dependence) (left hand side of Fig. 1). The decrease in individual fitness when conspecific density decreases is also known as an Allee effect (Stephens & Sutherland, 1999) and is often seen as a shortage of interactions among conspecifics at low density (Courchamp *et al.,* 1999).

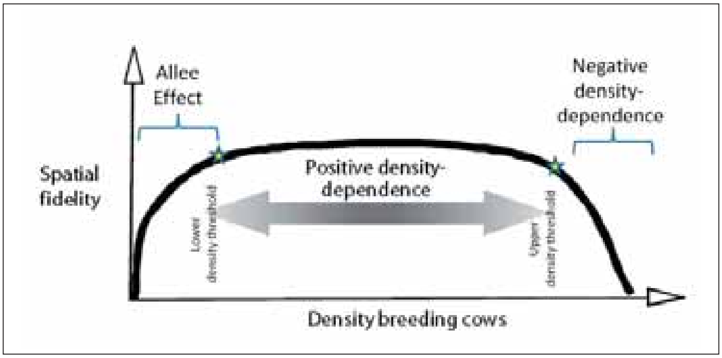

Fig. 1. Proposed curvilinear relationship between spatial fidelity and density of caribou on the calving ground.

Individual fitness increases with conspecific density through several mechanisms. Conventionally for caribou, predator-swamping is considered to be an advantage of gregarious calving (Bergerud *et al.,* 2008). McLellen *et al.* (2010) describe a relationship between population density, group size and predation rates for mountain caribou. Increased foraging is likely through reduced vigilance (Ims, 1990; Roberts, 1996; Childress & Lung, 2003; Mooring *et al.,* 2004) and through information from conspecifics' foraging. The cues that conspecifics learn from their neighbours about reproductive success, predators, and resources is termed 'public information' (Danchin *et al.,* 1998; Doligez *et al.,* 2003; 2004; Donahue, 2006; Boulinier *et al.,* 2008).

The Bathurst and Beverly herds are two herds where information on both the location of calving grounds and numbers of caribou has been monitored since the 1970s. For breeding cows on the calving grounds of at least the Bathurst and Beverly herds, as herd size increased, densities on the calving grounds also increased (Sutherland & Gunn, 1996; Gunn & Sutherland, 1997). Our conceptual model proposes that at some threshold, positive density-dependence shifts to negative density-dependence (right hand side of Fig. 1). We specify these two herds as we did not find a relationship between the size of the calving ground and population size in other herds (unpubl. data). By comparison for the George River herd in northern Quebec and Labrador, the calving grounds have changed in area relative to the number of breeding cows (Bergerud *et al.,* 2008; J. Taillon, pers. comm., 2010).

The simultaneous presence of positive and negative density-dependence was demonstrated for nest site fidelity and fledging success in a gregariously nesting sea bird colony (Kim *et al.,* 2009). For migratory tundra caribou, we suggest positive and negative density-dependence effects on individual fitness are expressed along a continuum of density values. At some threshold, negative density-dependence predominates and individual cows change their behaviour. Negative density-dependence is usually thought of as competition for forage but may also include increased risk of parasitism. For example, gregariousness was a risk factor for parasitism in red deer (*Cervus elaphus*; Vicente *et al.,* 2006). The risk of parasitism may increase as density (gregariousness) on the calving grounds increases. The peri-parturient rise in gastrointestinal nematode egg output caused Folstad *et al.* (1991) to predict that calving grounds "…might develop into transmission foci for parasites, where females and their susceptible calves would experience intense parasitic transmission." As caribou density increases, so does the density of fecal pellets and the risk of exposure to parasites (Folstad *et al.,* 1991).

This conceptual curvilinear relationship between density (gregariousness) and spatial fidelity on the calving ground approximates a 'flattened inverse U' with a steep portion at extremely high or low densities (Fig. 1). From this conceptual model, we suggest that fidelity to a traditional calving ground will be reduced at extremely high or low densities.

At extremely high densities, positive density-dependence shifts to negative. One possible mechanism for this could be forage competition, which causes cows to congregate in areas not recently used for calving (higher forage biomass and a lower risk of parasite exposure). The second possible mechanism for changes in spatial fidelity is when densities are so low that positive dependence breaks down—there are no longer gains to individual fitness as there are too few individuals. For example, we predict that calf survival would decrease, which was the case in 2007 as calf-cow ratios on the Beverly traditional calving ground were low (Johnson *et al.,* in press). Consequently, cows will shift to neighbouring calving grounds to maintain conspecific attraction, especially if cows have overlapped on the winter range or during pre-calving migration.

The locations of the Bathurst and Beverly herd's calving grounds have been mapped since the 1970s. For the Beverly herd, calving overlapped within a traditional calving ground for all 15 years between 1978 and 2002 when calving distribution was mapped during aerial surveys (Gunn *et al.,* 2007). Peak herd size was in 1994 when densities on the calving ground were visually estimated at 13.5 caribou/km^2.

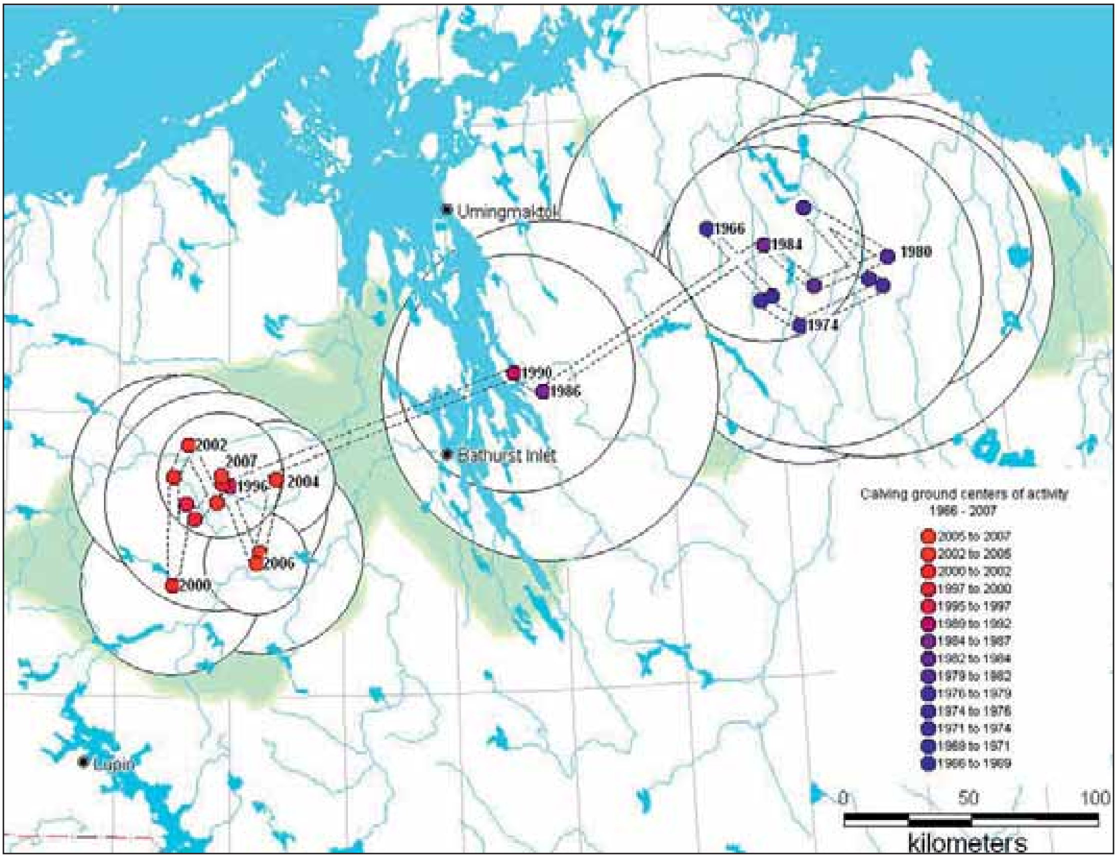

Fig. 2. Centroids of annual calving grounds at the peak of calving for the Bathurst herd, 1966 to 2007. The centroids are embedded in circles that are equivalent to the area of the annual calving ground; larger circles denote larger annual calving grounds (see Gunn *et al.,* 2008 for further explanation).

Subsequent monitoring was infrequent, but systematic strip transect surveys of the Beverly calving ground resulted in visually estimated densities of 4.0 and 0.4 caribou/km^2 in 2002 and 2007, respectively (Johnson *et al.,* in press).

Satellite collaring of cows in the Beverly herd did not start until 2006 (except one cow collared in 2001 which calved 4 of 5 years on the traditional Beverly calving grounds, with one non-breeding year). Since 2007, of the nine cows collared on the Beverly herd's winter or summer range with >1 year of calving on the Beverly calving ground, three remained on the Beverly calving ground for 2 years (Government of Northwest Territories, unpubl. data). Six cows moved to the neighbouring calving ground of the Ahiak herd about 250 km away (BABA, BAA, BA, BA0, B0A, B0A; B = Beverly calving ground, A = Ahiak calving ground, 0 = non-breeder). We suggest that the extreme low density in 2006-09 correlated with a reduced fidelity as cows maintained conspecific attraction by moving to a neighbouring calving ground.

The distribution of calving was not annually mapped until the use of satellite telemetry for some herds, including the Bathurst herd, starting in the mid-1990s. Gunn *et al.* (2008) estimated a centroid for each annual Bathurst calving ground between 1966 and 2007 based on aerial surveys or distribution of satellite-collared cows at the peak of calving (Fig. 2). There were the two periods (1966-1984; 1996-2007) when the centroids were clustered in the eastern and western parts of the calving range, linked by a period of directional shift between 1986 and 1996. The shifts between the consecutive 24 annual calving grounds averaged 17 km over 42 years (1966-2007) but were highly variable (3-120 km) (Table 1). The average yearly shift rate was 13 km (± 2.4 SE) for the 1966-1984 cluster of 10 centroids based on aerial surveys and when caribou densities were increasing, but had yet to reach a threshold density value that could trigger a change in calving ground fidelity.

Table 1. Size, distance between centroids, and direction of shift for successive peak calving grounds, determined by satellite collars and peak calving grounds for the Bathurst herd, NU (grey shading denotes consecutive years).

Shift dates	Peak calving ground area (sq km)	Distance between centroids (km)	Azimuth (°)
1966	8778		
1966-1970	6157	37	136
1970-1971	4275	5	245
1971-1974	6909	18	121
1974-1977	7180	36	64
1977-1978	11205	6	296
1978-1979	3113	37	318
1979-1980	6774	38	120
1980-1982	9429	31	249
1982-1984	3519	26	309
1984-1986	15096	104	236
1986-1990	5905	14	301
1990-1996	611	120	248
1996-1997	3472	3	291
1997-1998	1993	18	218
1998-1999	3950	7	330
1999-2000	3876	32	189
2000-2001	4731	43	1
2001-2002	3088	13	25
2002-2003	5758	25	153
2003-2004	1237	25	69
2004-2005	4932	26	193
2005-2006	1308	4	202
2006-2007	3785	37	338

The greater distances were between 1984 and 1996, based on only three aerial surveys over 13 years. The average yearly shift rate of the calving ground centroid was 21 km (± 4.0 SE) for the 1996-2007 cluster of 11 centroids when the densities of caribou on the calving ground were declining but had not reached the extreme low value to trigger an Allee Effect (see Table 8 in Gunn *et al.,* 2008 for details).

In between the two periods of overlap was a discontinuity as the 1984 and 1986 calving grounds did not overlap and were separated by 104 km. The 1986 and 1990 calving grounds overlapped, then the 1990 to 1996 calving grounds were also non-overlapping and their centroids were separated by 120 km. This shift resulted in a movement of the Bathurst calving ground from the east side to the west side of Bathurst Inlet; the distance between the centroids for the 1966-1984 grouping and the 1996-2007 grouping was 250 km (Fig. 2). The location of the annual calving ground overlapped between 1966 and 1984, when at the peak of calving, average density for the high density stratum was 203 caribou/km^2 (photographic estimate). Between 1986 and 2009, also based on photographic estimates, average densities declined from 111 to 7 caribou/km^2 (Nishi *et al.,* in press).

Discussion

We have proposed a mechanism leading to predictive insights about the spatial fidelity of migratory tundra caribou cows to their calving grounds. The mechanism is based on the two characteristics of migratory tundra caribou calving which are gregariousness and spatial fidelity. At extremely high or low levels of gregariousness (indexed by density), in response to negative or positive effects of density-dependence, spatial fidelity to the previous cumulative calving grounds will decline.

Typically, negative or positive effects of density are considered to be on rate of population growth. However, we identify the effects as behavioural – that the presence of conspecifics is both a positive and negative influence and likely acts along a continuum. To recognize these effects, we have to be aware of scale (individual to population) and variability (again individual, but also environmental). We also have to be aware of the dangers from the “tyranny of the dichotomous mind” (Dawkins, 2004), this being our tendency to emphasize distinct boundaries rather than continuums. Caution is needed in extrapolating from the shifts of individual cows to neighbouring calving grounds (based on satellite or conventional telemetry). It is uncertain how individual variation in calving behaviour becomes a shift in calving distribution relative to individual variability, as the expressions of individual variation may be the same behaviours that lead to shifts in distribution.

We have offered examples of changes in fidelity to annual calving grounds in two herds, each with close to 40 years of mapped annual calving grounds, with only two recorded examples of displacement to a currently unused area (Bathurst) or the Beverly cows partial shift to a neighbouring herd (Ahiak). For the Beverly herd, we suggest that extreme low densities correlate with a partial shift to a neighbouring calving ground as cows maintain conspecific attraction. For the Bathurst herd, peak high densities coincided with a shift to a calving area which was unoccupied and had not been used since decades earlier (Sutherland & Gunn, 1996). Then the degree of overlap in successive calving grounds was significantly greater during the decline in the number of breeding females (Gunn *et al.,* 2008).

We recognize that information about the reasons for changes in calving fidelity is incomplete. We lack information on whether the risk of parasitism and/or forage availability had changed on the Bathurst calving grounds in the early 1980s. We also do not have an understanding of how environmental variability plays into the relationship between calving fidelity and gregariousness—for example, Bathurst calving in 1986 occurred during a later snow melt (Sutherland & Gunn, 1996). Any relationship between calving ground fidelity and gregariousness will be complicated as the cows will be integrating current year's conditions with the previous year's performance on the calving ground (*sensu* colonial sea-birds which predicate nest site decisions on their previous fledging success and that of their neighbours; Danchin *et al.,* 1998).

The proposed curvilinear relationship between fidelity and density (gregariousness) accommodates the periodic changes in abundance typical of migratory tundra herds. The model also predicts that the greater the amplitude in densities, the more likely directional shifts will occur (negative density-dependence). For example, the George and Leaf River herds have high amplitude changes in herd size and shifts in calving distribution up to 400 km (Bergerud *et al.,* 2008; Couturier *et al.,* 2009). Between 1986 and 2003, the George River herd peaked in size at about 776 000 (±104 000) in 1993 before decreasing (Crete & Huot 1993, Manseau *et al*., 1996, Couturier *et al*., 2009) while the Leaf River herd probably peaked in 2001 and then started to decline (Couturier *et al*., 2009). When both the George River and Leaf River herds were increasing in size, their calving grounds directionally shifted north of the tree line. Then, as the herd began to decline, the size of calving ground of the George River herd increased and it started to shift south back toward the tree line. Bergerud *et al.* (2008:447) attributed the shift north to the cows reducing predation risk by spacing themselves away from wolves (*Canis lupus*), and the shift south to over-grazing. We note that the George River herd is atypical of all North American migratory tundra caribou herds, as the tundra portion of its annual range is only 11% (A. Gunn, unpubl. presentation 2008 CARMANET.ca). This may accentuate any relationship between density and rate of directional shifting in the calving ground.

At first sight, some movements of individual cows to another calving ground might seem counter to the concept that at high densities cows would not be expected to move to another high density calving ground. For example, rates of switching were annually variable between the George River and Leaf River herds. Boulet *et al.* (2007) recorded that 14 of 149 satellite-collared cows switched calving grounds (1986-2003) with herd-specific annual rates of switching calving grounds being 6.6% and 0.9% of the George River and Leaf River collared cows, respectively. Six of 13 cows (one cow had only two calving locations) reversed and returned to their natal calving ground. Two cows spent an equal number of years on either calving ground (6 and 8 years). The two calving grounds remained geographically separate by several 100 km. The George River herd had peaked when most of the cows switched to the Leaf River herd which was still increasing. However, without more information (densities on the calving ground, individual condition and parasite loads, habitat conditions) we are left with uncertainty.

We suggest directional shifts are more likely in mountainous terrain where herds may display either dispersed or gregarious calving behaviour. In the Alaskan mountains, there are two examples of herds with increasing population sizes that shifted their calving grounds. The new calving ground overlapped the calving area of a smaller and neighbouring herd (Davis *et al.,* 1986; Valkenburg *et al.,* 2003; Hinkes *et al.,* 2005). Although information on caribou densities on the calving grounds is not available, it is reasonable to assume that they were high for the larger herd. Between 1979 and 1987, the calving grounds of the smaller Yanert herd (500-1000 caribou) and the larger Delta herd (4000-8000 caribou) were only 10 – 50 km apart after the Delta herd's calving ground had shifted. In the second example, the smaller Kilbuck herd's (ca. 4000) traditional calving ground was 25 km away from the larger Mulchatna's (ca. 200 000) calving ground in 1994 (Hinkes *et al.,* 2005). The smaller mountain herds (Yanert and Kilbuck) had different calving strategies (scattered rather than gregarious) than the larger herds.

We acknowledge that other reasons, including weather and industrial development, can influence both individual cows (Carroll *et al.,* 2005) and calving ground locations (Cameron *et al.,* 2005). A variation in spatial fidelity, which is not the focus of this paper, is the effect of unusual weather during pre-calving migration. For example, late snow melt can mean extensive snowcover and cows calve before reaching the calving ground (e.g., Griffith *et al.,* 2002). Bergerud *et al.* (2008) remark that migrating cows halt before reaching the calving ground when snow cover is 100%. In coastal Alaska, Carroll *et al.* (2005) reported that during spring migration in May 2004, a combination of the Trans Alaska Pipeline, the Dalton Highway and the flooding Savaganirktok River delayed the Teshekpuk herd's pre-calving migration. Two of five collared cows calved before they reached the Teshekpuk herd's usual calving ground while the other three collared cows and many uncollared cows calved on the Central Arctic herd's calving ground. Attention must be paid to environmental conditions when interpreting unusual caribou movements, including apparent switching between calving grounds.

Further testing of the curvilinear relationship between gregariousness and spatial fidelity to calving grounds and how positive density-dependence shifts to negative density-dependence is necessary. Only a few herds have estimates of density of breeding cows on calving grounds, but many herds are monitored through satellite telemetry. We are investigating using nearest-neighbour distances between satellite-collared cows to estimate calving dispersion (the pattern of relative density, an index to gregariousness).

Our initial results for the Beverly and Bathurst herds are that the relationship between gregariousness and spatial fidelity is over a tenfold range in densities. Thus, we suggest fidelity to traditional calving grounds remains a robust hypothesis. We also suggest that changes in fidelity can be expected at either extremely low or high densities, which are relatively infrequent. Distinguishing between the two mechanisms for shifts in fidelity is key to caribou management and is indexed by whether the cows shift to an area with no or few cows, or an area with high densities. Instances when densities are so low that cows shift to maintain the advantages of gregariousness for calf survival are exceptional.

Understanding whether changes in spatial fidelity are predictable relates to designing calving ground protection as well as designating herds based on fidelity to calving grounds. Calls to protect the calving grounds of migratory tundra caribou are long-standing and frequent. For example, Inuit concerns prompted court action leading to the Department of Indian Affairs and Northern Development (Government of Canada) implementing Caribou Protection Measures to protect the calving and post-calving caribou of the Beverly and Qamanirjuaq herds in 1978 (BQCMB, 2004). Management of land use activities has not been extended to other herds in northern Canada, in part because of a perception about the mobility of calving grounds which argued against using land-based protection for calving grounds (Weihs & Usher, 2001).

We need to further test the conceptual relationship between fidelity and gregariousness and whether predictive thresholds are measurable for fidelity across a broad range of migratory tundra caribou calving grounds. We also expect that we need to re-examine the definition of "a herd's calving ground". Is the herd's calving ground the cumulative area used over time? What amount of data and years of survey are needed to adequately describe the extent of a herd's calving ground? Additionally, there is considerable diversity within migratory tundra caribou and their calving grounds – both ecological and in the amount of data available. We propose working within the CARMA network (http://www.carmanetwork.com/display/public/home) to collaborate using data from circumpolar herds to test and develop predictive relationships between spatial fidelity and gregarious behaviour for calving.

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Recent changes in summer distribution and numbers of migratory caribou on the southern Hudson Bay coast

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Abstract: The status of migratory woodland caribou inhabiting the coastal region in southern Hudson Bay is dynamic. The Pen Islands Herd within that region was defined in the 1990s, but opportunistic observations between 1999 and 2007 suggested that its status had significantly changed since the late 1980s and early 1990s. We undertook systematic surveys from the Hayes River, MB, to the Lakitusaki River, ON, in 2008 and 2009 to determine current distribution and minimum numbers of woodland caribou on the southern Hudson Bay coast from the Hayes River, Manitoba, to the Lakitusaki River, Ontario. We documented a significant change in summer distribution during the historical peak aggregation period (7-15 July) compared to the 1990s. In 2008 and 2009, respectively, we tallied 3529 and 3304 animals; however, fewer than 180 caribou were observed each year in the Pen Islands Herd's former summer range where over 10 798 caribou were observed during a systematic survey in 1994. Over 80% of caribou were in the Cape Henrietta Maria area of Ontario. Calf proportions in herds varied from 8% of animals in the west to 20% in the east. Our 2008 and 2009 systematic surveys were focused on the immediate coast, but one exploratory flight inland suggested that more caribou may be inland than had been observed in the 1980s-1990s. The causes of change in the numbers and distribution in the coastal Hudson Bay Lowlands and the association of current caribou with the formerly large Pen Islands Herd may be difficult to determine because of gaps in monitoring, but satellite telemetry, genetic sampling, remote sensing, habitat analysis, and aboriginal knowledge are all being used to pursue answers.

Key words: aerial survey; distribution; Hudson Bay; migratory; monitoring; Pen Islands Herd; population numbers; range shift; woodland caribou.

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Introduction

Woodland caribou (*Rangifer tarandus caribou*) are found throughout northern Ontario and Manitoba across the northern part of the boreal forest and in areas north to the shores of Hudson Bay (Armstrong, 1998). Within this range, two ecotypes of the species have been identified: forest-dwelling and forest-tundra (Courtois *et al.*, 2003) or alternatively sedentary and migratory (Bergerud, 1996; 2000). These ecotypes are distinguished on the basis of their calving strategies: females of the forest-dwelling ecotype disperse after winter to calve in isolation from one another, whereas members of the forest-tundra ecotype migrate north of the tree line to the Hudson Bay coast and aggregate during calving. While the forest-dwelling woodland caribou ecotype has been listed as Threatened in Canada both federally and provincially, the forest-tundra ecotype is not listed under any species-at-risk legislation in Canada. However, with increasing concern about globally synchronous declines in many caribou and reindeer herds (Vors & Boyce, 2009) closer examination of any changes in caribou populations is warranted.

Forest-tundra woodland caribou have been documented as occupying the southern Hudson Bay coast since the 1700s, however, large aggregations were not reported during the first half of the 1900s (Banfield, 1961). In 1979, incidental observations made in early July indicated that caribou were aggregating in significant numbers at the coast near the Ontario-Manitoba border (Abraham & Thompson 1998). Studies in the 1980s-1990s confirmed the presence of summer aggregations during the calving and post-calving period and this group was named the Pen Islands Herd (Thompson & Abraham 1994). By 1994, the herd had grown from about 2300 animals to nearly 11 000 when observed during the peak of calving season (7-15 July; Abraham & Thompson, 1998).

Opportunistic observations between 1999 and 2007 indicated that very few caribou were present in the former range of the Pen Islands Herd during calving and post-calving periods (Magoun *et al.*, 2005; OMNR, unpublished data). In contrast, caribou numbers during calving and post-calving had increased east of the Winisk River, while during the 1979 to 1999 period there were few caribou observed in that area. These opportunistic observations were not based on formal or systematic surveys, and did not cover the complete Hudson Bay coast. Thus, we recognized a need to establish whether there were still concentrations of caribou in the Pen Islands Herd coastal summer range and whether there were other areas of the southern Hudson Bay coast where caribou were forming summer aggregations. To help address these questions, we undertook a spring and summer aerial survey in 2008 and a summer survey in 2009.

Methods

Study area

Aerial surveys were conducted along the coast of southern Hudson Bay from the Hayes River, Manitoba in the northwest to the Lakitusaki River on the James Bay coast in the Hudson Plains Ecozone (ESWG, 1995), which generally corresponds with the boundaries of the Hudson Bay Lowlands ecozone of Angus Hills (Crins *et al.*, 2009). It is the largest semi-continuous peatland system in Canada and the world's third largest wetland (Riley, 1982; Abraham & Keddy, 2005). Land rises from tidal flats surrounding Hudson and James Bay to a maximum elevation of 240 m west of James Bay (Geological Survey of Canada, 1994). Vegetation across this area shows major north-south changes from treeless coastal tundra in the north to conifer-dominated boreal forest in the south (Riley, 2003). Wetlands, however, are the dominant landcover type at all latitudes covering more than 90% of the ecozone (Riley, 2003). The climate is significantly influenced by Hudson Bay with short cool summers and cold winters (Abraham & Keddy, 2005).

Methods

A fixed-wing survey (calving period, 24-28 May 2008) and two rotary-wing surveys (post-calving period, 10-15 July 2008 and 11-15 July 2009) were conducted in the immediate coastal area of southern Hudson Bay, Manitoba, and northern James Bay, Ontario. The time periods were chosen to match the previously known calving period and the period of highest aggregation post-calving (Thompson & Abraham, 1994). A Twin Otter airplane was used for the spring calving survey and flew at an altitude of 150 m AGL at speeds less than 100 knots. Bell Long Ranger and A-Star helicopters were flown for the summer post-calving surveys and flew at approximately 100 m AGL and speeds of less than 80 knots, slowing when needed. A combination of line transects and dynamic flight lines were flown; the line transects were located in areas of special interest (e.g. up to 30 km inland from coast). The dynamic lines were pre-determined to follow the James Bay and Hudson Bay coast and cover the area within 5 km of the coast where historical surveys had been done (Thompson & Abraham 1994) and were "dynamic" in the sense that they were not fixed point-to-point transects. There was a minimum of three observers to conduct the surveys. Of the observers, one was a navigator and the primary observation recorder. This person sat beside the pilot and recorded on datasheets and in a GPS unit a description and the location of each observation. All caribou seen within approximately 750 m of the aircraft were recorded and we deviated from the flight lines to obtain definitive counts and classifications and photographs, then the flight line was resumed. The other observers called their observations to the navigator and took photographs of caribou. In-flight estimates of caribou numbers by age-sex classes were generally done for small groups. Larger herds required post-flight analysis of photographs of the groups, which permitted more accurate counting and, with digital image enhancement, often enabled better discrimination of individuals and age and sex classes. Age was classed as calf, yearling or adult based on size and morphology differences. Adult sex was determined from external morphological characteristics when possible, but adults were counted in an "unknown adult" category if the sex was not discernable after image enhancement. Non-photographic observations of caribou groups included group sizes by age and sex class; observations of other species were also recorded (e.g. wolf, polar bear, wolverine, moose). Waypoints and track logs for all surveys were recorded on handheld GPS units (Garmin GPSmap76s).

In addition to the transects flown up to 30 km from the coast in certain sections, (see figures in Results for locations), caribou were recorded on a flight from Peawanuck to Big Trout Lake on 15 July 2009, and during inspection of winter habitat north of Big Trout Lake on 17 and 18 July 2009.

Data on past summer caribou numbers and distribution in southern Hudson Bay were compiled from published literature (Abraham & Thompson, 1998; Magoun *et al.*, 2005), unpublished survey reports, and unpublished Ontario Ministry of Natural Resources data. Data, including date and location of caribou observations; number, age and sex of animals; and survey effort (absence) were used to describe the status and distribution of the caribou in the coastal region over time.

Analysis

The aerial survey data were georeferenced, mapped and spatially grouped by coastline segment. Summary descriptive statistics were computed for the whole survey area and for each coastal segment for total number of animals, number of groups, and average group size and numbers and percentages in each age-sex class. In recognition that some animals or groups were likely missed, the number of animals we report represents a minimum of the number of caribou present at or near the Hudson Bay coastline. It is consistent with the method used to determine minimum numbers in the 1980s-1990s (Abraham & Thompson, 1998). Difficulties in consistently discriminating the sex of caribou in photographs led to an underestimation of numbers of adult female caribou, which would result in overestimation of calves per 100 cows. To provide some bounds on the likely values of cow:calf ratios, given the uncertainty in estimating cow numbers, two measures were computed in addition to calves per 100 cows: i) calves per 100 adult caribou, including those of unknown sex, and ii) calves as a percentage of all caribou observed.

Results

Three aerial surveys, flown in spring 2008 (calving period) and summer 2008 and 2009 (post-calving), totalled 15 survey days. They covered the southern Hudson Bay coast from the Lakitusaki River in the east to the Hayes River in the west and between 2600 and 3800 km of flight lines were flown (Table 1).

Numbers and herd composition

During the May 2008 calving survey, 409 caribou were observed with an average group size of 5.0 (Table 1). The calves constituted 8.8% of all caribou observed, and the overall ratio of calves per 100 adults was 9.7. The calf:cow ratio was 65.5 calves per 100 cows, a likely over-estimation that is an artefact of the particular difficulty in sexing the animals from the Twin Otter at this speed and height.

Table 1. Spring and summer caribou aerial surveys conducted in the coastal area of the Hudson Plains Ecozone in 2008 and 2009.

Survey Id	Dates	Survey Days	Km flown	Caribou Seen	# Groups	Mean Group Size
May-08	24-28 May 2008	3	3050	409	81	5.0
July-08	10-15 July 2008	6	2605	3529	88	40.1
July-09	11-15 July 2009	6	3740	3304	138	23.9

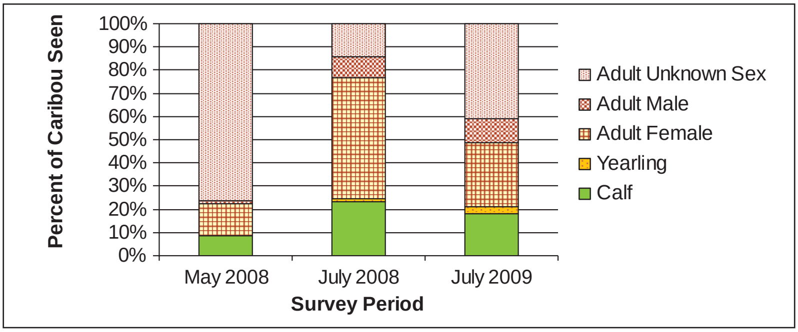

Fig. 1. Summary of age-sex composition of observed caribou for surveys conducted in May and July 2008 and July 2009 of the southern Hudson Bay coast from the Hayes River, Manitoba to Lakitusaki River, Ontario.

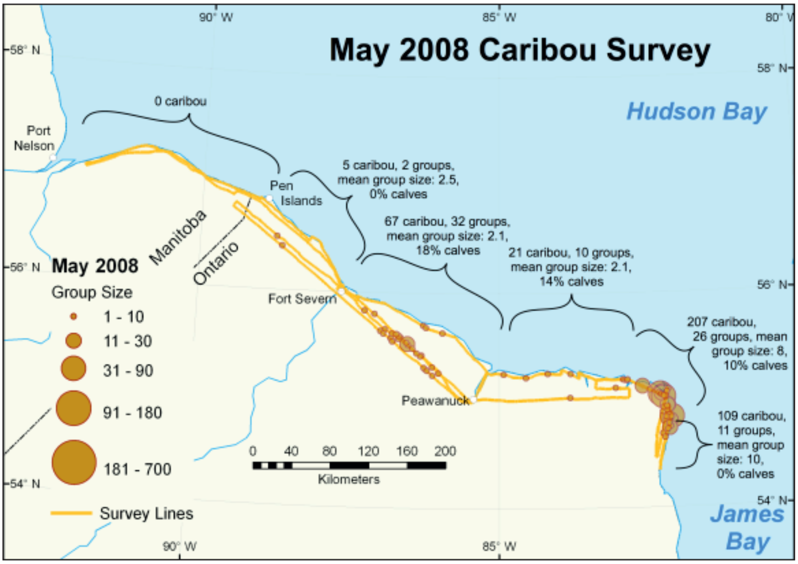

Fig. 2. Caribou distribution during May 2008 calving period aerial survey of the southern Hudson Bay coast from the Hayes River, Manitoba to Lakitusaki River, Ontario.

The post-calving surveys of July 2008 and 2009 had total minimum counts of 3529 and 3304 caribou, respectively. Average group size was 40 in 2008 (n= 88) and 24 in 2009 (n= 138) and ranged from 1 to 544 during these surveys (Table 1). The calf indices computed from the main post-calving surveys were 30.4 and 20.7 calves per 100 adults for 2008 and 2009, respectively; calves as a percentage of the total number of caribou were 23.1% in 2008 and 16.1% in 2009 and calves per 100 cows were 44.0 in 2008 and 61.5 in 2009 (Table 2, Fig. 1).

Geographic distribution

The calving period survey (May 2008) showed the majority of observed caribou (>300) to be near Cape Henrietta Maria at the eastern end of the southern Hudson Bay coast in Ontario (Fig. 2). There were relatively few animals west of Peawanuck (<75) and even fewer still (<10) west of Fort Severn, which historically was the Pen Islands Herd calving area.

Table 2. Age and sex description in percent of observed caribou for each aerial survey (number of animals seen in brackets) in the coastal area of the Hudson Plains Ecozone.

Survey Id	Total caribou	Adult male	Adult female	Yearling	Unknown age or sex	Calf	Calves/ 100 cows[1]	Calves/ 100 adults[2]
May-08	409	1.5 (6)	13.4 (55)	0 (0)	76.3 (312)	8.8 (36)	65.5	9.7
July-08	3529	8.1 (285)	52.4 (18.5)	1.2 (41)	15.3 (539)	23.1 (814)	44.0	30.4
July-09	3304	10.2 (337)	27.0 (892)	3.2 (106)	43.0 (1420)	16.1 (549)	61.5	20.7

[1] Calves/100 cows may be overestimated and should be interpreted with caution; this is because discrimination of sex was difficult and there were large numbers of caribou for which assignment of age or sex class was not made.

[2] The adult class does not include yearlings, but does include the Unknown age or sex class, which are assumed to not be calves.

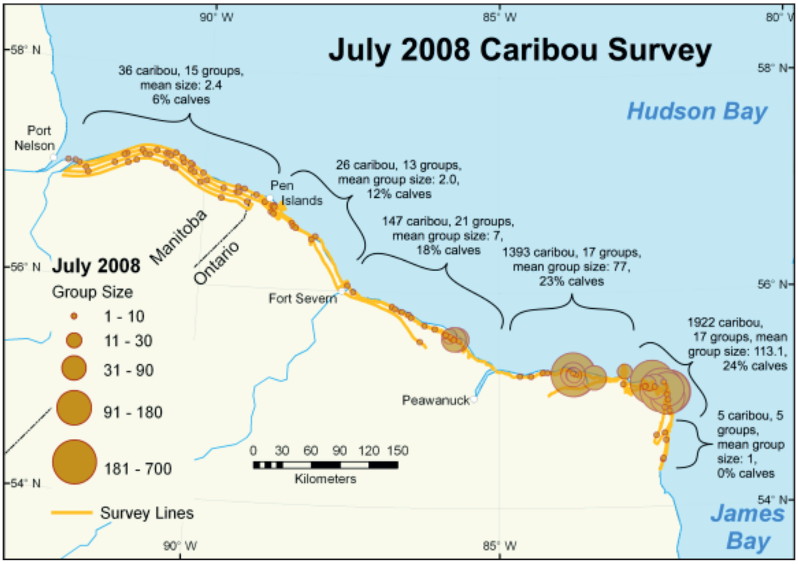

Fig. 3. Caribou distribution during July 2008 post-calving period aerial survey of the southern Hudson Bay coast from the Hayes River, Manitoba to Lakitusaki River, Ontario.

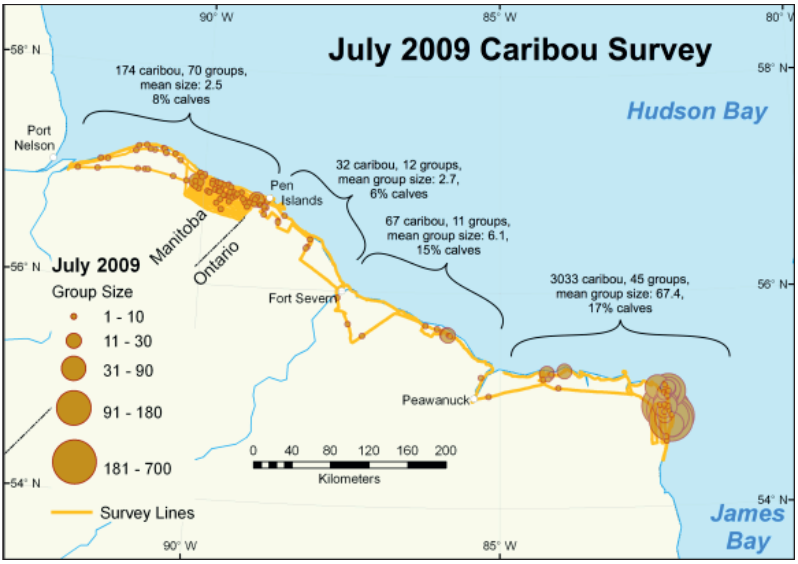

Fig. 4. Caribou distribution during July 2009 post-calving period aerial survey of the southern Hudson Bay coast from the Hayes River, Manitoba to Lakitusaki River, Ontario.

The distribution of caribou during the post-calving survey in July 2008 (Fig. 3) exhibited a similar pattern to the May 2008 survey; the majority of caribou (>1900) were around Cape Henrietta Maria, with another 1400 just west of the Cape. Few animals were found west of Peawanuck (<210) and fewer still were west of Fort Severn (<63). The post-calving survey of 2009 (Fig. 4) had a pattern very similar to 2008. The majority of caribou (>3000) were in the Cape Henrietta Maria area, with few animals (<300) located west of Peawanuck and fewer west of the Severn River (<210). It is interesting to note that in Manitoba, within close proximity (5 km) of the coast, only 75 caribou were observed in 2009.

The inland transects within 30 km of the coast in Ontario had very few caribou and no large aggregations. On 14 July 2009, we flew 5 transects along beach ridges spaced approximately 5 km apart from 25 km inland to the coast from Hook Point, Ontario (Fig. 4). The coastal transect covered an area of the flight line of 12 July. There were no caribou on the 4 inland transects, confirming their adherence to the immediate coast. The 2009 survey in the Manitoba portion of the range included more inland area than in 2008, extending 30 km inland adjacent to the Ontario border (Fig. 4); in this area only 100 caribou were sighted, approximately equal numbers as were at the coast. On the flight from Peawanuck to Big Trout Lake on 15 July 2009, few caribou and no large aggregations were observed. However, on 17 July, 6 groups totalling 108 (mean 18, range 1 to 75) were observed and on 18 July, 14 groups totalling 350 (mean 24, range 1 to 129) were observed north of Big Trout Lake. Observations of similar groups near the community of Shamattawa, Manitoba, in late July have been reported to VT and DH in each of the past few years.

On the coast in general, larger groups of caribou were observed in the east, in the area of Cape Henrietta Maria. This trend was evident at calving time in

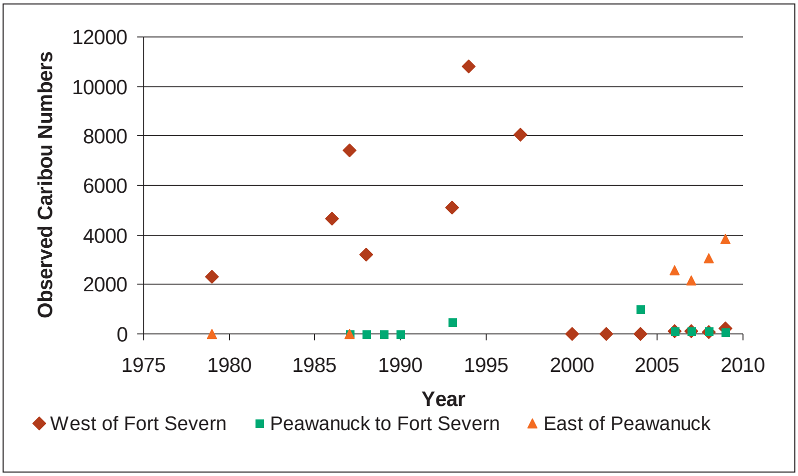

Fig. 5. Summary of total caribou observed at peak of post-calving aggregation in July caribou surveys of the southern Hudson Bay coast from the Hayes River, Manitoba to to Lakitusaki River, compiled from published and unpublished survey reports 1979–2009.

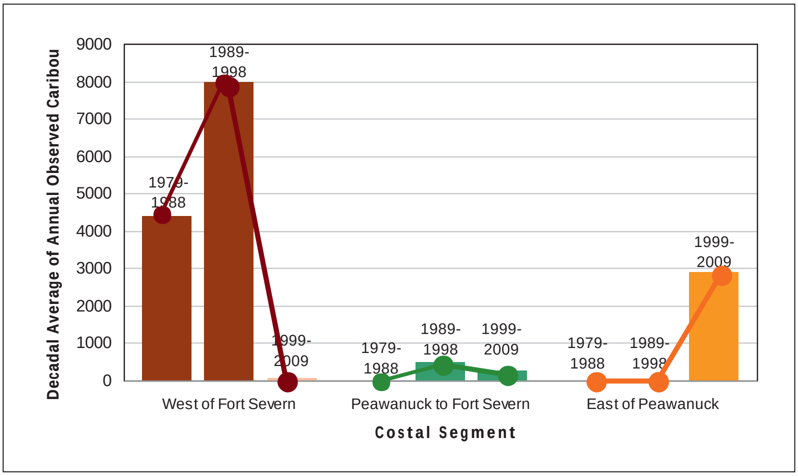

Fig. 6. Trends in annual number of caribou observed at peak of post-calving aggregation in July on the Southern Hudson Bay coast from the Hayes River, Manitoba to Lakitusaki River, Ontario, by coastal segment, averaged by decade.

May (Fig. 2), but was much more pronounced during the July post-calving period in both years (Figs. 3, 4). West of Fort Severn mean group size did not exceed 3 and was less than 7 west of Peawanuck; while to the east, mean group sizes were larger by more than an order of magnitude. There was a similar increasing trend in the calf indices in both post-calving surveys from west (7% and 8% west of Fort Severn in 2008 and 2009, respectively) to east (24% and 17% at Cape Henrietta Maria in 2008 and 2009, respectively).

The compiled past and current data, aggregated by decade and broken down by coastal segment (Figs. 5, 6), clearly show the changes in coastal distribution of caribou over the last 30 years, with dramatic declines in the west after 1999 and rising numbers in the eastern segments.

Discussion and conclusion

Summer caribou population data from the Hudson Bay coastal area showed a steady increase in the number of caribou using the coast near the Pen Islands from the late 1970s to the mid-1990s (Abraham & Thompson, 1998; Magoun *et al.*, 2005). The summer caribou concentrations in the Pen Islands area increased notably from 2300 in 1979 to reach a peak estimate of 10 798 animals in 1994. During the 1980s and 1990s, summering animals were found mostly around the Manitoba-Ontario border near the Pen Islands and few were found east of the Winisk River (Abraham & Thompson, 1998; Magoun *et al.*, 2005, OMNR unpublished data). However, in the past decade there has been a change in the distribution of caribou along the southern coast of Hudson Bay, Manitoba and Ontario, during the calving and post-calving periods from predominance of animals occurring in the western portion to predominance in the eastern portion of the Hudson Bay coast. By the early 2000s, the majority of incidental and opportunistic caribou observations were made in the Cape Henrietta Maria area and very few observations were made west of the Severn River (Magoun *et al.*, 2005). Our 2008 and 2009 summer survey data confirm and quantify this significant change. These two years of systematic surveys plus data from opportunistic observations in 2006 and 2007 (Figs. 5 and 6; Abraham, *et al., 2010;* OMNR unpublished data) produced similar geographic patterns in numbers, distribution and calf percentages, indicating that this is not an ephemeral change.

The average group sizes in July 2008 (40) and 2009 (24) are significantly smaller than the mean group sizes recorded by Thompson & Abraham (1994) for the period of peak aggregation (cf. 1060, range 209-1978). That difference and the gradient in group size we recorded from west to east may simply be an outcome of the relative density of animals, with large groups less likely to form when overall densities are low. The difference in group size raises the possibility that the timing of the peak of aggregation has changed, and indeed as the timing of peak calving appears to occur later, based on the May 2008 survey, so too might the peak of aggregation be later. Further examination of weekly or biweekly trends is warranted.

Bergerud (1996) identified a threshold of 12-15% calves in a herd in late winter as a requisite for population stability. West of the Severn River during post-calving surveys, we observed a range of 6% to 12% calves in the caribou groups, which is indicative of a herd in decline. In the Cape Henrietta Maria area these values were 24% and 17% in 2008 and 2009, respectively, which suggests that the population of animals in this area is in much better condition than those to the west. Thompson & Abraham (1994) reported values of 24.4% and 29.6% calves for the Pen Islands Herd in 1987 and 1988, respectively, at a time when the herd would have been increasing toward the maximum number (10 798) observed in 1994. Scholten & Chenier (1997) estimated 15% of the Pen Islands Herd were calves in a 1997 survey (8058 animals observed) when the herd was at or past its highest numbers.

The observation of over 450 animals in 20 groups as far inland as Big Trout Lake and the local reports from Shamattawa raises questions of the annual range and possible origin/association of these animals relative to the current and former coastal animals, as well as questions about their movement behaviour, and their ecotype identity. These group sizes are unexpected for the forest-dwelling ecotype at any time of year, but especially summer, and their behaviour is suggestive of the migratory forest-tundra ecotype. Are they remnants of the former Pen Islands Herd with altered spatial and temporal behaviour?

The evidence from our surveys is that the former coastal calving and post-calving grounds of the Pen Islands Herd have been essentially abandoned. If the Cape Henrietta Maria animals represent the descendants of the Pen Islands Herd, then a significant shift in calving grounds of this migratory ecotype has occurred. Calving grounds are usually thought to be quite stable (Russell *et al.,* 1993). If the inland animals represent the descendants of the Pen Islands Herd, then a significant change in summer habitat use or timing of use has occurred. Both possibilities deserve further investigation.

The change in summer distribution and in numbers, between the Hayes River, Manitoba, and Cape Henrietta Maria, Ontario, may have several causes. The minimum numbers in 2008 and 2009 are less than one-third of the estimated peak Pen Islands numbers in 1994. Is this evidence of a population decline since the 1990s, or simply a redistribution and imperfect sampling? The incidental observations near Big Trout Lake might support the redistribution idea but adequate sampling of the vast interior is a daunting task. A combination of causes for the change may be more likely, including: differential mortality of animals in western versus eastern parts of the Hudson Plains Ecozone due to differences in predation and hunting pressure, nutritional stress due to range deterioration, redistribution of western animals in response to habitat change or to disturbance in the western area; and/or differential natality (e.g. intrinsic growth of the eastern group of animals where predation pressure, including hunting, may be lower and where forage quality may be higher).

Lack of continuous monitoring during the recent period of greatest change makes distinguishing among these alternative hypotheses difficult. However, collaring programs have been initiated in both Ontario and Manitoba, which will enhance our knowledge of current seasonal movement patterns of caribou in all parts of the Hudson Bay Lowland and by illuminating the link between winter concentration areas and the summer coastal distribution, may allow inferences to historical changes. Collaring will also allow identification of calving grounds and perhaps even calving behaviour. Genetic samples obtained during our surveys and collected through other survey and research initiatives at other times (including historical samples from the Pen Islands) will provide additional insight into fine-scale genetic structure in caribou in the Hudson Plains Ecozone, which in turn may provide important clues about long-term caribou movement and adaptation to a changing environment. At minimum, these studies will help delineate the contemporary boundary between forest dwelling and forest-tundra ecotypes.

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The effect of fire on spatial separation between wolves and caribou

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Abstract: Fire management is an important conservation tool in Canada's national parks. Fires can benefit some species, while others may be negatively impacted. We used GPS and VHF collar data for 47 wolves from 12 separate packs and 153 caribou from 5 separate herds, and resource selection analysis to model the effects of fire on these species' habitat and potential interactions. Resource selection modeling showed that wolves select for burned areas and areas close to burns, presumably due to the presence of primary prey (i.e., elk and moose), while caribou avoid burns. Fire reduced the amount of high quality caribou habitat (a direct effect), but also increased the probability of wolf-caribou overlap (an indirect effect). We delineated a spatial index of caribou "safe zones" (areas of low overlap with wolves), and found a positive relationship between the proportion of a herd's home range represented by "safe zone" in winter and population size (P = 0.10, n=4). While currently-planned prescribed fires in Banff and Jasper reduced the amount of quality caribou habitat by up to 4%, they reduced the area of "safe zones" by up to 7%, varying by herd, location, and season. We suggest that conservation managers should account for the indirect, predator-mediated impacts of fire on caribou in addition to direct effects of habitat loss.

Key words: *Canis lupus*; fire; *Rangifer tarandus caribou*; resource selection; spatial separation; wolf; woodland caribou.

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Introduction

Woodland caribou (*Rangifer tarandus caribou*) are classified in Alberta as *threatened* both provincially (under the Alberta Wildlife Act) and nationally (under the Species at Risk Act), and are declining likely due to resource extraction activities that are altering predator-prey dynamics (Alberta Woodland Caribou Recovery Team, 2005; Wittmer *et al.*, 2005). Human activities such as forestry are thought to increase densities of primary prey, which in turn increase densities of predators (Seip, 1992; Wittmer *et al.*, 2007). Moreover, linear features such as roads and seismic lines created by human development may enhance predator efficiency (James & Stuart-Smith, 2000). High levels of human development in Alberta from forestry and oil and gas development are related to declines in almost all provincial caribou herds (McLoughlin *et al.*, 2003; Sorensen *et al.*, 2008). Banff and Jasper National Parks in Alberta (Banff and Jasper) have historically maintained populations of woodland caribou, although numbers in both parks have declined since the 1980s. The cause of declines within the national parks where resource extraction does not occur is unclear, but is also hypothesized to be related to predation.

Recovery of wolf (*Canis lupus*) populations in Banff and Jasper during the 1970s appears to have coincided with caribou declines (Hebblewhite *et al.*, 2010). A possible mechanism explaining this relationship is apparent competition; where secondary prey experience increased predation pressure due to a shared predator's response to primary prey (Holt, 1977; DeCesare *et al.*, 2010). Under the apparent competition hypothesis, increased predation pressure on secondary prey may be the result of an increased number of predators (numerical response), or increased spatial overlap between predators and secondary prey (aggregative response) (Holt & Lawton, 1994; Berryman & Gutierrez, 1999). Caribou are thought to have historically avoided the affects of apparent competition by minimizing spatial and temporal overlap with wolves; a strategy termed the Spatial Separation Hypothesis (Bergerud *et al.*, 1984; James *et al.*, 2004). In the National Parks, primary prey populations (i.e., elk (*Cervus elaphus*) and moose (*Alces alces*)) increased during decades of wolf control. As a result, following recolonization, wolves likely exceeded historically common densities and caused declines of caribou due to increased predation (Hebblewhite *et al.*, 2007b; Hebblewhite *et al.*, 2010). Persistence of caribou in Banff and Jasper may therefore be tied to densities of wolves and primary prey, as well as habitat-related spatial factors that affect overlap between wolves, primary prey, and caribou.

Parks Canada has an active fire management program with goals of restoring historic fire cycles, reducing the risk of catastrophic fires near townsites and adjacent provincial lands, and of managing mountain pine beetle outbreaks (Parks Canada, 2005). While fire can improve habitat for some species, it may be directly detrimental to species (such as caribou) that rely on older seral stage forests. For instance, southern mountain caribou in British Columbia prefer late-seral forests where the abundance of arboreal lichens is highest (Terry *et al.*, 2000; Johnson *et al.*, 2004). Previous studies of caribou resource selection within Banff and Jasper showed that caribou selected forest stands older than 75 years of age (Shepherd *et al.*, 2007). Rupp *et al.* (2006) used landscape-scale fire and climate simulations to show that increased fire frequency would have negative effects on the availability of winter caribou habitat in east-central Alaska. Conversely, elk and moose both respond positively to the increased forage within burned areas (Tracy & McNaughton, 1997; Karns, 1998; Maier *et al.*, 2005; Mao *et al.*, 2005; Sachro *et al.*, 2005). Despite their reliance on old forests, Bergerud (1974) suggested that the direct loss of lichen forage due to fire or logging was not sufficient to cause observed declines in caribou populations. Fire may reduce caribou habitat quality directly through removal of lichen biomass. However, fire may also act to reduce caribou populations by altering apparent competition dynamics by increasing primary prey and predator densities and/or the spatial overlap of these species with caribou.

It may be possible to mitigate effects of fire on caribou by assessing how fire influences overlap between wolves and caribou and identifying areas of high overlap. Recent applications of resource selection function (RSF) modeling to predator-prey theory have suggested that RSF models can be used to estimate overlap using two independent RSF models. Therefore, we estimated wolf–caribou overlap in Banff and Jasper using wolf and caribou RSF models. Under the spatial separation hypothesis, we predicted that most predation would occur where the probability of overlap between wolves and caribou was greatest. Conversely, we identified areas with low probability of wolf and caribou overlap to delineate caribou "safe zones" where caribou had an extremely low probability of wolf-caused mortality. We then tested the indirect effects of fire on wolf-caribou overlap by measuring the effects of simulated prescribed fires and the resulting change in "safe zone" habitat. Finally, we compared the indirect effects of fire on safe zones to the direct loss of high quality caribou habitat due to fire. We predicted that fire would increase the amount of wolf–caribou overlap, effectively reducing the "safe zones" for caribou.

Study area

Our study area was defined by the movements of radio-collared caribou and wolves along the eastern slopes of the Canadian Rockies in Banff and Jasper National Parks (hereafter referred to as Banff and Jasper) in the province of Alberta and a small adjacent area of British Columbia, a combined area of approximately 67 000 km^2 (Fig. 1). Topography ranges from 896 m to 3739 m ASL in elevation, and climate is characterized by long, cold winters, and short summers with most precipitation occurring in spring. Banff is 6858 km^2 and Jasper is 11 228 km^2 in area. Vegetation is classified into three broad ecoregions: montane, subalpine, and alpine. The montane is dominated by lodgepole pine (*Pinus contorta*) interspersed

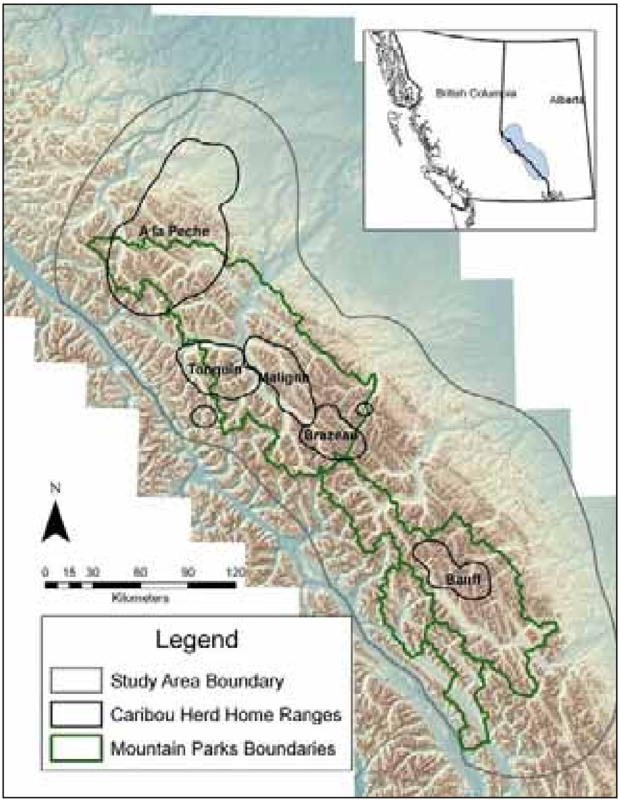

Fig. 1. Annual 99% adaptive kernel home ranges of five woodland caribou herds utilizing Banff and Jasper National Parks, Alberta (2001 - 2008).

with Englemann spruce (*Picea engelmanii*) and willow (*Salix* spp.) areas, aspen (*Populus tremuloides*) parkland, and grassland. Sub-alpine and alpine ecoregions are comprised of Engleman spruce, subalpine fir (*Abies lasiocarpa*) and lodegepole pine forest interspersed with willow-shrub riparian communities, subalpine grassland, grading to open shrub-forb meadows in the alpine ecoregion (Holland & Coen, 1983).

Hewitt (1921) noted that caribou were historically "abundant" in the Canadian Rockies. Jasper may have sustained populations of mountain caribou ranging from 435 to 700 individuals into the early 1970s following decades of wolf control in Alberta (Stelfox, 1974; Gunson, 1992). Wolves recolonized Banff and Jasper in the early 1970s (Carbyn, 1974; Dekker *et al.*, 1995; Paquet *et al.*, 1996). Today, the mountain national parks support 4 extant caribou herds, containing an estimated population of 237 individuals (Fig. 1). In March 2009, all known individuals (*n*=4) in Banff were killed in an avalanche, and the herd was likely extirpated (Hebblewhite *et al.*, 2010). Of the remaining herds, the Tonquin (*n*=74) and A La Pêche (*n*=150) are thought to be stable or declining, while the Maligne (*n*=4) and Brazeau (*n*=9) have declined to low population levels (DeCesare *et al.*, 2011).

The mammalian community of predators include wolves, grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*), cougars (*Puma concolor*), wolverine (*Gulo gulo*), lynx (*Lynx canadensis*), and coyotes (*Canis latrans*). Ungulate species besides caribou include moose, elk, mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), bighorn sheep (*Ovis canadensis*), and mountain goats (*Oreamnos americanus*). Wolves rely primarily on elk as prey in the southern end of this ecosystem (Hebblewhite *et al.*, 2004), but shift towards moose along a north-south gradient as moose become more abundant (Kuzyk *et al.*, 2005; Franke *et al.*, 2006).

Methods

We captured and radio-collared wolves and caribou from 2001 to 2010 to obtain location data used to develop resource selection function models. Study animals were captured via leg-hold trap (wolves) or via helicopter net-gunning and darting by trained personnel (wolves and caribou), under approved university and government animal handling protocols (University of Montana Animal Use Protocol 059-09MHWB-122209). We outfitted adult animals with either very high frequency (VHF) or LOTEK (Aurora, ON) global positioning system (GPS) radiocollars (LOTEK models GPS 2000, 2200, 3300, 4400). GPS collar data was standardized to a 4-hour acquisition interval for both species with an average fix location error of 33 m (Hebblewhite *et al.*, 2007a).VHF-collared animals were located from fixed-wing or rotary-wing aircraft approximately once per month.

From 2001 to 2007, 40 female caribou from the 5 herds were captured and fit with GPS collars. From 1980 to 2007 an additional 113 caribou were fit with VHF collars. From 2002 to 2009, 28 wolves from 12 packs in Banff and Jasper were captured and fit with GPS collars, and an additional 19 wolves were fit with VHF collars during that same period. All GPS locations acquired prior to 2008 were used in model training. GPS locations acquired after 2007 were standardized to a single location per day, combined with all VHF collar locations, and used for model validation (see supplementary materials Tables 1, 2 and 3 for further information regarding telemetry data).

Resource Selection Functions

We developed seasonal resource selection functions (RSFs) for both wolves and caribou. We identified two seasons based on the elevational migration of caribou in the study area: winter (December to May) and summer (June to November) (McDevitt *et al.*, 2009). Recent studies have demonstrated that caribou populations are most influenced by factors operating at large-landscape scales (Rettie & Messier, 2000; McLoughlin *et al.*, 2005; Sorensen *et al.*, 2008), and that factors influencing caribou habitat should be investigated at large spatial scales (Environment Canada, 2008). Therefore, we evaluated caribou resource selection at the second-order scale, assessing the selection of home range resources within the regional landscape (Johnson, 1980). We evaluated selection using a used-available design by comparing the proportionate use of resources to their proportionate availability within a logistic regression framework (Hosmer & Lemeshow, 2000; Manly, 2002). We sampled availability using a 3:1 ratio of random available locations to telemetry locations. Random available locations were drawn from within the study area boundary defined by a 99% adaptive kernel (Worton, 1989) based on the combined locations of all study animals (Fig. 1). We used a generalized linear mixed-effects modeling (GLLAMM) framework to account for unbalanced sample sizes between individual radio-collared animals and to treat the individual animal as the most appropriate sample unit (Gillies *et al.*, 2006). The used-available design results in a relative probability function of selection because true unused locations are not sampled, but this relative probability is appropriate to rank habitat quality (Johnson *et al.*, 2006).

We overlaid caribou and wolf telemetry data on raster layers (30m resolution) in a geographic information system (GIS; ArcGIS 9.3) to quantify the underlying resources (habitat) associated with each location. Habitat variables included landcover (i.e., dominant vegetation), topography (i.e., elevation, slope, etc.), and human use (i.e., distance to infrastructure) (see supplementary materials Table 4 for complete description of all candidate variables).

To characterize vegetation we used seamless GIS coverages of forest crown closure (0–100%), landcover, and forest species composition (0–100% coniferous) for the entire study area developed with Landsat 5 Thematic Mapper (TM) or Landsat 7 TM sensor data (McDermid *et al.*, 2009). We also used the Normalized Difference Vegetation Index (NDVI) as a measure of the biomass of green forage biomass at a 250 m^2 scale obtained from Moderate Resolution Spectroradiometer (MODIS) data; NDVI has been shown to be related to ungulate and carnivore resource selection in recent studies (Pettorelli *et al.*, 2005; Hebblewhite *et al.*, 2008). However, because NDVI only indexes ungulate forage biomass reliably in open habitats, we only used NDVI in open habitats using the landcover model above to develop an open/closed mask for NDVI (e.g., Hebblewhite *et al.*, 2008). We used a digital elevation model (DEM) to derive layers of elevation, slope, and aspect.

As both caribou and wolves respond to human use and linear features (e.g., James & Stuart-Smith, 2000; Hebblewhite *et al.*, 2005b), we used vector geodatabases of towns, roads, seismic lines, and trails to create raster layers of the distance of each pixel to the nearest of each of these human-use linear or point features. Roads were classified as either primary (i.e., paved) or secondary (i.e., gravel) and a separate layer of the distance to each was created. A single trail layer was created by combining trails within the parks with seismic lines outside. We assumed that human use of both was similar and therefore that animal response to each would also be similar. Previous studies have shown that wolves selected areas close to edges and stream banks for travel (Hebblewhite *et al.*, 2005a; Bergman *et al.*, 2006). Therefore, we included GIS layers representing the straight-line distance to streams and forest edges.

Fire and stand age layers were obtained from Parks Canada for the National Parks, and from Alberta Sustainable Resource Development for areas outside the parks (White *et al.*, 2003; Van Wagner *et al.*, 2006). Caribou have been shown to avoid burned areas up to 50 years post burn, while primary prey use declines about that same time (Peck & Peek, 1991; Joly *et al.*, 2003). Therefore, we classified burns as any area where a fire had occurred since 1950, limiting the affects of fire to those within 50-60 yrs of our wildlife data collection.

We used a manual stepwise model building method described by Hosmer & Lemeshow (2000) to create "best" models that described the resource selection of both species. This pluralistic model building approach best reflects the balance between prediction and mechanism as achieved through regression-type models (Stephens *et al.*, 2005). Candidate variables were considered if biologically relevant, ecologically plausible, non-confounded, and uncorrelated at a correlation coefficient of $|r| < 0.5$ (Hosmer & Lemeshow, 2000). We considered both linear and non-linear (quadratic) responses to continuous variables for both species and used a combination of graphical and Akaike information criteria (AIC) based methods to determine how a response was best modeled. First, frequency histograms of used and available distance locations were plotted then compared to the predicted values of a univariate model to graphically depict each species' response. Secondly, the AIC values of univariate models fit as a linear and quadratic response were compared in order to gauge if modeling as a quadratic improved fit (Burnham & Anderson, 1998). We followed the same procedure for all continuous covariates in which we expected potential non-linear resource selection patterns, including elevation (selection for intermediate elevations), distances to human activity, distance to burns, etc.

We used both within-sample and out-of-sample validation techniques to test the predictive ability of our models (Boyce *et al.*, 2002). Within-sample validation first consisted of standard logistic regression diagnostics and goodness-of-fit measures including variance inflation factors (VIFs), classification tables and the area under the receiver operating characteristic (ROC) curves (Fielding & Bell, 1997; Hosmer & Lemeshow, 2000). We also used k-fold cross-validation to estimate Spearman's rank correlation (rho) statistics correlating model predictions to subsets of withheld data (Boyce *et al.*, 2002). Finally, we used telemetry data, which we had withheld from model development entirely to asses model predictions again with Spearman's rank correlation (see supplementary materials Tables 1, 2 and 3 for description of data used in validation). This out-of-sample validation provided a robust measure of model performance (Fielding & Bell, 1997).

Overlap and probability of wolf predation on caribou.

We treated RSF models for caribou and wolves as habitat ranking models, and used them to assess wolf-caribou overlap by subtracting the caribou RSF from the wolf RSF (sensu Neufeld, 2006). Continuous RSF maps were categorized into 10 equal-area (km^2) habitat bins based on the predicted values of random locations (Boyce *et al.*, 2002). We estimated the wolf-caribou overlap index subtracting the binned wolf RSF model from the binned caribou RSF model. This generated a spatial overlap index from -10 to +10, where high values indicate high quality caribou habitat and low quality wolf habitat, and low values indicate low quality caribou habitat and high quality wolf habitat. We overlaid this index layer with our out-of-sample telemetry locations to graphically depict the frequency of use by each species across this overlap index. We used this overlay of withheld locations and overlap index to visually estimate a cut point at which high quality caribou habitat existed with little probability of wolf use, referring to these areas as caribou "safe zones". We hypothesized that most predation events would occur where the probability of overlap between wolves and caribou was greatest. We tested this hypothesis by obtaining the overlap index scores of suspected and confirmed wolf-caused caribou mortalities. Mortality locations were obtained from both collared caribou, and uncollared caribou discovered by parks staff when investigating wolf GPS locations, and those reported to Parks staff by the public.

Evaluating the direct and indirect effects of fire with burn scenarios

We modeled the direct and indirect effects of 3 future burn scenarios on caribou using Parks Canada's current prescribed fire plan, and two randomly located "wildfire" scenarios. The first scenario was created by simply adding all of the prescribed fires currently planned by Parks Canada within Banff and Jasper. Secondly, we simulated a single 1% wildfire within each caribou home range (interior wildfire), and thirdly, we simulated wildfires outside of caribou home ranges but within a 14-km buffer zone surrounding the home ranges (buffer wildfire). A 14-km buffer was chosen as it was the mean distance of avoidance of burns across seasons determined from our caribou resource selection results (see RSF results below).

In 2000, a wildfire was ignited by lightning in Jasper on the southeast corner of the Tonquin caribou herd's home range. The fire consumed 1028 ha of forest, or approximately 0.7% of the Tonquin caribou's range. Using this naturally occurring fire as a template of the extent of probable future events, we simulated wildfires in our GIS burn layers representing 1% of each of the five caribou home ranges. These burns were created by selecting at random the largest contiguous forest block with a stand origin closest to 1862, the mean stand origin of Parks Canada's current planned prescribed fires, and adding adjacent forest polygons until the desired burn size was achieved. GIS layers of planned prescribed fires were obtained for Banff and Jasper for use in simulations.

We projected our original RSF models onto landscapes created under each burn scenario and quantified changes in the amount of high quality caribou habitat and caribou "safe zones" within each herd's home range using Hawthtools Zonal Statistics (Hawth's Analysis Tools for ArcGIS v.3.27). To assess the direct effects of fire on caribou we quantified the change in the amount of high quality caribou habitat according to the caribou RSF model. We identified high quality caribou habitat using a caribou RSF bin rank of 8 or higher because 85% of all out-of-sample caribou telemetry locations occurred in habitat ranks of 8 or greater. To assess the indirect effects of fire on caribou we quantified the change in the amount of caribou "safe zone". We quantified the relative change in the indirect effects of fire (safe zone loss) and direct effects of fire on caribou habitat (RSF loss) between herds, and fire type (planned prescribed fire, interior wildfire, or buffer wildfire) using a two-way analysis of variance (ANOVA) (Zar, 1999).

Population consequences of overlap between wolves and caribou

To test for the consequences of increased overlap between wolves and caribou on caribou population dynamics, we investigated the relationship between the amount of "safe zone" within each caribou herd (n=4) and herd-specific estimates of abundance, mean annual population growth rate, and adult female survival rates using data from complementary studies (Hebblewhite *et al.*, 2010; DeCesare *et al.*, 2011). Based on previous studies of spatial separation in mountainous terrain in BC (Seip, 1992), we expected that greater levels of spatial separation and larger areas of safe habitat would be positively correlated with larger caribou populations, higher caribou survival rates, and higher population growth rates. We tested this hypothesis by examining how the amount of winter, summer, and amount of seasonal change of safe zones affected these three demographic metrics across the 4 extant caribou herds using linear regression (Banff was excluded from this analysis as no demographic data existed for this extirpated herd).

A prediction of the apparent competition hypotheses is that caribou ranges with more "safe zone" habitat would have larger population size, higher adult female survival rates, and higher population growth rates due to increased spatial separation between wolves and caribou.

Results

Resource selection (RSFs)

In summer, wolves selected herb and shrublands at both high and low elevations (supplementary material Table 5). Burned areas were strongly selected as well as areas close to burns. Deciduous forests and alpine barren ground were avoided. Selection decreased with distance to stream banks. Wolves avoided secondary roads, while selection declined with distance from primary roads and trails showing selection for areas with human activity at this second-order scale. Geographically, wolf resource selection appeared to be a generalized function of low elevation valley bottoms throughout Banff and Jasper. The model ROC value of 0.89 showed excellent discrimination, and both within-sample k-fold cross-validation (rho = 0.99) and validation using withheld out-of-sample data showed high predictive ability (rho = 0.98, P < 0.01).

In summer, caribou selected both low elevation and high elevation alpine herb and shrublands (supplementary material Table 5). Intermediate levels of greenness or NDVI in open habitats, presumably related to maximum forage quality (Hebblewhite *et al.*, 2008), were also selected. Caribou strongly avoided burned areas, even more strongly than the ice and rock landcover class. Caribou selection as a function of distance to burned areas was best modeled as a quadratic with use maximized at a distance of approximately 18 km. They selected moderate elevations with the highest probability of use at 1982 m. Our top summer caribou model accounted for approximately 50% of variation in summer resource use. The ROC value of 0.93 showed excellent discrimination of used/available locations. K-fold cross validation revealed excellent predictive capacity (rho = 0.99), however the model only adequately predicted withheld or out-of-sample locations (Spearman rank correlation rho = 0.67, P = 0.03)

In winter, wolves preferred open conifer forests, as well as low herb and shrublands (supplementary material Table 6). Burned areas were also strongly selected for, and selection declined linearly with distance to burn indicating selection for areas close to burns. Over and above their avoidance of high elevations, wolves also strongly avoided alpine areas and rock and ice during winter. Selection also declined with distance to stream banks and in open canopy forests. In winter, wolves selected for low-intermediate elevations (probability of use was highest at 1817 m). The model showed similar ability to discriminate between used and available locations as our summer wolf model, and validated well. The ROC value of 0.89 shows excellent discrimination. Both within-sample k-fold cross-validation (rho = 0.99), and validation using reserved out-of-sample data (rho = 0.98, P < 0.01) showed high predictive ability.

In winter, caribou selected for conifer forests and alpine herb and shrublands, while avoiding both low elevation and alpine barren ground (supplementary material Table 6). Burned areas were completely avoided, precluding a burn coefficient in the model (perfect predictability); however,; burned areas are included in the model intercept. Use based on distance to burned areas was best modeled as a quadratic function with use maximized at a distance of approximately 10 km. Our top winter model validated very well showing high ROC values (0.88), and outstanding within-sample k-fold (rho = 0.99) and out-of-sample Spearman rank correlation (rho = 0.98, P < 0.01).

Overlap and probability of wolf predation on caribou

We found the greatest number of wolf-killed caribou where their probability of spatial use was approximately equal to that of wolves, and therefore probability of overlap highest (Fig. 2). Overlap between wolves and caribou appeared to be negligible at overlap index values of positive 5 or above. We chose this overlap value of ≥ 5 as a cut-point to delineate caribou safe zones for the remainder of the analysis.

The seasonal strength of spatial separation by wolves varied between individual caribou herds as measured by the degree of safe zone within their home range. The A La Pêche had the greatest amount of safe zone habitat, followed by the Tonquin, Brazeau, Banff, and Maligne herds (Table 1). Spatial separation between wolves and caribou increased during winter for all herds, with the amount of safe zone at least doubling during that season.

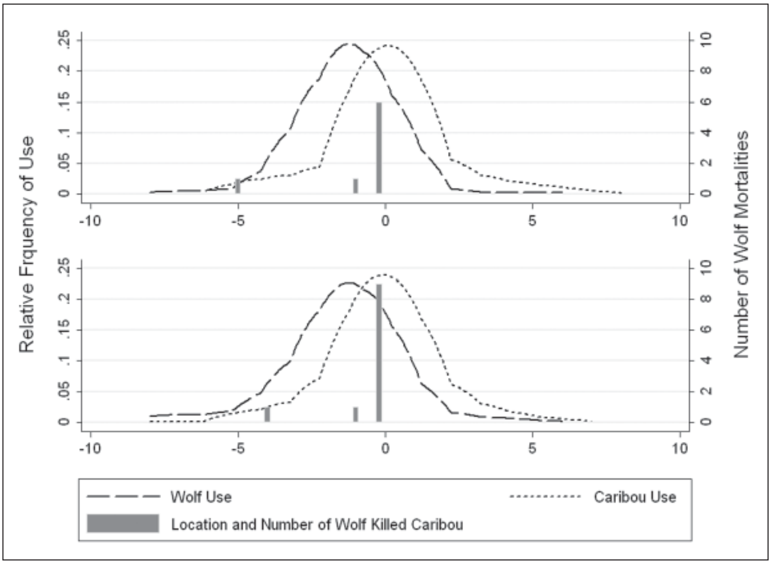

Fig. 2. Seasonal overlap of caribou and wolves showing relative probability of use as a function of the difference between summer (top) and winter (bottom) caribou and wolf resource selection models, and location and frequency of caribou mortalities (black bars). Note the X axis is the difference between binned RSF values of caribou and wolves, such that high values (10) represent safe areas for caribou, and low values (-10) represent high wolf use areas.

Table 1. Total area in km^2 and % of home range contained within safe zone habitat (with low wolf–caribou overlap) during winter and summer in the Canadian Rockies.

Herd	Season	Area (km^2)	% of Home Range
A La Pêche	Summer	902.2	14.7
A La Pêche	Winter	1580.2	25.9
Banff	Summer	60.3	5.9
Banff	Winter	92.8	9.2
Brazeau	Summer	73.5	6.8
Brazeau	Winter	131.1	12.3
Maligne	Summer	1.2	0.1
Maligne	Winter	3.8	0.3
Tonquin	Summer	59.4	3.9
Tonquin	Winter	235.6	15.6

Evaluating the direct and indirect effects of fire

The effects of fire on quality caribou habitat (direct effects) varied based on season, location of burn, and herd or home range size. ANOVA confirmed that the direct habitat-related effects of burn scenarios (prescribed, interior, buffer) on the percent of high quality habitat within caribou ranges were not significant ($P = 0.978$), and that the main differences in habitat quality were driven by seasonal differences between winter and summer ($P<0.005$) (Table 2). Considering only the effects of direct habitat loss due to loss of high quality caribou habitat, currently planned prescribed fires showed proportional (1%:1%) reductions in habitat of the A La Pêche, Banff, and Maligne herds (Table 3). A 1 % interior burn within a herd's home range caused an average of 1% habitat loss in winter, but a 2.3% loss in summer. Also, logically, burns on the periphery of caribou ranges (within a 14-km buffer) had negligible effects on direct habitat loss (Table 3).

In comparison to the direct habitat-related effects of fires, the indirect predation risk effects of burns varied with season, herd, and type of fire (Table 3). ANOVA revealed much greater interaction between

Table 2. ANOVA results for the effects of burn scenarios, season, and herd status on the percentage of caribou ranges occurring in high quality caribou habitat from RSF models, measuring the direct effects of fire on caribou. Seasons were winter and summer, and burn scenarios were prescribed burns, interior area, and buffer area burns. No interactions were significant. Overall adjusted R^2 for the model was 0.831, n=40 landscape burn experiments.

	Partial SS	df	MS	*F*	*P*-value
Model	3.333	12	24.88	24.88	<0.0005
Season	3.227	1	192.77	192.7	<0.0005
Herd	0.102	4	1.53	0.218	0.218
Burn Scenario	0.003	3	0.06	0.06	0.978
Residual	0.519	31	0.0167		
Total	3.852	39			

Table 3. Percentage areal reduction (%) in habitat quality and amount of safe zone by herd following simulated 1% prescribed, within home range, and within buffer zone fires. Values greater than equal losses to the 1% fire are bolded, indicating indirect effects of fire were important.

Herd	% Habitat Loss			% Safe Zone Loss		
	Prescribed Fire	Interior Fire	Buffer Fire	Prescribed Fire	Interior Fire	Buffer Fire
			Summer			
A La Pêche	-1	-2.7	-0.4	-2.2	-0.2	-0.1
Banff	-1.2	-4	<-0.1	-2	**-3.6**	-0.2
Brazeau	-0.6	-2.3	<-0.1	-1	-2.4	<-0.1
Maligne	-1.5	**-1.9**	-0.2	<-0.1	<-0.1	<-0.1
Tonquin	-0.5	-0.8	<-0.1	-0.2	<-0.1	<-0.1
Mean	-1	-2.3	-0.15	-1.1	-1.3	-0.1
			Winter			
A La Pêche	-0.5	-1.2	-0.2	-7.4	-0.3	<-0.1
Banff	-0.3	-1.5	<-0.1	-2.7	**-3.8**	<-0.1
Brazeau	-0.4	-1.2	<-0.1	<-0.1	-4.6	<-0.1
Maligne	-0.5	-1.1	-0.1	<-0.1	-0.1	<-0.1
Tonquin	-0.4	<-0.1	<-0.1	<-0.2	<-0.1	<-0.1
Mean	-0.4	-1	-0.1	-2.1	-1.8	<-0.1

Table 4. ANOVA results for the effects of burn scenarios, season, and herd status on the percentage of caribou ranges occurring in safe zone habitat, measuring the indirect effects of fire on caribou mediated via increased wolf–caribou overlap. Seasons were winter, summer, and burn scenarios were prescribed burns, interior area, and buffer area burns. Both season*herd and burn*herd 2-way interaction were significant. Overall adjusted R^2 for the model was 0.985, n=40 landscape burn experiments.

	Partial SS	df	MS	*F*	*P*-value
Model	0.21	24	0.0088	107.71	<0.0005
Season	0.035	1	0.0348	427.28	<0.0005
Herd	0.151	4	0.0376	462.26	<0.0005
Burn Scenario	0.002	3	0.0007	8.81	0.0013
Season*Herd	0.018	4	0.0045	55.37	0.0021
Burn*Herd	0.005	12	0.0004	5.07	0.08
Residual	0.001	15	0.0001		
Total	0.211	39	0.0054		

season, burn scenarios, and herds such that the effects of fires differed substantially between burn scenarios and herds (Table 4). The single greatest effect on a herd was a 7% loss in winter safe zone within the A La Pêche home range resulting from a currently planned prescribed fire (Table 3). Similar to habitat loss, however, the greatest impact appears to be from fires located directly within the interior area, with the Banff and Brazeau herds showing 2-5% losses of safe zone following fire (representing 1% of that herd's home range). Fires in the buffer zones surrounding the caribou home ranges had little effect on the amount of safe zone within (Table 3).

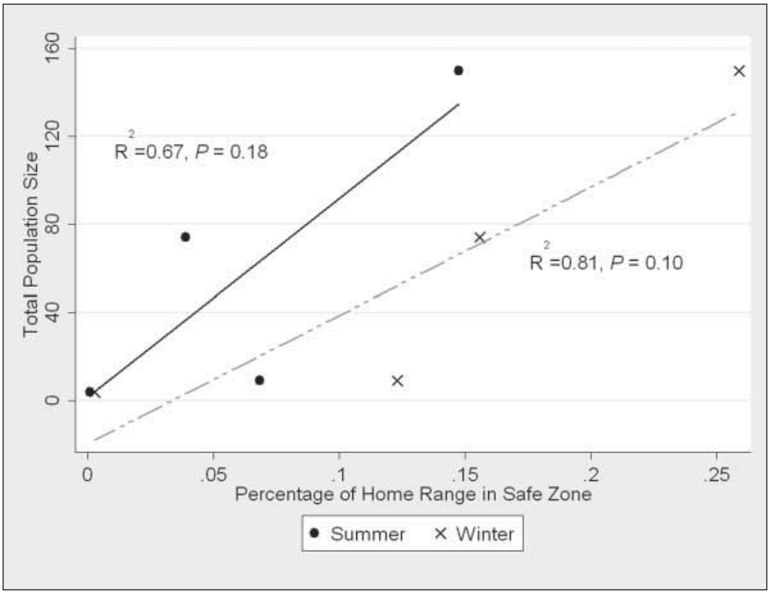

Fig. 3. Habitat-population relationships between percentage of home range consisting of safe zone within each caribou herd, and estimated population size of the caribou herd during winter and summer.

Population consequences of spatial separation between wolves and caribou

There was a positive relationship between the proportion of a herd's home range represented by "safe zone" and population size among the 4 caribou herds, although the relationship was marginally significant during winter (P = 0.10, n=4) but non-significant during summer (P = 0.18, n=4) (Fig. 3). There were similar positive effects of spatial separation on adult female caribou survival rates and population growth rate, although neither relationship was significant. Expressing separation as the proportion (%) that the safe zone increased during winter also showed that as spatial separation increased during winter, survival and population growth rate increased. These relationships may be biologically significant however a lack of sample size (n=4) limited statistical power.

Discussion

Our results suggest that spatial separation from wolves at broad, landscape scales is an important strategy for caribou to avoid mortality, and that fire will increase the amount of overlap between wolves and caribou with potentially negative consequences for caribou populations. Our support for the spatial separation hypothesis agrees with the results of many previous studies of caribou resource selection (Apps *et al.*, 2001; McLoughlin *et al.*, 2005; Wittmer *et al.*, 2005) that indicated that, for example, "…the spatial distribution of woodland caribou largely reflects a behavioral response to risk" (Fortin *et al.*, 2008). Our results show that the highest probability of caribou and wolf overlap occurs in areas where each species has an equal probability of use (i.e., areas near zero in terms of RSF difference), and it is in these same areas where the majority of wolf-caused caribou mortalities occur (Fig. 2). McLoughlin *et al.* (2005) showed similar results from boreal caribou in northern Alberta. Therefore, identifying areas of overlap between wolves and caribou is an important factor when considering how changes in landscape configuration induced by fire could affect wolf movements and caribou predation risk.

Our resource selection models show selection of landscape variables similar to the findings of past research on both species (e.g., Apps *et al.,* 2001; Hebblewhite & Merrill, 2008). In summer, caribou and wolves showed similar selection for both low and high elevation (alpine) herb and shrub landcover classes; for wolves, this is presumably in response to increased prey availability. In winter, wolf selection for low elevation shrub and herb landcover classes, in conjunction with caribou selection for alpine herb and shrub, may create an elevational separation between the species; while selection by both for open conifer forests provides opportunity for overlap in that landcover type.

Wolves selected for burned areas in both seasons, while caribou avoided burns in both seasons (complete avoidance in winter), ostensibly suggesting that burns would be areas of strong separation between wolves and caribou. However, due to the linear response of wolves to distance to burned areas, their probability of use is increased not only in the burned area itself, but also in the surrounding areas. It follows that if a burn occurs in preferred caribou habitat, the probability of overlap between the two species increases by a greater proportion than simply the size of the fire.

Despite the limitations of having only 4 caribou herds to examine between-herd demographic consequences of spatial separation, our results support the demographic benefit of spatial separation from wolves over very large spatial scales. Total population size was positively correlated with the percentage of safe zone within a herd's home range during winter (P=0.10, n=4). The seasonal, but not total, estimates of spatial separation were weakly correlated with survival, lambda, and population size. Taken together, these results support the results from other studies that showed large patches of low predation risk caribou habitat are required for the long-term persistence of Boreal and Mountain populations of woodland caribou in Canada (Lessard, 2005; Wittmer *et al.*, 2005; Courtois *et al.*, 2007; Fortin *et al.*, 2008). These results also support the results of recent demographic population viability models by DeCesare *et al.* (2011) that show almost certain extirpation of the caribou herds with low spatial separation (Maligne and Brazeau herds), but continued persistence and growth of the Tonquin herd which has more safe habitat.

We investigated the direct habitat loss and indirect predation risk effects of fire on caribou using spatial simulations of planned prescribed and natural fires. The direct effects of fire on caribou habitat itself were minimal. Burning 1% of a caribou home range reduced the abundance of high-quality caribou habitat throughout the range by an average of 2% in summer and 1% in winter. The direct effects of fire were unaffected by the position of the fires in the interior of the caribou range.

In contrast, the indirect effects of prescribed and natural fire on caribou were often greater than the direct effects, and varied across herds and burn scenarios. Fire in caribou range increased wolf use of the burned and surrounding area which in turn resulted in a decrease in safe habitat. On average, burning 1% of the landscape reduced the amount of safe habitat by ~2%, and this effect was most pronounced for fires occurring in the interior of their home ranges, and especially for a prescribed burn planned in the A La Pêche caribou home range (Table 3). This suggests that spatial arrangement of burns will be critical for evaluating effects of prescribed burn plans on caribou.

In the Canadian Rockies, we found caribou tended to select areas along the continental divide at higher elevations dominated by old-growth spruce and subalpine fir and with low fire frequency (Van Wagner *et al.*, 2006). In contrast, wolves tended to select lower elevation, more early seral habitats that historically would have been spatially separated because of fire history (White *et al.*, 2003; Van Wagner *et al.*, 2006), probably contributing to the viability of caribou. Regardless, our results show that when fire overlaps current caribou habitat, there is increased overlap with wolves, and that that has potential population consequences. Given the *threatened* status of southern mountain woodland caribou, maintenance of current caribou populations and distribution is an important management objective. Our results suggest Parks Canada managers should seek to spatially separate fires from caribou ranges when trying to restore both caribou populations and fire on the landscape—two potentially conflicting objectives. This is especially true because of potential changes to fire cycles due to fire suppression, climate change, and increased drought in Rocky Mountain areas (Schoennagel *et al.*, 2004).

Our fire scenarios did not consider a range of potential fire sizes or configurations evaluated in other wildlife-fire modeling efforts (Turner *et al.*, 1994). Even so, our results are conservative because we modeled the effect of only burning 1% of a caribou range, which equated to fire sizes of 10-61 km^2. Within the last decade, several fires in our study area were larger than the 1% burns we evaluated. With the potential for increased fire frequency resulting from the interacting effects of climatic change, historic fire suppression, and increased fuel loads (Brown *et al.*, 2004; Schoennagel *et al.*, 2005; Rupp *et al.*, 2006), large stand-replacing fires are possible in and adjacent to caribou ranges. Linking our caribou and wolf spatial overlap models to probabilistic and dynamic landscape fire simulations as used in Alaska (Rupp *et al.*, 2006) would be useful for evaluating the susceptibility of caribou in the National Parks to future fires.

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Supplementary tables

S-table 1. Number of radiocollared caribou monitored in Banff and Jasper National Parks, and total number of locations used in model development and validation.

Season	Herd	Model Training		Model Validation	
		Animals	Locations (mean, range)	Animals	Locations (mean, range)
Summer	A la Peche	10	8895 ($\bar{x}$=889, 212 - 2031)	72	924 ($\bar{x}$=13, 1 - 192)
	Banff	2	2125 ($\bar{x}$=1062, 954 - 1171)	2	31 ($\bar{x}$=15, 12 - 19)
	Brazeau	6	4521 ($\bar{x}$=735, 154 - 1523)	11	94 ($\bar{x}$=8, 3 - 13)
	Maligne	9	9329 ($\bar{x}$=1036, 187 - 2417)	10	94 ($\bar{x}$=9, 1- 22)
	Tonquin	8	4974 ($\bar{x}$=621, 152 - 1590)	17	204 ($\bar{x}$=12, 1 - 18)
Winter	A la Peche	15	11868 ($\bar{x}$=791, 341 - 1964)	78	1193 ($\bar{x}$=15, 1 - 245)
	Banff	2	1957 ($\bar{x}$=978, 880 - 1077)	2	36 ($\bar{x}$=18, 11 - 25)
	Brazeau	6	5220 ($\bar{x}$=870, 612 - 1244)	12	185 ($\bar{x}$=15, 3 - 27)
	Maligne	9	9336 ($\bar{x}$=1037, 374 - 2377)	8	95 ($\bar{x}$=11, 6 - 29)
	Tonquin	8	5058 ($\bar{x}$=632, 87 - 1553)	17	299 ($\bar{x}$=17, 3- 72)
		75		229	

S-table 2. Number of animals from each wolf pack monitored during summer in Banff and Jasper National Parks, and total number of locations used in summer model development and validation 2002 - 2009.

Park	Pack	Model Training		Model Validation	
		Animals	Locations (mean, range)	Animals	Locations (mean, range)
BANFF	Bow Valley	1	932 ($\bar{x}$= 932, N/A)	0	N/A
	Ranch	3	1859 ($\bar{x}$= 619, 561 - 675)	0	N/A
	Cascade	2	1218 ($\bar{x}$= 609, 164 - 1054)	0	N/A
	Red Deer	4	2037 ($\bar{x}$= 509, 193 - 775)	0	N/A
	Wildhorse	1	770 ($\bar{x}$= 770, N/A)	0	N/A
JASPER	Medicine	4	767 ($\bar{x}$= 191, 26 - 464)	3	60 ($\bar{x}$= 20, 2 - 32)
	Berland	1	625 ($\bar{x}$= 625, N/A)	0	N/A
	Brazeau	4	657 ($\bar{x}$= 164, 8 - 604)	1	1 ($\bar{x}$= 1, N/A)
	Maligne	1	319 ($\bar{x}$= 319, N/A)	2	3 ($\bar{x}$= 1.5, 1 - 3)
	Signal	4	760 ($\bar{x}$= 190, 3 - 328)	5	212 ($\bar{x}$= 42, 1 - 118)
	Sunwapta	2	1037 ($\bar{x}$= 518, 439 - 598)	4	316 ($\bar{x}$= 79, 2 - 158)

S-table 3. Number of animals from each wolf pack monitored during winter in Banff and Jasper National Parks, and total number of locations used in winter model development and validation 2002 – 2009.

Park	Pack	Model Training		Model Validation	
		Animals	Locations (mean, range)	Animals	Locations (mean, range)
BANFF	Bow Valley	1	39 (x̄= 39, N/A)	0	N/A
	Ranch	3	1472 (x̄= 490, 253 - 813)	0	N/A
	Cascade	4	1261 (x̄= 315, 31 - 961)	0	N/A
	Red Deer	4	1734 (x̄= 433, 217 - 743)	0	N/A
	Wildhorse	3	1067 (x̄=355, 103 - 544)	0	N/A
JASPER	Medicine	4	1859 (x̄= 464, 110 - 734)	4	33 (x̄= 8, 4 - 15)
	Berland	1	361 (x̄= 361, N/A)	0	N/A
	Brazeau	4	2616 (x̄= 654, 314 - 933)	2	71 (x̄= 35, 3 - 68)
	Maligne	1	602 (x̄= 602, N/A)	3	14 (x̄= 4, 2 - 7)
	Rocky	1	132 (x̄= 132, N/A)	1	2 (x̄= 2, N/A)
	Signal	6	1879 (x̄= 313, 6 - 595)	7	251 (x̄= 35, 1 - 107)
	Sunwapta	2	1384 (x̄= 692, 489 - 895)	6	361 (x̄= 60, 4 - 186)

S-table 4. Terrain and landcover GIS layers (canidate variables) used in predictive RSF models for caribou and wolves, Banff and Jasper national parks.

Variable	Variable Type	Range of Values	Description
Topography			
North	Categorical	0.1	North aspects from 315° to 45°
South	Categorical	0.1	South aspects from 135° to 225°
East	Categorical	0.1	East aspects from 45° to 135°
West	Categorical	0.1	West aspects from 225° to 315°
Flat	Categorical	0.1	No aspect (slope = 0)
Slope	Continuous	0–6827%	Percent slope (equivalent to 0 – 90°)
Elevation	Continuous	553–3955m	Elevation in meters
Landcover			
Alpine Barren	Categorical	0.1	Barren ground between 2200 and 2700m.
Alpine Herb	Categorical	0.1	Alpine meadows above 2200m.
Alpine Shrub	Categorical	0.1	Shrub communities above 2200m.
Burn	Categorical	0.1	Areas burned 1950 to present.
Closed Conifer	Categorical	0.1	Coniferous forest with >50% canopy closure and >70% conifer composition.
Deciduous Forest	Categorical	0.1	Deciduous dominated forests <30% coniferous.
Ice and Rock	Categorical	0.1	Permanent ice, snow and alpine rock above 2700m.
Low Barren	Categorical	0.1	Barren but possible still productive ground below 2200m.
Low Herb	Categorical	0.1	Grasslands below 2200m
Low Shrub	Categorical	0.1	Shrub stands below 2200m.
Mixed Forest	Categorical	0.1	Forests >30% and <70% coniferous.
Open Conifer	Categorical	0.1	Coniferous forest with <50% canopy closure and >70% conifer composition.
Wetlands and Water	Categorical	0.1	Water and wetlands at all elevations.
Bank Distance	Continuous	0–6951m	Distance to water's edge from both directions.
Burn Distance	Continuous	0–105670m	Distance to any burn occurring after 1950.
Edge Distance	Continuous	0–15531m	Distance to boundary between open and closed canopy from either direction.
Hard Distance	Continuous	0–6728m	Distance to the closest hard edge.
NDVI	Continuous	0–8759	Mean NDVI in open habitats
Open Distance	Continuous	0–15557m	Single direction distance to open canopy (i.e. value within open canopy is 0)
Human Use			
Primary Road Distance	Continuous	0–48247m	Distance to paved road.
Secondary Road Distance	Continuous	0–56075m	Distance to gravel road.
Trail Distance	Continuous	0–40972m	Distance to trails inside the parks and cutlines outside.
Water Distance	Continuous	0–6951m	Single direction distance to water.

S-table 5. Wolf and Caribou summer resource selection function (RSF) model for Banff and Jasper National Parks. Covariates without coefficients were non-significant in our stepwise model selection process and thus categorical variables (landcover type and aspect) without coefficients are included in the model intercept. For distance variables a positive coefficient shows avoidance (i.e., use increases with distance) while negative coefficients show selection (i.e., use decreases with distance). Squared variables are quadratic terms. All variables included in the models were significant at a level ≤ 0.01

	Wolf Summer		Caribou Summer	
Variable	Coef.	Std. Err.	Coef.	Std. Err.
LANDCOVER				
Burn	1.177	0.0656	-3.967	0.7119
Closed Conifer			-0.221	0.0303
Ice and Rock			-2.627	0.1004
Deciduous Forest	-0.527	0.2151		
Low Elevation Barren Ground			-0.976	0.0553
Low Elevation Herb	0.547	0.0671	0.954	0.0458
Low Elevation Shrub	0.605	0.0504	0.8	0.0393
Open Conifer	0.966	0.0429		
Alpine Barren	-0.444	0.0939		
Alpine Herb	1.239	0.1007	1.743	0.0449
Alpine Shrub	1.234	0.1368	1.486	0.0599
Mean NDVI			5.25E-04	2.21E-05
Mean NDVI^2			-9.61E-08	3.98E-09
Distance to Burn	-0.00012	3.16E-06	2.14E-04	5.24E-06
Distance to Burn^2			-5.84E-09	1.86E-10
Distance to Stream Bank	-0.00063	3.72E-05		
TOPOGRAPHY				
Elevation	0.0134	0.0004	0.0103	0.0003
Elevation^2	-0.000003	1.20E-07	-2.59E-06	8.17E-08
Slope	-0.051	0.0011	-0.05	0.0007
East Aspects	0.338	0.04	-0.441	0.0278
South Aspects	0.463	0.0417	-0.283	0.0279
West Aspects	0.188	0.0434		
North Aspects			-0.182	0.0282
HUMAN USE				
Distance to Primary Road	-0.00007	2.38E-06	1.31E-04	4.45E-06
Distance to Primary Road^2			-5.97E-09	1.40E-10
Distance to Secondary Road	0.00006	1.28E-06	1.83E-04	3.45E-06
Distance to Secondary Road^2			-1.98E-09	7.17E-11
Distance to Trail	-0.0003	1.02E-05	3.20E-05	1.44E-05
Distance to Trail^2			-2.88E-08	1.74E-09
(Model intercept)	-12.49	0.374	-15.1	0.282

S-table 6. Wolf and Caribou winter resource selection function (RSF) models for Banff and Jasper National Parks. Covariates without coefficients were non-significant in our stepwise model selection process and thus categorical variables (landcover type and aspect) without coefficients are included in the model intercept or constant term. For distance variables a positive coefficient shows avoidance (i.e., use increases with distance) while negative coefficients show selection (i.e., use decreases with distance). Squared variables are quadratic terms. All variables included in the models were significant at a level ≤ 0.01.

	Wolf Winter RSF		Caribou Winter RSF	
Variable	Coef.	Std. Err.	Coef.	Std. Err.
LANDCOVER				
Burn	0.543	0.0559		
Ice and Rock	-2.171	0.2749	-4.123	0.2045
Closed Conifer			0.338	0.0247
Open Conifer	0.748	0.0376	0.892	0.0316
Alpine Barren Ground	-0.671	0.1073	-0.566	0.0412
Alpine Herb			1.016	0.049
Alpine Shrub			1.144	0.0638
Low Elevation Barren Ground			-1.064	0.0503
Low Elevation Shrub	0.421	0.0423		
Low Elevation Herb	0.544	0.053		
Distance to Burn	-0.00014	2.94E-06	0.00025	5.44E-06
Distance to Burn^2			-1.30E-09	2.64E-10
Distance to Stream Bank	-0.0007	3.45E-05		
Distance to Open Canopy	-0.0013	6.25E-05		
Distance to Hard Edge			0.0024	9.84E-05
Distance to Hard Edge^2			-2.40E-06	1.10E-07
TOPOGRAPHY				
Elevation	0.015	0.0005	0.01	0.00018
Elevation^2	-4.00E-06	1.35E-07	-3.00E-05	5.02E-08
Slope	-0.038	0.0009	-0.039	0.0006
East Aspects	0.189	0.0303	-0.467	0.0206
South Aspects	0.24	0.0318	-0.316	0.0223
Flat Aspects			0.194	0.0398
HUMAN USE				
Distance to Secondary Road	6.03E-05	1.15E-06	0.0002	2.76E-06
Distance to Secondary Road^2			-3.00E-09	5.90E-11
Distance to Trail	-0.00024	8.19E-06	-0.0001	3.53E-06
Distance to Primary Road	-5.60E-05	2.04E-06		
(Model intercept)	-11.72	0.369	-12.69	0.155

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Using movement behaviour to define biological seasons for woodland caribou

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Abstract: Terrestrial mammals are strongly influenced by seasonal changes in environmental conditions. Studies of animal space use behaviour are therefore inherently seasonal in nature. We propose an individual-based quantitative method for identifying seasonal shifts in caribou movement behaviour and we demonstrate its use in determining the onset of the winter, spring dispersal, and calving seasons. Using pooled data for the population we demonstrate an alternate approach using polynomial regression with mixed effects. We then compare individual onset dates with population-based estimates and those adopted by expert consensus for our study area. Distributions of individual-based onset dates were normally distributed with prominent modes; however, there was considerable variation in individual onset times. Population-based estimates were closer to the peaks of individual estimates than were expert-based estimates, which fell outside the one-tailed 90% and 95% sample quantiles of individually-fitted distributions for spring and winter, respectively. Both expert- and population-based estimates were later for winter and earlier for both spring and calving than were individual-based estimates. We discuss the potential consequences of neglecting to corroborate conventionally used dates with observed seasonal trends in movement behaviour. In closing, we recommend researchers adopt an individual-based quantitative approach and a variable temporal window for data set extraction.

Key words: biological inference; quantitative methods; seasonal onset behaviour; temporal variation; woodland caribou.

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Introduction

The life history traits of mammals are in no small part a function of the bioclimatic environments in which they live (Klein, 1982). In the northern boreal forest of Canada, the biological activity of terrestrial mammals is regulated by seasonal shifts in temperature and precipitation which, in turn, directly or indirectly influence the quality and availability of forage and refuge habitat (Pruitt, 1957; Telfer & Kelsall, 1984; Post & Stenseth, 1999). Members of the Cervidae family, for example, exhibit growth dormancy in winter when the metabolic demands of thermoregulation are high and plant nutrients essential for body tissue development are in short supply (Irving *et al.*, 1955; Wood *et al.*, 1962; McEwan, 1970). Likewise, displacements are limited at this time in order to minimize heat loss and the depletion of body reserves (McEwan & Whitehead, 1970; Ozoga & Gysel, 1972; Gates, 1979; Ferguson & Elkie, 2004). Spring, in contrast, is a time of increased energetic expenditure when the demands of pregnancy reach their peak and female cervids prepare to give birth (Moen, 1976). Forest-dwelling woodland caribou (*Rangifer tarandus caribou*) make concerted movements away from wintering areas at this time as a means of attaining low densities and thereby reducing detection by predators (Bergerud & Page, 1987; Cumming & Beange, 1987; Rudolph, 2011). The punctuated movements of spring dispersal come to an abrupt halt at parturition, when nursing caribou become virtually immobile, functionally limited in their movements for up to several weeks until calves are vigorous enough to travel (Lent, 1966; Espmark, 1971; Clutton-Brock & Guiness, 1975). This period coincides with the emergence of high-quality plant vegetation required for lactation and, consequently, calf development (Klein, 1990; Lantin *et al.*, 2003; Post *et al.*, 2003).

Like many species, caribou exhibit shifts in biological activity that parallel changes in their natural environment. For this reason, investigations of their space use behaviour tend to differentiate between seasons based on conventional knowledge of populations, climatic conditions, and plant phenology (*e.g.* Rettie & Messier, 2000; Brown *et al.*, 2003, Apps *et al.*, 2001; Jones *et al.*, 2007; Hins *et al.*, 2009). Few studies, however, recognize and account for temporal variation in seasonal processes, which could have important consequences for biological inference. Calving, for example, is a relatively predictable biological event that tends to be well defined for populations based on field observations (Rettie & Messier, 2001). Despite this, the peak onset of calving can vary annually by as much as 15 days (Eloranta & Nieminen, 1986; Cameron *et al.*, 1993; Post & Klein, 1999; Flydal & Reimers, 2002). Furthermore, calving times for individuals within a population may vary by as much as a month or more (Bergerud, 1975; Eloranta & Nieminen, 1986; Rettie & Messier, 1998; Post & Klein, 1999; Ferguson & Elkie, 2004). Conceivably, then, failure to account for either source of variation (whether individual or annual) could mean including several weeks of migratory behaviour in a characterization of caribou calving site selection.

However accurate the dates we choose, using a fixed temporal window to study seasonal phenomena may generate biased results due to inter-individual variation. Given the variable and often unpredictable behaviour of free-ranging animals (Gustafson & Gardner, 1996; Johnson *et al.*, 2001; Gustine, 2005), we propose an approach to analyzing seasonal space use that accounts for individual variation in seasonal onset times. We argue that by varying the temporal window of analysis to more effectively capture the biological phenomenon under investigation, we can improve ecological studies by reducing misclassification, thereby improving biological inferences.

A number of quantitative approaches have been used to identify seasonal shifts in the behaviour of woodland caribou. These require *a priori* biological knowledge and can be rule-based (Mahoney & Schaefer, 2002; Saher & Schmiegelow, 2005; Courbin *et al.*, 2009) or model-based (Ferguson & Elkie, 2004; Dyke, 2008; Vander Wal & Rodgers, 2009). We propose a model-based approach called recursive partitioning, which can be used to locate changes in the distribution of movement parameters over time using iterative analyses of variance (ANOVA) and prior knowledge of species life history. We demonstrate how this approach can be used to delineate three contrasting seasonal periods in the annual life cycle of woodland caribou: winter, spring dispersal, and calving. Finally, we compare the results of this approach with 1) dates obtained using polynomial regression with pooled data (population estimates), and 2) dates adopted by expert consensus (conventional estimates) for our study area in northern Quebec.

Study area

The study area comprises a 109,116 km^2 tract of boreal forest in northern Quebec situated between 49°52’ and 51°46’N and 71°17’ and 79°31’W (Fig. 1). Part of the black spruce-feathermoss bioclimatic domain, it is dominated by black spruce (*Picea mariana*) in association with feathermoss (*Pleurozium schreberi*) and/or various lichen species. Jack pine (*Pinus banksiana*) and balsam fir (*Abies balsamea*) occur to a lesser extent, in addition to trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), tamarack (*Larix laricina*), and (rarely) balsam poplar (*Populus balsamifera*). Forest understory is dominated by mosses and ericaceous shrubs with few herbaceous species. The western flank of the region forms part of the Clay Belt and is dominated by large sphagnum bog and fen complexes. Terrain is broad and mildly sloping with occasional topographic relief. Elevation ranges from 45 to 825m and there are numerous rivers and waterways interconnecting the region. Treed wetlands and upland forest intersperse with bog/fen complexes and lichen or shrub-dominated uplands with occasional rock barrens. The region receives approximately 960 mm of precipitation annually with monthly average temperatures ranging from -19° (January) to + 16° (July) Celsius.

Constituting Québec’s second-largest timber supply region, the study area encompasses both the northern limit of commercial forestry activity and the southern limit of continuous woodland caribou distribution (Courtois, 2003). Primary disturbances include forest fire (100-500 year fire cycle; Bergeron et al. 2001) and forest harvesting, which is presently concentrated in the southern portion of the study area. Large mammal species in addition to forest-dwelling woodland caribou include, moose (*Alces alces*), wolf (*Canis lupus*) and black bear (*Ursus americanus*). Reliable population estimates are unavailable,

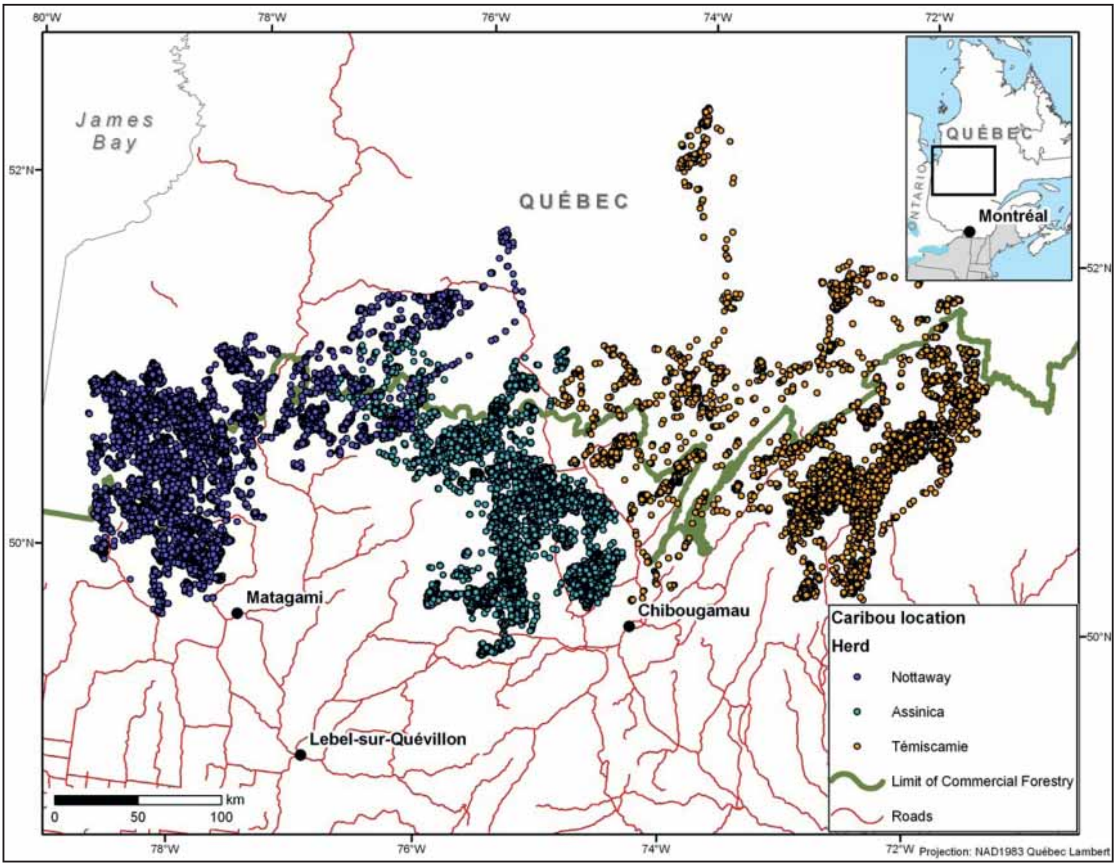

Fig. 1. Location of study area in the northern boreal forest of Quebec. Depicted are GPS telemetry locations transmitted by 26 collared female woodland caribou dispersed across three regional populations: the Nottaway, Assinica, and Témiscamie. Primary road networks are also depicted along with the current limit of commercial forestry.

but caribou densities are estimated to be between 1.5 and 2.1/100 km^2, with individuals occupying average annual home ranges of ~4386 km^2 (St-Pierre *et al.*, 2006). In the northern sector, infrequent range overlap takes place with populations of the tundra-forest ecotype of woodland caribou (*Rangifer tarandus caribou*) (Courtois *et al.*, 2003).

Methods

Caribou capture and GPS telemetry

Animal relocation data were obtained via GPS (Global Positioning System) collar transmitters (Telonics model TGW 3680) fitted on 26 female caribou by members of the Québec Ministry of Natural Resources and Wildlife in March 2004 and January 2005. Captures were conducted using ASTAR 350BA or EC120 helicopters and a net gun (Potvin & Breton, 1988). Individuals sampled were evenly distributed across three regional populations: the Nottaway (west), Assinica (central), and Témiscamie (east) (Fig. 1). Collars were programmed to transmit locations every seven hours and data was compiled in March 2007. Relocations were filtered for positional accuracy in order to remove large location errors: those based on 4 or more satellites (3-D) were eliminated if they had corresponding horizontal dilution of precision (HDOP) values greater than or equal to 25, whereas those based on 3 satellites (2-D) were eliminated if they had HDOP values greater than or equal to 8 (Dussault *et al.*, 2001). The Horizontal Dilution of Precision reflects the horizontal accuracy (latitude/longitude) of GPS position fixes by adjusting the error estimates according to the geometry of the satellites used. This resulted in a roughly 4% data reduction per individual.

Although movement rates have been known to vary among female caribou according to reproductive status (Paré & Huot, 1985; Fancy & Whitten, 1991; Ferguson *et al.*, 1998), high pregnancy rates are pervasive in woodland caribou populations so we assumed no error due to variation in reproductive condition (Parker, 1981; Rettie & Messier, 1998).

In order to render our data temporally uniform, we reduced data sets to one relocation per individual per day, retaining that relocation obtained closest to 12:00 noon. Because estimates of movement rates may be biased when fix interval varies (Johnson *et al.*, 2002), distance calculations based on more than one consecutive day between successive relocations were not retained for analyses. Furthermore, individual-year combinations comprising less than 100 observations were eliminated from analyses. Resulting sample sizes ranged from 231 to 365 ($\bar{x}$ = 319).

Temporal focus of study

We chose the winter, spring and calving seasons because they represent critical periods in the annual life cycle of woodland caribou (Darby & Pruitt, 1984; Environment Canada, 2008). We were also particularly interested in characterizing spring dispersal behaviour of boreal caribou (Rudolph, 2011). Our goal, therefore, was to identify peak onset dates for the winter, spring dispersal, and calving periods on an individual basis through quantitative analysis of movement patterns. We began by calculating two movement parameters for each individual: movement rate (km/day) and net displacement (km). Movement rate was logarithmically transformed to improve normality. Net displacement was defined as the Euclidean distance between an animal's location on any given day and its location on January 10 of the same year; this date was chosen as the "anchor" point because most individuals were found to have settled into their wintering areas by this time. We then proceeded to calculate daily averages for each parameter (individuals and years pooled). Visualizing trends in pooled averages over time permitted us to identify temporal neighbourhoods corresponding with seasonal changes in the movement behaviour of our study population. All computations were done using R Version 2.9.0 (R Development Core Team 2010) (R code is available through the authors upon request).

Individual-based modeling

In order to minimize noise attributed to periodic variation in individual movement behaviour (e.g. circadian rhythms), prior to proceeding we applied a 4-term (1 observation/day) smoothing window (moving average) over the raw movement parameters observed for each individual-year time-series (Rudolph, 2011). We chose 4 terms because correlograms of residual distances (y) over time (x) demonstrated a significant recurring pattern every 4 days for the majority of individual-year distributions based on Moran's *I*.

We used the R package rpart to model movement rate (km/day) and net displacement (km) as a function of Julian day (origin = January 1) using recursive partitioning to progressively subdivide the smoothed values into temporally homogenous groups (De'ath & Fabricius, 2000; Therneau *et al.*, 2010). Smoothed movement rates were log-transformed to improve normality. The rpart algorithm iteratively performs analyses of variance to produce a univariate regression tree in which temporally discrete blocks are optimally partitioned so as to maximize the between-groups sums of squares (Therneau & Atkinson, 2011). A complexity parameter is incorporated to permit only those partitions which improve the explained variance by an established threshold (i.e. $\Delta R^2 >= 0.01$). Cross-validation is employed to obtain the predicted error, and the optimal tree is determined based on the lowest estimate plus or minus one standard error.

In order to determine individual onset dates for winter, spring dispersal and calving, we conducted two recursive partitioning exercises (one for each parameter or response variable) for each individual-year distribution. Due to inherent variation in movement behaviour, there were occasionally numerous statistically plausible choices for the onset of a given season, which necessitated *a priori* knowledge of caribou biology. The first model (log(movement rate) ~ Julian day) provided the candidate breakpoints. Since spring dispersal is generally demarcated by important displacements from late winter ranges to traditional calving areas (Courbin *et al.*, 2009), breakpoints obtained via the second model (net displacement ~ Julian day) gave weight to our final choice of onset dates, in particular with respect to the beginning and end of spring dispersal (Fig. 2).

In order to provide enough data to effectively capture the onset of winter, we included the previous year in recursive partitioning exercises when selecting for these dates. Individuals displaying erratic behaviour (i.e. considerable deviation from mean observed pattern) and those missing data during critical periods of interest were excluded from subsequent analyses for the year(s) in question. Once the onset dates of winter, spring dispersal, and calving had been determined for every qualifying individual-year data sequence, population means (µ) and their associated standard errors (SE) were estimated for each season using a non-parametric bootstrap procedure (Efron & Tibshirani, 1986). Means were considered the most appropriate summary statistic given that individual onset dates were normally distributed.

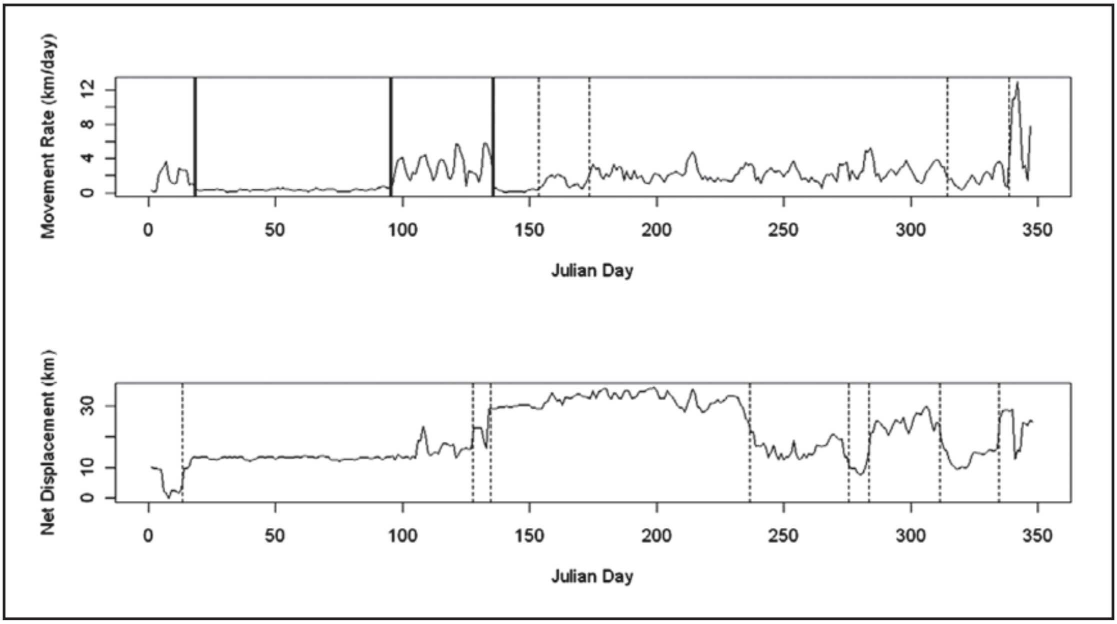

Fig. 2. Example output from two recursive partitioning exercises conducted using GPS telemetry locations emitted daily by one female caribou of Northern Quebec in 2005. Model 1 (log(distance)~Julian day) is depicted above and Model 2 (net displacement~Julian day) is depicted below. Dashed lines represent candidate splits of the univariate regression trees and solid black lines represent splits chosen to delimit the onset of (from left, above) winter, spring dispersal, and calving. Because important changes in net displacement may be indicative of spring dispersal, breakpoints obtained via Model 2 (below) informed our choice of final onset dates when more than one candidate split was obtained by Model 1 for a given season.

Population-based modeling

As a point of comparison, we developed a population-based polynomial regression model with mixed effects in order to estimate the onset dates of winter, spring dispersal, and calving periods based on season-specific shifts in movement rate (log-transformed to improve normality) as a function of Julian day (origin = Jan. 01). This is similar to the approach published by Ferguson & Elkie (2004); however because we were working with a sample of a much larger population and wished to take into account individual and annual variability in seasonal onset behaviour, a random intercept was specified for each individual and each nested individual-year combination. Specifying the grouped structure of the data ensured that the individual animal was considered the sample unit and that population estimates were unaffected by variable sample sizes (Gillies *et al.*, 2006). Population-based models were estimated using Maximum Likelihood and the R package nlme (Pinheiro *et al.*, 2010). Polynomials were independently re-centered about their respective means (orthogonal polynomials) to facilitate convergence and eliminate correlation between terms. The model takes the following form:

$y_i = X_i\beta + Z_ib_i + \varepsilon_i$, where:

$X_i\beta = \beta_0 + \beta x + \beta x^2 + \beta x^3 + \ldots + \beta x^k$ is the standard linear model structure for the fixed effects component, and:

$Z_i bi = b_1x + b_2x^2 + b_3x^3 \ldots + b_kx^k$, where b_k is the variance-covariance matrix of the random effects and ε_i is an estimation of the residual error.

We compared a series of candidate models in which polynomial terms were sequentially added and Akaike's Information Criterion for small sample sizes (AIC_c) was calculated iteratively to identify the best candidate model based on the principle of parsimony. In order to define at least three seasons, we began with five terms and sequentially added up to 25 polynomial terms, stopping at the first model in the sequence where ΔAIC_c ceased to be negative, the best candidate model being the one immediately prior. Inflection points in the fitted curve indicated season-specific changes in movement rate, and these were obtained by solving for x=0 in the second derivative of the fixed effects component of the regression equation (Ferguson & Elkie, 2004).

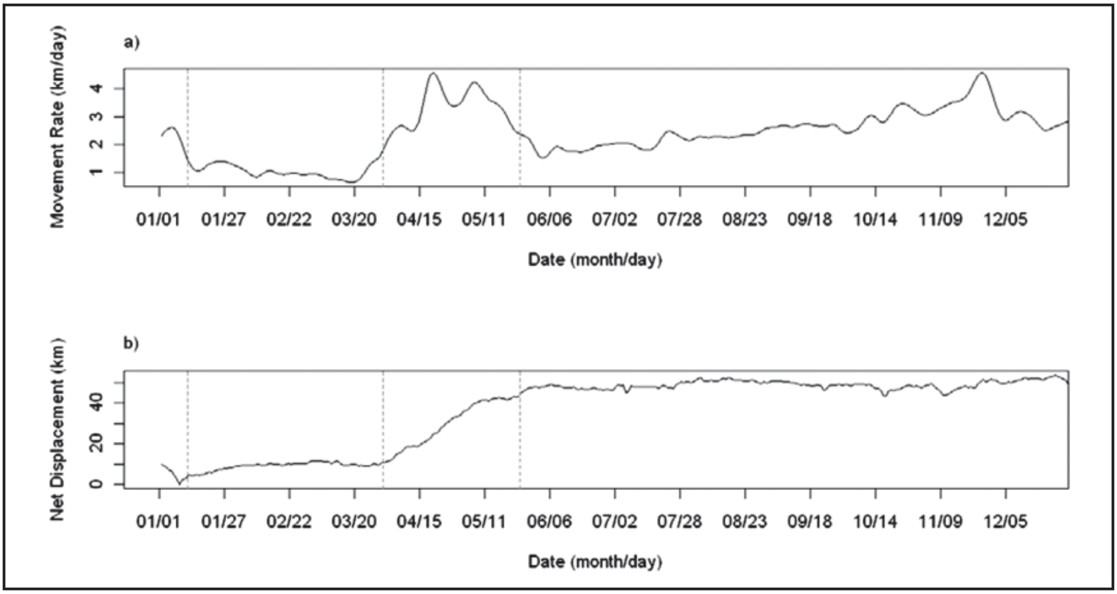

Fig. 3. Mean daily a) movement rate (smoothed) and b) net displacement of 26 female woodland caribou from Northern Quebec pooled across 3 years (2004–2007). Movement parameters (1 observation/day per individual) were derived from GPS locations transmitted from ARGOS telemetry collars. The onset of late winter is marked by a significant drop in movement rate in early January (1st dashed line from left). The onset of spring dispersion is marked by a sudden increase in both movement rate and net displacement in early April, followed by a drop in both variables in late May that marks the onset of calving (rightmost pair of dashed lines).

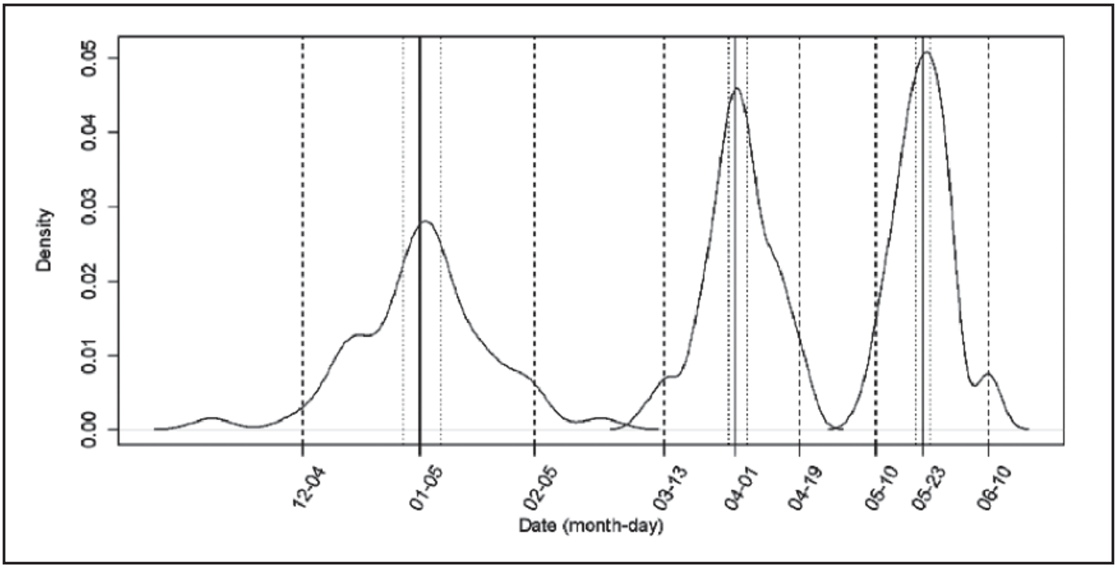

Fig. 4. Distribution of individual onset dates determined via recursive partitioning for 26 female caribou from Northern Quebec pooled over three years. Movement rate (km/day) and net displacement (km) were derived from GPS locations transmitted from ARGOS telemetry collars. The two parameters were subsequently modeled as a function of time using iterative analyses of variance (ANOVA). Onset dates for all three seasons were normally distributed with prominent modes. Solid lines indicate peak (population) onset dates for the winter (Jan. 5; n=50), spring dispersal (April 1; n=55), and calving (May 23; n=62) periods. Dotted lines indicate the 95% confidence intervals about the means (peak onset dates) and dashed lines indicate the 95% sample confidence intervals.

Table 1. Peak annual onset dates for the winter, spring dispersal, and calving seasons as determined by individual-based recursive partitioning (2004-2007). Also shown are sample sizes (n = number of collared caribou from which onset dates were derived), 95% bootstrap confidence intervals (Lower CI, Upper CI), standard errors about the mean estimates, and overall season length. An estimate of season length for winter 2007 was not possible as no GPS locations were recorded beyond March 2007.

Year	Season	*n*	Lower CI	Peak Onset	Upper CI	S.E. (days)	Length (days)
2005	winter	13	9-Jan	17-Jan	27-Jan	4.5	74.8
2006	winter	21	30-Dec	5-Jan	11-Jan	3.4	81.2
2007	winter	16	19-Dec	28-Dec	6-Jan	4.4	n/a
2004	spring	12	6-Apr	11-Apr	15-Apr	2.3	44.5
2005	spring	22	31-Mar	2-Apr	5-Apr	1.4	50.0
2006	spring	21	24-Mar	28-Mar	2-Apr	2.3	55.1
2004	calving	18	22-May	25-May	29-May	1.7	15.0
2005	calving	25	20-May	23-May	26-May	1.6	20.4
2006	calving	19	18-May	21-May	25-May	1.6	25.8

Results

Average distances travelled per day (pooled for all individuals and years) are shown in Fig. 3a. Corresponding with the onset of late winter, a significant drop in movement rate was noted to take place in early January. A sudden increase in movement rate in early April corresponded with the onset of spring dispersal, followed by a substantial drop in movement rate which indicated the start of calving in late May. Between January 10 and June 30, the minimum daily average distance was 530 m on March 16 while the maximum daily average distance was 5.93 km on April 21. The maximum distance recorded in one day was 54.6 km by caribou 2003014 on May 9.

Average net displacement per day (pooled for all individuals and years) is depicted in Fig. 3b, which reveals a distinct migratory pattern from early April until late May. On average there was little departure from wintering areas until the onset of spring dispersal, at which time animals proceeded to travel consistently further away from their wintering areas, reaching a maximum daily average displacement of 49.3 km from their wintering grounds on June 6. The maximum net displacement recorded for one animal between January 10 and June 15 was 208.8 km by caribou 2003008 on June 09, 2005.

Individual-based models

The distributions of seasonal onset dates determined via individual-based recursive partitioning are shown in Fig. 4. Peak onset of late winter occurred on January 5th (+/- 5.2 days, $n = 50$, $s = 18.64$), spring dispersal on April 1nd (+/- 2.5 days, $n = 55$, $s = 9.73$), and calving on May 23th (+/- 2.0 days, $n = 62$, $s = 7.78$). Distributions exhibited prominent modes in all three cases, and Anderson-Darling tests of residual values ($f(x) = x - \bar{x}$) indicated no significant departure from normality. Sample 95% confidence intervals ranged from Dec. 04 – February 05 for winter, March 13 – April 19 for spring dispersal, and May 10 – June 10 for calving. Peak onset times over three years varied from Dec. 28 (2007) to Jan. 17 (2005) for winter (20 days), from March 28 (2006) to April 02 (2005) for spring (5 days), and from May 21 (2006) to May 25 (2004) for calving (4 days) (Table 1).

Winter was the longest season at $\mu = 78.6$ days, followed by spring dispersal at $\mu = 50.6$ days, and finally calving at $\mu = 20.2$ days. Based on the statistics of unique individuals, the longest period observed for winter behaviour was 130 days, for spring dispersal behaviour 80 days, and for calving behaviour 58 days. Minima and maxima were Nov. 9 and February 24 for winter (107 days), March 8 and April 22 for spring dispersal (45 days), and May 6 and June 13 for calving (38 days).

The onset of late winter (2005 vs. 2007: $F = 9.70$, $P < 0.01$) and spring dispersal (2004 vs. 2006: $F = 15.0$, $P < 0.001$) tended to be progressively earlier from 2004 to 2007. This may have been attributed to higher early snowfall (for winter) and/or higher March temperatures (for spring) in latter years. Latitude had no significant influence on onset dates regardless of season. Lastly, although age and experience can influence the timing of ovulation and therefore calving (Bergerud, 1975;

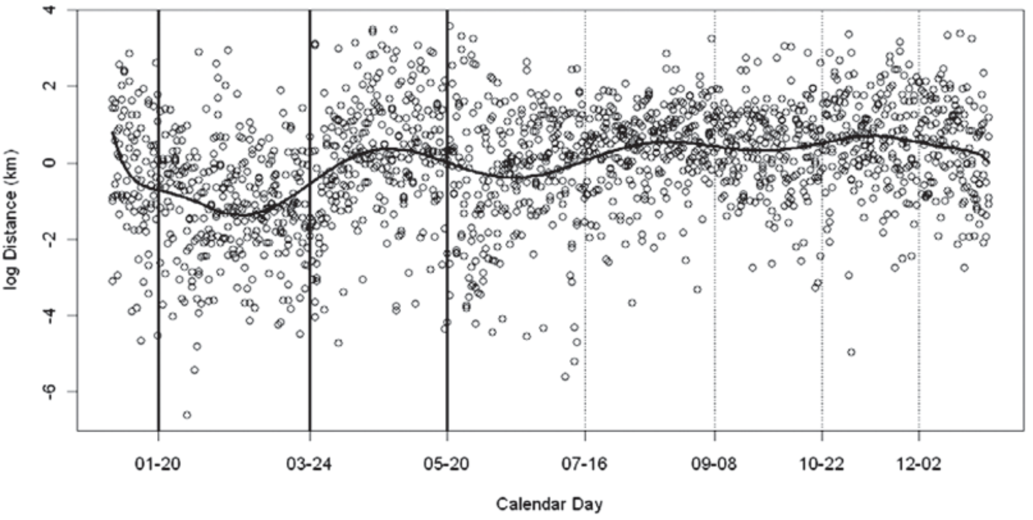

Fig. 5. Distance (in km, log-transformed) travelled per day over time by 26 woodland caribou tracked using GPS telemetry in Northern Quebec. Shown are raw values and the fitted curve of an 11th order polynomial regression model. Inflection points were obtained by solving for x=0 in the second derivative of the fixed effects component of the regression equation. Solid lines indicate the estimated peak onset of the winter (January 10), spring dispersion (March 24), and calving (May 20) periods, while dotted lines indicate latter seasons of potential biological interest (most likely representing summer, fall, rut, and early winter).

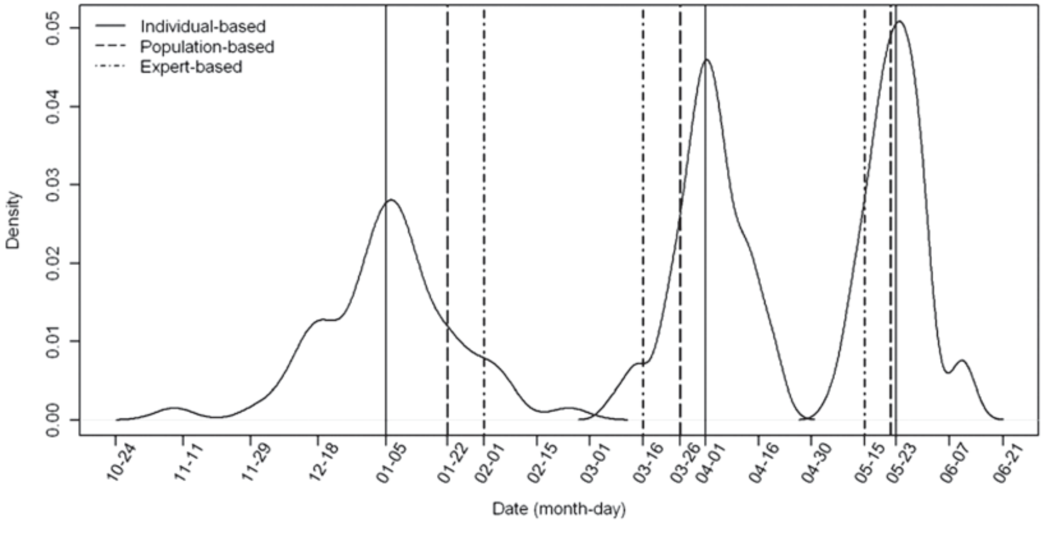

Fig. 6. Comparison of peak onset dates corresponding with (from left to right) the winter, spring dispersal, and calving periods. Dates were obtained using three methods: a) individual-based recursive partitioning (solid lines), b) mixed polynomial regression with pooled data (dashed lines) and c) expert consensus (dot-dashed lines). Conventional estimates for spring and winter were outside the respective one-tailed 90% and 95% sample quantiles of the individually-fitted distributions. Analyses were conducted using movement parameters derived from GPS telemetry locations of 26 female woodland caribou in Northern Quebec.

Flydal & Reimers, 2002; Langvatn *et al.*, 2004), morphometric data available for our population was not complete enough to support or refute this.

Population-based model

Adding progressive polynomial terms to the prospective regression model continued to substantially reduce AIC_c until a twelfth term was added, at which time the net change in AIC_c became positive. Therefore the final population-based model contained eleven polynomial terms and took the following form (jd = Julian day):

$$\hat{Y} = 1.08 - 0.301 + 2.16\times10^{-2}\,(jd)^2 - 8.18\times10^{-4}\,(jd)^3 + 1.71\times10^{-5}\,(jd)^4 - 2.11\times10^{-7}\,(jd)^5 + 1.63\times10^{-9}\,(jd)^6 - 7.97\times10^{-12}\,(jd)^7 + 2.51\times10^{-14}\,(jd)^8 - 4.92\times10^{-17}\,(jd)^9 + 5.44\times10^{-20}\,(jd)^{10} - 2.60\times10^{-23}\,(jd)^{11} + Zibi + \varepsilon i$$

Relative to the fixed intercept, there was considerable variation in the random intercepts for “id” and “year within id” (16.6% and 18.1%, respectively). Solving for $x=0$ in the second derivative of the fixed effects component of the regression equation allowed us to determine the estimated peak onset dates of the three biological seasons of interest for our study population: late winter (January 20), spring dispersal (March 24) and calving (May 20) (Fig. 5).

Comparison of Methods

With respect to quantitative methods (individual- vs. population-based), estimates of winter were 16.6 days apart ($p = 0.20$), with the pooled estimate occurring later (Fig. 6). Estimates of spring dispersal were 7 days apart ($p = 0.21$), with the individual-based estimate occurring later. The least difference occurred among estimates of peak onset for calving, with the pooled estimate preceding the individual-based estimate by only 1.6 days.

Estimates of peak winter onset differed greatly between individual- and expert-based (conventional) approaches, with the conventionally defined period occurring close to a full month (26.6 days) later than it was found to occur by recursive partitioning (Fig. 6). Conventional estimates for the onset of spring dispersal, likewise, preceded the observed mean date by over two weeks (16.9 days). Again the least amount of difference between estimates was observed for peak calving time, with conventional dates preceding individual-based results by just over a week (8.6 days). The conventional estimate for winter was outside the one-tailed 90% sample quantiles of the individually-fitted distribution; the estimate for spring was outside the one-tailed 95% sample quantiles.

Discussion

By delineating seasonal shifts in movement behaviour using individual-based recursive partitioning, we were able to capture both individual and annual variation in the seasonal onset behaviour of woodland caribou. In terms of individual variation, the onset of calving alone spanned up to 38 days in length from the earliest recorded observation (May 6) to the last (June 13). In terms of annual variation, over three years peak onset varied by up to 20 days for winter, although only 4-5 days for spring and calving. These findings, particularly with respect to calving, corroborate with what has been documented elsewhere for woodland caribou (Bergerud, 1975; Rettie & Messier, 1998; Ferguson & Elkie, 2004), barren-ground caribou (Cameron *et al.*, 1993; Post & Klein, 1999), and Eurasian reindeer (Eloranta & Nieminen, 1986; Flydal & Reimers, 2002).

Despite the fact that individually-estimated onset dates were normally distributed with prominent modes for all three seasons, consensus-based estimates of peak onset dates were outside the one-tailed 90% and 95% confidence intervals observed for winter and spring, respectively. This suggests that researchers should use caution when adopting conventionally accepted seasonal periods in biological investigations of seasonal phenomena. As shown by our example, a quantitative approach using pooled data rendered considerably more accurate estimates of peak shifts in seasonal behaviour. In fact, if we had used recursive partitioning on the pooled data instead of polynomial regression, we would have obtained peak estimates roughly identical to the mean values reported from individual-based estimates (Rudolph & Drapeau, unpubl. data).

Seasonal changes in movement rates have been documented for a great number of species (Moen, 1978; Jingfors, 1982; Garner *et al.*, 1990; Covell *et al.*, 1996; Schneider *et al.*, 2000; Brito, 2003). By modeling these changes we can derive inflection points marking the boundaries between statistically distinct periods of biological interest. This is typically achieved through some form of non-linear curve-fitting, and may be applied to individual (individual-based) or pooled (population-based) distributions. Vander Wal & Rogers (2009), for example, approximated the cumulative annual distance travelled by individual moose with a sigmoidal relationship. Movement rates of woodland caribou, however, tend to be fairly irregular over time, and such trends can be difficult to approximate in a single model formula. We built on Ferguson & Elkie’s (2004) use of polynomial regression by adding random intercepts to control for individual and annual variation in movement rates, allowing us to identify up to 8 distinct biological seasons using differential calculus. Dyke (2008) obtained similar results for woodland caribou in central Canada, circumventing distributional assumptions using non-parametric LOESS (locally weighted scatterplot smoothing) curves fitted to individual time-series distributions. Disadvantages of this method include sensitivity to the choice of smoothing factor and inability to derive inflection points mathematically.

Fieberg & Delgiudice (2008) explored several methods for estimating the timing of migration in white-tailed deer using interval-censored data. For the most part, however, these approaches require advanced computing skills and are unlikely to be used by most wildlife managers (Fieberg & Delguidice, 2008). Furthermore, time-to-event models require knowledge of when the event (e.g. migration) has occurred, which (in the case of migration) may not be possible for animals that do not have strictly defined summer and winter ranges.

Despite the prevalence of increasingly complex movement models (e.g. Smouse *et al.*, 2010), we demonstrate a relatively simple quantitative approach to defining biological seasons using iterative analyses of variance (ANOVA) and prior knowledge of species life history. Recursive partitioning works by maximizing the between-groups sums of squares along a temporal gradient; it is non-parametric and may be applied in any circumstance where changes in the movement parameter(s) of a species are known to reflect seasonal shifts in its annual life cycle. It is also fairly robust to missing values (Therneau & Atkinson, 2011), although it is best used with high-fix GPS telemetry data (>= 1 observation/day). We do not recommend it be used without scrutiny, however, for even with smoothed data stochastic variation is likely to result in more inflection points than are biologically justified, at least at the individual level. For this reason we chose only seasons we were able to distinguish via changes in movement rates, closely supervising candidate splits and retaining only those that made sense from a biological point of view (optionally, users may increase the complexity parameter, or the minimum admissible increase in R^2, to reduce the number of candidate splits). In parallel we also modeled changes in net displacement to support our final choice of individual onset dates for the beginning and end of spring dispersal. In a similar manner, Shuter (2011) modeled two separate movement parameters - displacement and linearity - to identify seasonal onset dates for woodland caribou in northwestern Ontario using univariate regression trees.

We recognize that many variables can influence seasonal onset behaviour in terrestrial mammals (Monteith *et al.*, 2011). Accordingly, researchers may wish to consider any number of additional explanatory variables in the model (e.g. temperature, altitude, snow depth, plant phenology, species life-history characteristics). Shuter (2011), for example, included photoperiod along with Julian day as independent variables. In the case where a fixed temporal window is deemed adequate yet individual variation is still of interest, one may consider obtaining population-level estimates (peak onset dates) using a random effects-expectation maximization (RE-EM) tree (Galimberti & Montanari, 2002; Sela & Simonoff, 2010).

Conclusion

Animals such as woodland caribou exhibit marked trends in movement behaviour that reflect seasonal variation in the relative importance of foraging, reproduction, energy conservation, and predator avoidance. For this reason the study of animal space use patterns tends to be inherently seasonal in nature. However, the timing of seasonal events in the life cycle of animals may vary considerably from year to year and/or among individuals. This raises concern as to the prudence of adopting fixed time periods in the analysis of seasonal space use behaviour (e.g. habitat selection), for they may introduce unwanted bias in the form of observations that are not strictly representative of the biological activity under investigation.

Our study provides evidence that dates determined by expert consensus and conventionally used to differentiate seasonal periods may not always be representative of the biological phenomena for which they were intended. We recommend researchers consult the biological signal of their study population using quantitative methods and other first-hand knowledge in order to verify the accuracy of the dates, and consequently the appropriateness of the data, used. Wherever possible, we also recommend varying the temporal window used to extract observations based on individually determined seasonal onset dates (e.g. Apps et al. 2001), for doing so should reduce misclassification and potentially erroneous bias in subsequent analyses of habitat selection.

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Prey specialization and morphological conformation of wolves associated with woodland caribou and moose

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Abstract: Morphological analysis of wolves associated with woodland caribou in late succession boreal coniferous forests north of the commercial cut line and those associated with moose in early succession boreal deciduous forests south of the commercial cut line were studied in Ontario. So-called "moose-wolves" could readily be distinguished from "caribou-wolves" in both genders using a few morphological measurements. Wolves associated with woodland caribou were significantly smaller in most measurements, and increased in size within seven years post-harvest as moose totally replaced caribou in the ecosystem. Whether this change in wolf morphology is related to micro-evolutionary change, the migration of larger "moose-wolves" into the area, or both, remains unclear.

Key words: caribou; logging; moose; morphology; wolf diet; wolves.

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Introduction

Historically, woodland caribou (*Rangifer tarandus caribou*) dominated most of the Boreal Forest Biome throughout Canada (Bergerud, 1974) and few moose (*Alces alces*) existed in the northeast of Ontario prior to the mid-1800s (Krefting, 1974). Woodland caribou originally extended as far south as Manitoulin Island and north to approximately 46° latitude (Cumming and Beange, 1993). However, since the 1880s this subspecies has disappeared in the southern part of the range. The present range distribution is north of 50° latitude (Cumming & Beange, 1987; Cumming & Beange, 1993), which approximates the northern limit of commercial timber harvest between Cochrane and Kenora (Racey *et al.,* 1991). Moose have benefited from early succession forests created by timber harvest (Krefting, 1974) and it has been hypothesized that wolves increase pack sizes (Bergerud, 1974; Messier, 1985; Seip, 1992; Rettie & Messier, 1998) and body mass (Hillis, 1990; Mallory & Hillis, 1995) due to increased prey size. This shift in the predator–prey system is hypothesized to result in the extirpation of local woodland caribou populations due to greater wolf numbers and wolf body mass and the loss of prime habitat (Hillis, 1990; Seip, 1992; Mallory & Hillis, 1995). Bergerud (1990) hypothesized that rareness was an anti-predator strategy of caribou, and Lariviere *et al.* (2000) and Cumming (1975) suggested the clumping strategy of caribou would fail when moose were present in high densities. Evidence indicates that disturbance has a major negative impact on caribou (Schaefer & Pruitt, 1991; Cumming, 1992; Antoniak, 1993; Chubbs *et al.,* 1993; Cumming & Beange, 1993; Antoniak & Cumming, 1996; Hillis *et al.,* 1998; Hillis & Mallory, 2004). Woodland caribou are now listed as vulnerable by COSEWIC because of the historical recession of their range associated primarily with commercial logging (Brown *et al.,* 2003). No declines in caribou have been recorded in undisturbed Ontario populations. The primary goals of this study were: (1) to assess the status of woodland caribou in northwestern Ontario, (2) to understand habitat utilization by this subspecies, and (3) to understand the impact of human-related land use activities on this species and its predators.

Moose are the largest member of the Cervidae and are found only in boreal forest dominated by spruce, fir, and pine, where disturbance is a major factor shaping the vegetative communities (Odum, 1983; Telfer, 1984; Karns, 1998). In late winter, moose are commonly found on south-facing slopes at higher elevations, in association with protective cover; while in summer they are found near water with abundant aquatic plants (Karns, 1998). Moose numbers were few in the area north of Lake Superior until the early twentieth century; due to the predominance of old growth coniferous forest, and have only recently become common in response to logging and other disturbance (Peterson, 1953, 1955; DeVos, 1958; Karns, 1998). Since the middle of the twentieth century, moose populations have shown positive growth across the continent (Bergerud, 1981; Crete, 1987; Thompson & Euler, 1987; Karns, 1998), which is believed to be due to a reduction in predators, reduced deer populations in the north due to the reversion of farmland to forest, larger clearcuts, and increased legal protection (Aldous & Krefting, 1946; Karns *et al*., 1974; Peek *et al*., 1976; Hicks, 1986; Boer, 1992; Alexander, 1993; Bontaites & Guftason, 1993; Morris & Elowe, 1993; Karns, 1998; Peek, 1998).

Resource partitioning facilitates the coexistence of sympatric ungulates and may take the form of spatial or temporal segregation, species-specific preferences for forage or plant parts, and different feeding heights (Stelfox & Taber, 1969; Hudson, 1976; Boer, 1992). Woodland caribou and moose inhabiting the Boreal Forest have limited competition (Davis & Franzmann, 1979; Fuller & Keith, 1981; Boer, 1992), as caribou prefer herbaceous forbs and deciduous foliage in summer and arboreal and ground lichens in the winter, while moose consume woody browse in winter and aquatic succulents, forbs, and deciduous foliage in summer (Dodds, 1960; Darby & Pruitt, 1984; Eastman & Ritcey, 1987; Servheen & Lyon, 1989; Boer, 1992; Proceviat, 2003; Proceviat *et al*., 2003).

Woodland caribou and moose populations may also remain segregated by habitat partitioning and seasonal altitudinal preferences (Boer, 1992). Caribou prefer mature coniferous forest much of the year, open fens during the rut, and frozen lakes and large rivers during the late winter (Bergerud, 1974; Fuller & Keith, 1981; Darby & Pruitt, 1984; Servheen & Lyon, 1989; Boer, 1992; Wilson, 2000; Metsaranta, 2002; Brown *et al.,* 2003; Metsaranta *et al.,* 2003). Moose are associated with aquatic habitats in summer and prefer upland conifer areas with shrub layer in late winter (LeResche *et al*., 1974; Cairns & Telfer, 1980; Boer, 1992; Hillis & Mallory, 2004).

It is hypothesized that the decline in woodland caribou (*Rangifer tarandus caribou*) in Ontario is due in part to predation. Since moose predation exposes wolves to greater risk of injury or death (Weaver *et al.,* 1992; Mallory *et al.,* 1994), natural selection would favor larger wolves in habitats dominated by moose and smaller wolves in habitats dominated by caribou. As wolves select for the most common ungulate in the system (Lamothe & Parker, 1989), if moose dominate, the increased numbers of wolves and selection for larger wolves would subject the smaller, less common caribou to increased predation risk and population decline into a “predator pit” or local extirpation (Mallory *et al*., in press). Presumably, if the smaller prey is more abundant, natural selection would result in smaller-sized wolves (less food) and the larger, less common prey would present a more dangerous prey choice and tend to be avoided by the predator, resulting in sustained or increasing populations of the larger prey species.

Material and methods

Wolf carcasses were obtained from trappers across northwestern Ontario between 1997 and 1998 and wolf scats were collected from moose and caribou ranges. Necropsy procedures for wolf carcasses were followed as outlined by Roffe *et al.* (1996) and measurements were taken as described by Hillis (1990) and Mulders (1997). Wolf skulls were fleshed and dried prior to cleaning by dermestid beetles and the suture between the basiosphenoid and basioccipital bones was checked for ossification to identify adult animals. Only skulls of adults were used in the statistical analysis (Kolenosky & Stanfield, 1975; Skeel & Carbyn, 1977; Mulders, 1997). A total of 45 cranial, mandibular, and dental measurements to the nearest

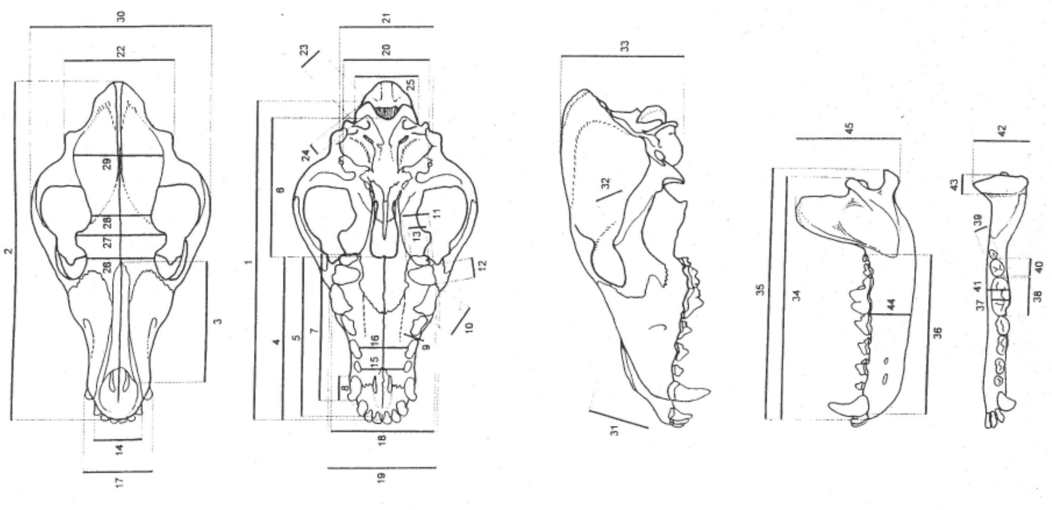

Fig. 1. Cranial, mandibular, and dental parameters (n = 45) taken from adult moose- and caribou-wolves (*Canis lupus*). Corresponding descriptions are listed in Table 1.

0.01 mm were taken using digital calipers (Fig. 1; Appendix 1).

Total body weight with skin removed was measured to the nearest 0.5 kg using a Salter Scale (up to 100 kg) and external body measurements were made to the nearest mm with a fiberglass measuring tape (Fig. 2). A Sartorius Electronic Balance (up to 4 kg) was used to weigh internal organs to the nearest 0.1 g. Differences in morphology between wolves (*Canis lupus*) from caribou range and those from moose ranges were analyzed. Adipose tissue depth measurements were made to the nearest mm with calipers and kidney fat was estimated as described by Harder & Kirkpatrick (1996).

Wolf stomach and scat contents were washed through a 0.21-mm sieve and hairs were selected randomly and rinsed in methyl salicylate. Imprints of each hair were made in clear nail polish for prey species identification (Adorjan & Kolenosky, 1969). Scats were stored in plastic Whirlpak bags and autoclaved to kill endoparasites before handling. Each sample was assigned either a single prey category or—when there were multiple prey items in the stomach or scat—the most abundant item was used (Floyd *et al.*, 1978; Weaver, 1993). Frequencies (%) were calculated within each prey category to allow comparisons among the 3 different habitat types: (1) no disturbance, (2) 0 to 7 years post-harvest, and (3) more than 7 years post-harvest.

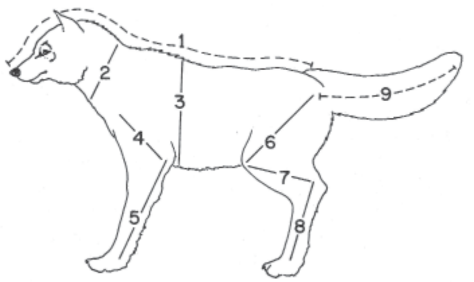

Fig. 2. External morphological measurements taken from wolf (*Canis lupus*) specimens from northwestern Ontario (1—contour length; 2—neck girth; 3—chest girth; 4—humerus length; 5—ulna length; 6—femur length; 7—tibia length; 8—tarsal length; 9—tail length).

Statistical analyses were used to identify differences between items in wolf diets, skull morphology, and body and organ morphology for males and females. All multivariate and univariate statistical analyses were done using a SPSSx program, and Discriminant Analysis was used to identify differences in skull and body measurements that best distinguished the wolves from caribou and moose ranges, while Student's *t*-tests, Mann-Whitney U, and Kruskal-Wallis one-way Analysis of Variances were performed on adipose parameters (Zar, 1974).

Results

Wolf diet

Stomach and scat contents were analyzed from undisturbed areas (stomachs - *n* = 94; scats - *n* = 16) and from recently logged woodland caribou range 0 to 7 years post-harvest (stomachs - *n* = 89; scats - *n* = 12). Only wolf stomach contents (*n* = 110) were analyzed from logged moose ranges greater than 7 years post-harvest. The percentage of caribou in wolf diets declined significantly, from 21% in areas with no disturbance, to 6% in areas where logging had occurred during the previous 0 to 7 years ($c^2(1) = 7.259$; $P<0.01$) and to 0% in areas logged earlier than 7 years (Fig. 3). The percentage of moose in the diet of wolves was 37% in areas of no disturbance and 33% in areas logged approximately 0 to 7 years earlier and 49% on ranges where logging had occurred earlier than 7 years. The presence of white-tailed deer (*Odocoileus virginianus*) in wolf diets also increased significantly from 0% on ranges with no disturbance to 6% on ranges with logging approximately 0 to 7 years earlier and 9% on ranges where logging had occurred more than 7 years earlier ($c^2(2) = 8.400$; $P<0.025$). In contrast, the percentage of beaver (*Castor canadensis*) in wolf diets declined from 26% on ranges with no disturbance to 22% in ranges with logging approximately 0 to 7 years earlier and to 12% on ranges where logging had occurred more than 7 years earlier. Significant changes in prey classified as "Other" were 0% on ranges with no disturbance, 28% on ranges with logging approximately 0 to 7 years earlier, and 14% on ranges where logging had occurred more than 7 years earlier ($c^2(1) = 4.024$; $P<0.05$); prey diversity was highest in ranges 0 to 7 years post-harvest and lowest in ranges with no disturbance (Fig. 3).

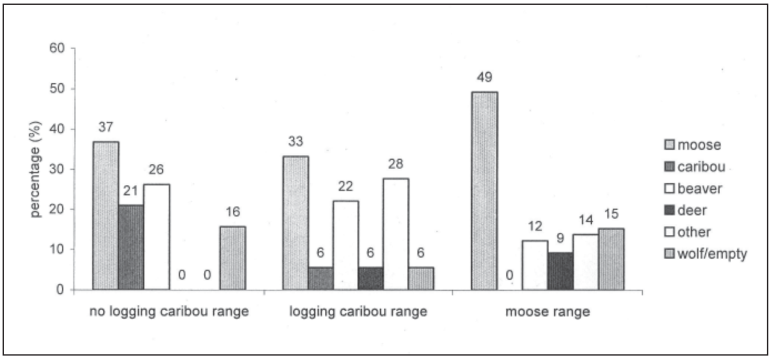

Fig. 3. Percentage of stomach and scat contents of *Canis lupus* in three different habitats (no logging-caribou range; logging-caribou range; logged-moose range) from northwestern Ontario.

Skull morphology

Male wolves

A comparison of the means of adult male wolf skull measurements using a Student's *t*-test and a nonparametric Mann-Whitney U test is presented in Table 1. Canonical Discriminant Analysis was used to find which of 45 skull measurements best discriminate between moose- and caribou-wolves. Sixty-nine (64%) of the 107 wolf skulls were excluded from the Discriminant Analyses, as they were juveniles or damaged. Twenty-three skulls of adult male wolves were used, 7 from areas within the undisturbed range of woodland caribou and 16 from ranges more than 7 years post-harvest, where moose predominated and caribou were absent. Male moose-wolves had significantly ($P<0.05$) larger values on numerous skull measures including: Mandible Width, Length of Premolar ^{4}, Zygomatic Breadth, Cheek T W, and Width Across the 1st Molars.

The maximum Zygomatic Breadth, which is associated with bite force (Wiersma, 2001), differed significantly between adult male moose- and caribou-wolves from the two ranges (F = 8.3; $P=0.009$). Zygomatic Breadth entered the discriminant function first and explained 28% of the variance, and the Occipital Condyle Width entered the function next and accounted for an additional 19% of the variance. Only the first five measurements were allowed to enter the Discriminant Analysis to ensure that multiple measurements that vary similarly did not influence the results. Once the 5 measurements had entered the function, only 23% of the variance in all skull measurements remained to be explained, thus 77% of the variance was accounted for by the measurements listed in Table 2. A Wilks' Lambda value of 0.23 indicated that there was a highly significant difference between the two groups of adult male wolves using the 2 value from Table 2 (2(5) = 27.15; $P<0.001$). The discriminant function effectively assigned 100% of the male wolves that were used to generate the function to the range from which they were collected. When the function was tested on adult male wolves not used to generate the function, it correctly classified 95.7% to their respective ranges.

Female wolves

One-way Analysis of Variance and Canonical Discriminant Analysis were used to find which of 45 skull measurements best discriminated between adult female moose- and caribou-wolves. Measurements were made on 19 skulls: 8 wolves were from the undisturbed woodland caribou range and 11 from the moose-dominated and caribou-absent range, where logging had occurred more than 7 years earlier. Adult female moose-wolves had significantly larger values ($p<0.05$) in Length of Premolar ^{4} and Width Between the 2nd Premolars (Table 3).

A One-way Analysis of Variance indicated that adult female caribou-wolves had greater Palatal Width across the 2nd Premolars (mean = 35.1 mm) than adult female moose-wolves (mean = 33.5 mm, F = 5.9; $P=0.03$). Wilks' Lambda indicated that 26% of the variance between the 2 groups was accounted for by the Palatal Width measurement and the five measurements accounted for 85% of the variance. The Wilks' Lambda value (0.15) for the entire function and its 2 value indicated that the two groups separated well using the function. When the Discriminant Analysis was used to calculate discriminant scores (D) for each skull, the function correctly assigned 100% of the adult female wolves used to generate the function to their respective ranges. When the function was tested on wolves not used to generate the function, it correctly assigned 94.7% of them to their respective ranges, with only one of the 19 wolves being erroneously classified as a caribou-wolf (Table 4).

Body morphology

Male wolves

Table 5 compares the morphological parameters of adult male wolves collected from undisturbed caribou ranges and ranges where logging had occurred more than 7 years earlier and where moose dominated and caribou were absent. Levene's test for equality of variances was used to select the appropriate *t*-test. Two-tailed Student's *t*-test significance was confirmed by non-parametric Mann-Whitney *U* tests and the results of these analyses indicated that adult male moose-wolves were larger than adult male caribou-wolves. Adult male moose-wolves had higher Body Mass (31.6 kg) compared to adult male caribou-wolves (24.7 kg). Male moose-wolves also had greater mean Neck Girth (397.1 mm) than male caribou-wolves (344.3 mm). In addition, adult male moose-wolves had greater Heart, Lung, Liver, and Spleen Weights (Table 5).

Discriminant analysis

Male wolves

Twenty male adult wolves were used for a Discriminant Analysis with 8 body measurements and 5 organ weights (Table 6). One-way Analysis of Variance indicated that adult male caribou-wolves had smaller Neck Girths (mean = 335.00 mm) than moose-wolves (mean = 395.70 mm, n = 20, F = 25.700; $P<0.001$). Neck Girth entered the discriminant function on the first step and accounted for 59% of the variability between wolves from the two areas. Neck Girth and Kidney Weight were the only two variables to enter the function and accounted for 65% of the total variance. Wilks' Lambda value for the function was 0.35 and its 2 value in Table 6 indicated that there was a significant difference ($P<0.001$) between the two groups of wolves using the body measurements listed. When scores were calculated for each male wolf used to generate the discriminant function, it correctly assigned 83% of the male wolves to their respective areas. When applied to wolves not used to generate the function, 88% of them were correctly classified (Table 6).

Female wolves

Comparisons of the mean organ masses and external body measurements of adult female wolves from undisturbed woodland caribou ranges and ranges where logging had occurred more than 7 years earlier were compared (Table 7). Levene's test for equality of variances was used to select the appropriate *t*-test. Two-tailed Student's *t*-test significance was confirmed by non-parametric Mann-Whitney *U* tests. The results indicated that no significant differences existed between the female moose-wolves and female caribou-wolves ($P>0.05$).

Discriminant analysis—Female wolves

Seventeen adult female wolves were used for a Discriminant Analysis using 8 body measurements and 5 organ weights (Table 8). One-way Analysis of Variance indicated no differences in the means of body measurements between adult female moose-wolves and adult female caribou-wolves. The Heart Weight (F = 1.900; P = 0.185) entered the discriminant function on the first step and accounted for 11% of the variability between adult female wolves from the two ranges. Kidney Weight and Neck Girth were the only other variables that entered the function and accounted for 50% of the total variance. Wilks' Lambda value for the function was 0.50 and its 2 value in Table 8 indicated that there was a significant difference (P = 0.025) between the two groups of adult female wolves using the body measurements listed. The function correctly classified 86% of the wolves used to generate the function. When applied to a sample of 22 wolves not used to create the function, it correctly classified 73% (Table 8).

Table 1. Skull morphology of adult male wolves (*Canis lupus*) collected from undisturbed woodland caribou ranges and disturbed moose ranges, where logging had occurred more than 7 years earlier. Levene's test for equality of variances was used to select the appropriate *t*-test (equal variances assumed or not). Two-tailed Student's *t*-test significance was confirmed by non-parametric Mann-Whitney U tests (C = caribou range, M = moose range, Wt = weight w[g] (unless otherwise indicated), Lth = length [mm], $P< 0.05$*, $P<0.01$**, $P<0.001$***).

Variable	Rangev	N	Mean	S.E.M.	*t*-value	Signif.	Mann-W U
Condy L	C	7	215.12	14.96	-0.786	0.461	0.789
	M	16	226.99	2.04			
I^1-Sag C	C	7	256.19	4.25	-0.642	0.528	0.789
	M	16	259.06	2.32			
Nasal L	C	7	95.02	3.49	-0.702	0.49	0.593
	M	16	97.10	1.27			
I^1-Palat	C	7	125.53	2.29	-0.669	0.511	0.738
	M	16	126.94	0.99			
I^2-Palat	C	7	123.64	2.33	-0.778	0.459	0.548
	M	16	125.59	0.92			
Pos Pal L	C	7	99.59	1.09	1.190	0.247	0.095
	M	16	97.66	0.96			
C^1-M^2	C	7	106.23	1.33	-0.496	0.625	0.738
	M	16	107.00	0.85			
W of C^1	C	7	14.16	0.38	-2.033	0.055	0.066
	M	16	15.06	0.24			
W of P^4	C	7	13.93	0.22	-0.274	0.786	0.815
	M	16	14.02	0.20			
L of P^4	C	7	25.78	0.45	-1.426	0.169	0.109
	M	16	26.51	0.28			
W of M^1	C	7	20.43	0.24	-0.982	0.338	0.688
	M	16	20.80	0.29			
L of M^1	C	7	16.71	0.31	-0.490	0.629	0.442
	M	16	16.88	0.18			
W of M^2	C	7	14.01	0.26	1.077	0.294	0.483
	M	16	13.62	0.21			
I^3 to I^3	C	7	35.42	0.86	0.016	0.987	0.738
	M	16	35.41	0.50			
P^1 to P^1	C	7	32.04	0.64	-1.313	0.203	0.350
	M	16	33.11	0.46			
P^2 to P^2	C	7	34.95	0.72	-1.709	0.102	0.095
	M	16	36.51	0.51			
C^1 to C^1	C	7	48.83	1.10	-2.015	0.057	0.061
	M	16	50.94	0.50			
M^1 to M^1	C	7	77.73	0.90	-2.118	0.046*	0.027*
	M	16	80.29	0.69			
CheekTW	C	7	79.67	1.09	-2.491	0.021*	0.033*
	M	16	82.82	0.69			
Pos ForW	C	7	72.92	3.17	-1.955	0.064	0.181
	M	16	77.41	0.70			
Aud BulW	C	7	17.75	0.82	-0.764	0.453	0.738
	M	16	18.45	0.49			
Occ CreW	C	7	80.38	1.53	-1.555	0.135	0.256
	M	16	82.52	0.63			
CondyleW	C	7	12.41	0.35	0.577	0.570	0.229
	M	16	12.15	0.25			
CondyleL	C	7	26.83	0.59	1.709	0.102	0.102
	M	16	25.83	0.29			

Variable	Rangev	N	Mean	S.E.M.	*t*-value	Signif.	Mann-W U
Occ ConW	C	7	50.87	0.78	1.542	0.138	0.061
	M	16	49.37	0.54			
InterOrW	C	7	44.34	1.16	-1.255	0.223	0.256
	M	16	46.21	0.84			
PostorbW	C	7	60.54	2.13	-1.618	0.120	0.161
	M	16	64.78	1.46			
TemFosW	C	7	41.38	0.77	-0.303	0.765	0.688
	M	16	41.74	0.70			
PariTempW	C	7	66.66	0.69	-1.002	0.328	0.462
	M	16	67.55	0.50			
ZygomB	C	7	135.59	2.94	-2.888	0.009**	0.013*
	M	16	143.56	1.32			
M^1 to Orb	C	7	41.18	1.39	-0.393	0.698	0.640
	M	16	41.70	0.62			
Jugal H	C	7	18.93	0.39	-1.793	0.090	0.333
	M	16	19.95	0.40			
SagC-AudB	C	7	86.52	2.13	-0.516	0.611	0.841
	M	16	87.51	0.88			
Sym-AngPr	C	7	190.12	3.40	-0.177	0.861	0.947
	M	16	190.67	1.43			
Sym-Condy	C	7	186.34	3.22	-0.318	0.754	0.841
	M	16	187.31	1.46			
C^1 - M^3	C	7	119.19	1.24	-0.613	0.547	0.548
	M	16	120.09	0.80			
W of P^4	C	7	11.36	0.16	-1.107	0.281	0.256
	M	16	11.65	0.15			
L of P^4	C	7	28.95	0.38	-2.159	0.043*	0.038*
	M	16	30.24	0.36			
W of M^1	C	7	9.22	0.18	0.012	0.990	0.789
	M	16	9.21	0.15			
L of M^1	C	7	12.17	0.29	-0.165	0.871	0.789
	M	16	12.22	0.13			
Mandib W	C	7	14.00	0.22	-2.719	0.013*	0.019*
	M	16	14.99	0.22			
Art ConW	C	7	11.61	0.93	-1.164	0.284	0.570
	M	16	12.73	0.23			
Art Con L	C	7	32.59	0.87	-1.160	0.259	0.789
	M	16	33.53	0.39			
H of Ramus	C	7	30.69	0.68	-0.563	0.580	0.867
	M	16	31.21	0.53			
AngP-CorP	C	7	76.44	2.26	-0.540	0.595	0.688
	M	16	77.63	1.09			

Table 2. Canonical Discriminant Analysis of skull measurements of adult male moose- and caribou-wolves (n = 23).

Variable	Wilk's Lambda	Change in Rao's V	Std. Canonical Discrim. Fun. Coef
Zygom B	0.72	8.3	1.66
Occ Con W	0.53	10.2	-0.51
SagC-AudB	0.40	12.3	1.48
M1 to Orb	0.29	21.0	-1.10
I^3 to I^3	0.23	18.2	-0.77

Canonical Correlation Coefficient = 0.88 2 value (5) = 27.15; P<0.001

Function D = ((-0.37*v 14)-(0.24*v 25)+(0.27*v 30)-(0.38*v 31)+(1.12*v 38))-31.46

Table 3. Morphological measurements of adult female wolves (*Canis lupus*) collected from undisturbed woodland caribou ranges and disturbed moose ranges, where logging had occurred more than 7 years earlier. Levene's test for equality of variances was used to select the appropriate *t*-test (equal variances assumed or not). Two-tailed Student's *t*-test significance was confirmed by non-parametric Mann-Whitney U tests. (C = caribou range, M = moose range, Wt = weight [g], Lth = length [mm]), $P < 0.05$*, $P<0.01$**, $P<0.001$***).

Variable	Range	N	Mean	S.E.M.	*t*-value	Signif.	Mann-W U
Condy L	C	8	213.35	2.70	2.211	0.041	0.137
	M	11	222.97	3.51			
I^1-Sag C	C	8	240.70	3.10	0.792	0.439	0.509
	M	11	244.14	2.75			
Nasal L	C	8	88.11	1.73	0.573	0.574	0.509
	M	11	89.49	1.50			
I^1-Palat	C	8	119.48	1.72	0.615	0.546	0.509
	M	11	121.17	2.17			
I^2-Palat	C	8	118.29	1.69	0.475	0.641	0.680
	M	11	119.56	2.11			
Pos Pal L	C	8	92.56	1.36	0.237	0.815	0.836
	M	11	93.04	1.48			
C^1-M^2	C	8	101.02	1.23	0.607	0.552	0.509
	M	11	102.20	1.51			
W of C^1	C	8	13.37	0.21	-0.451	0.657	0.869
	M	11	13.21	0.31			
W of P^4	C	8	13.20	0.37	-1.411	0.176	0.186
	M	11	13.83	0.27			
L of P^4	C	8	24.47	0.39	-2.129	0.057	0.048*
	M	11	25.40	0.20			
W of M^1	C	8	19.55	0.50	-0.544	0.594	0.137
	M	11	19.84	0.28			
L of M^1	C	8	16.11	0.14	0.009	0.993	0.679
	M	11	16.11	0.21			
W of M^2	C	8	13.64	0.22	1.071	0.299	0.680
	M	11	14.31	0.67			
I^3 of I^3	C	8	33.84	0.60	-0.343	0.736	1.000
	M	11	34.05	0.29			
P^1 to P^1	C	8	30.66	0.58	1.178	0.256	0.091
	M	11	31.58	0.32			
P^2 to P^2	C	8	33.49	0.45	2.433	0.026*	0.026*
	M	11	35.10	0.47			
C^1 to C^1	C	8	46.27	0.56	0.769	0.453	0.109
	M	11	46.87	0.42			
M^1 to M^x	C	8	76.03	0.96	0.914	0.373	0.409
	M	11	77.20	0.71			
Cheek TW	C	8	77.29	0.99	0.919	0.371	0.509
	M	11	78.42	0.74			
Pos For W	C	8	70.64	2.01	-1.372	0.188	0.248
	M	11	73.69	1.21			
Aud BulW	C	8	16.71	0.46	0.283	0.780	0.804
	M	11	16.93	0.66			
Occ CreW	C	8	78.69	1.32	0.091	0.928	0.869
	M	11	78.86	1.21			
CondyleW	C	8	11.07	0.24	1.298	0.212	0.283
	M	11	11.58	0.32			
Condyle L	C	8	25.02	0.35	1.236	0.233	0.364
	M	11	25.69	0.41			

Variable	Range	N	Mean	S.E.M.	*t*-value	Signif.	Mann-W U
Occ Con W	C	8	47.60	0.72	0.816	0.426	0.322
	M	11	48.46	0.73			
InterOr W	C	8	42.80	0.81	0.098	0.923	0.741
	M	11	42.91	0.71			
Postorb W	C	8	60.05	1.76	0.066	0.948	1.000
	M	11	60.21	1.15			
TemFosW	C	8	39.53	0.78	-0.965	0.348	0.364
	M	11	40.51	0.65			
Pari-TempW	C	8	65.35	0.84	-0.677	0.507	0.409
	M	11	66.14	0.78			
Zygom B	C	8	132.17	2.01	1.259	0.225	0.248
	M	11	135.56	1.50			
M^1 to Orb	C	8	38.16	0.41	0.649	0.525	0.509
	M	11	38.71	0.83			
Jugal H	C	8	18.00	0.46	-0.520	0.610	0.650
	M	11	18.30	0.37			
SagC-AudB	C	8	83.22	1.34	-0.024	0.981	0.869
	M	11	83.27	1.15			
SymAngPr	C	8	177.35	2.22	1.721	0.103	0.083
	M	11	182.79	2.08			
Sym-Condy	C	8	174.89	2.44	1.666	0.114	0.160
	M	11	180.27	1.73			
C^1-M^3	C	8	113.74	1.33	0.398	0.696	0.741
	M	11	114.50	1.28			
W of P^4	C	8	10.79	0.12	-1.369	0.189	0.090
	M	11	11.07	0.15			
L of P^4	C	8	28.22	0.37	-0.307	0.762	0.509
	M	11	28.39	0.39			
W of M^1	C	8	8.67	0.17	-1.061	0.304	0.409
	M	11	8.88	0.12			
L of M^1	C	8	11.82	0.22	-0.071	0.944	0.934
	M	11	11.84	0.16			
MandibW	C	8	13.72	0.28	0.579	0.570	0.321
	M	11	13.95	0.24			
Art ConW	C	8	10.75	0.58	-1.063	0.303	0.741
	M	11	11.40	0.32			
Art Con L	C	8	31.14	0.53	-0.167	0.870	0.934
	M	11	31.28	0.61			
H of Ramus	C	8	28.03	0.59	1.909	0.073	0.021
	M	11	29.44	0.27			
AngPCorP	C	8	72.16	0.80	0.573	0.574	0.741
	M	11	72.90	1.06			

Table 4. Canonical Discriminant Analysis of skull measures of adult female moose- and caribou-wolves (*n* = 19).

Variable	Wilk's Lambda	Change in Rao's V	Std. Canonical Discrim. Fun. Coef
P^2 to P^2	0.74	5.9	-1.87
L of P^4	0.49	11.8	1.77
Pos For W	0.34	15.0	0.90
Art Con L	0.27	13.7	1.24
L of P^4	0.15	47.7	-1.12

Canonical Correlation Coefficient = 0.92 2 value (5) = 27.22; $P<0.001$

Function D = ((2.03*v10)-(1.31*v 16)+(0.19*v 20)-(0.94*v 38)+(0.68*v 43))-13.97

Table 5. Morphological parameters of adult male wolves (*Canis lupus*) collected from undisturbed woodland caribou ranges and ranges where logging had occurred more than 7 years earlier where moose dominated and caribou were absent. Levene's test for equality of variances was used to select the appropriate *t*-test (equal variances assumed or not). Two-tailed Student's *t*-test significance was confirmed by non-parametric Mann-Whitney U tests (C = caribou range; M = moose range; Wt = weight [g] (unless otherwise indicated); Lth = length [mm]), $P < 0.05$*, $P<0.01$**, $P<0.001$***).

Variable	Range	N	Mean	S.E.M.	*t*-value	Significance	MannWU
Body Wt (kg)	C	7	24.7	2.5	-3.162	0.005**	0.014*
	M	17	31.6	1.0			
Contour Lth	C	7	123.1	2.8	-1.108	0.280	0.191
	M	17	130.5	4.1			
Tail Lth	C	6	410.0	17.7	-2.045	0.055	0.079
	M	15	448.9	9.8			
Neck Girth	C	7	344.3	14.1	-4.375	0.000***	0.003**
	M	17	397.1	5.3			
Chest Girth	C	7	590.7	29.6	-2.163	0.007**	0.079
	M	17	657.1	8.2			
Humerus Lth	C	7	215.7	6.2	-1.669	0.109	0.114
	M	17	225.3	2.7			
Ulna Lth	C	6	248.3	14.6	-0.757	0.317	0.941
	M	16	259.9	4.4			
Front Paw Lth	C	2	103.0	18.0	-0.281	0.753	1.000
	M	3	108.3	6.0			
Front Paw Wth	C	2	76.5	11.5	0.552	0.529	1.000
	M	3	70.0	2.5			
Femur Lth	C	7	249.3	5.6	-0.278	0.784	0.723
	M	17	251.2	3.7			
Tibia Lth	C	7	239.3	6.9	-0.518	0.610	0.796
	M	17	242.4	2.6			
Tarsal Lth	C	5	169.0	5.6	-1.376	0.188	0.286
	M	13	175.4	2.0			
Hind Paw Lth	C	2	92.5	17.5	-0.234	0.781	1.000
	M	3	96.7	3.3			
Hind Paw Wth	C	2	67.5	4.5	1.496	0.232	0.248
	M	3	61.3	1.9			
Heart Wt	C	7	203.5	70.5	-3.159	0.005**	0.014*
	M	17	424.5	34.6			
Lung Wt	C	7	503.0	42.1	-2.311	0.031*	0.033*
	M	17	667.1	41.8			
Liver Wt	C	7	632.5	67.2	-2.074	0.050*	0.028*
	M	17	862.2	64.9			
Kidney Wt	C	7	189.0	20.4	-1.451	0.161	0.070
	M	17	230.0	16.0			
Spleen Wt	C	7	45.1	7.7	-2.788	0.011*	0.027*
	M	16	68.7	4.5			

Table 6. Canonical Discriminant Analysis of body measures of adult male moose- and caribou-wolves.

Variable	Wilk's Lambda	Change in Rao's V	Std. Canonical Discrim. Fun. Coef
Neck Girth	0.41	25.7	0.76
Kidney Weight	0.35	8.2	0.50

Canonical Correlation Coefficient = 0.81 2 value (2) = 18.0 $P<0.001$
Function D = ((0.031*neck) + (0.015*kid)-14.95

Table 7. Morphological measurements of adult female wolves (*Canis lupus*) collected from undisturbed woodland caribou ranges and moose ranges. Levene's test for equality of variances was used to select the appropriate *t*-test (equal variances assumed or not). Two-tailed Student's *t*-test significance was confirmed by non-parametric Mann-Whitney U tests (C = caribou range; M = moose range; Wt = weight [g]; Lth = length [mm]), $P< 0.05$*, $P<0.01$**, $P<0.001$***).

Variable	Range	N	Mean	S.E.M.	*t*-value	Significance	MannWU
Body Wt (kg)	C	8	24.7	2.2	1.007	0.326	0.151
	M	17	22.7	0.9			
Condylo-basal Lth (cm)	C	8	118.9	3.6	0.027	0.979	0.632
	M	14	118.8	2.0			
Tail Lth	C	5	406.0	29.8	-0.094	0.926	0.402
	M	13	408.2	8.9			
Neck Girth	C	8	328.1	11.1	-0.883	0.388	0.471
	M	14	340.1	8.0			
Chest Girth	C	8	599.4	26.4	1.265	0.221	0.132
	M	14	568.8	10.6			
Humerus Lth	C	8	213.1	7.1	1.289	0.212	0.086
	M	14	204.7	2.9			
Ulna Lth	C	6	241.7	13.0	0.407	0.689	0.347
	M	12	236.7	5.9			
Femur Lth	C	8	233.1	6.3	-0.358	0.724	0.629
	M	14	235.1	2.4			
Tibia Lth	C	8	224.5	7.5	0.011	0.991	0.389
	M	14	224.4	2.3			
Tarsal Lth	C	6	164.2	4.9	-0.686	0.503	0.642
	M	11	167.2	1.9			
Heart Wt	C	8	427.6	65.3	1.961	0.027*	0.101
	M	14	292.4	21.9			
Lung Wt	C	8	643.2	63.6	1.454	0.162	0.152
	M	14	530.3	46.2			
Liver Wt	C	8	654.1	70.5	0.262	0.796	0.785
	M	14	633.2	44.9			
Kidney Wt	C	8	168.0	13.7	0.107	0.916	1.000
	M	14	166.2	10.4			
Spleen Wt	C	7	55.3	11.7	0.355	0.659	0.765
	M	14	50.9	3.8			

Table 8. Canonical Discriminant Analysis of body measures of adult female moose- and caribou-wolves (n = 17).

Variable	Wilk's Lambda	Change in Rao's V	Std. Canonical Discrim. Fun. Coef
HeartWeight	0.89	1.93	-1.85
KidneyWeight	0.58	9.02	1.47
Neck Girth	0.50	4.05	0.53

Canonical Correlation Coefficient = 0.71 2 value (3) = 9.4; P = 0.025

Function D = ((0.017*neck)-(0.018*heart)+(0.039*kid)-6.51

Table 9. Condition indices of adult male wolves (*Canis lupus*) collected from undisturbed woodland caribou ranges (caribou range) and disturbed moose ranges. Levene's test for equality of variances was used to select the appropriate t-test (equal variances assumed or not). Two-tailed Student's t-test significance was confirmed by non-parametric Mann-Whitney U tests (C = caribou range; M = moose range, P< 0.05*, P<0.01**, P<0.001***).

Variable	Range	N	Mean	S.E.M.	t-value	Significance	MannWU
Sterum Fat (mm)	C	7	7.0	2.8	-0.824	0.419	0.373
	M	17	12.3	3.9			
Rump Fat (mm)	C	7	5.1	2.0	-0.424	0.676	0.617
	M	15	6.2	1.4			
Back Fat (mm)	C	7	3.9	1.9	-1.036	0.312	0.126
	M	17	8.7	2.9			
Inguinal Fat (mm)	C	7	21.9	6.1	-0.777	0.446	0.547
	M	16	28.9	5.3			
Mesentary Fat (index)	C	7	2.1	0.5	-0.806	0.429	0.505
	M	17	2.5	0.2			
Total External Fat (index)	C	7	2.1	0.6	0.045	0.965	0.870
	M	17	2.1	0.3			
Total Internal Fat (index)	C	7	2.1	0.6	-0.702	0.490	0.534
	M	17	2.5	0.3			
Kidney Fat Index	C	7	41.7	13.7	-0.440	0.665	0.462
	M	16	47.9	7.1			

Condition indices

The condition of moose- and caribou-wolves determined by adipose measurements is presented in Tables 9 and 10. Levene's test for equality of variances was used to select the appropriate t-test and two-tailed Student's t-test significance was confirmed by non-parametric Mann-Whitney U tests. No significant differences were found in adipose tissue of moose- and caribou-wolves; however, adipose indices were greater in moose-wolves for all variables measured.

Male wolves

A comparison of condition indices of adult male wolves collected from undisturbed woodland caribou ranges and disturbed moose-dominated ranges with no caribou was undertaken (Table 9).

Female wolves

A comparison of condition indices of adult female wolves collected from undisturbed woodland caribou ranges and disturbed moose ranges with no caribou was undertaken and no significant differences were found (Table 10).

Wolf injuries

Old skeletal injuries distinguished by calcification (Phillips, 1984) were evident in 4 of the 106 wolves. Three of the 4 injured wolves were males from moose range. Male injures included a crushed anterior end of the nasal bones, a shattered humerus and scapula, a cracked and deformed premaxilla, and a cracked back of the skull where the occipital and sagittal crests meet. The single adult female caribou-wolf had a cracked sagittal crest.

Table 10. Condition indices of adult female wolves (*Canis lupus*) collected from undisturbed woodland caribou ranges and disturbed moose ranges. Levene's test for equality of variances was used to select the appropriate *t*-test (equal variances assumed or not). Two-tailed Student's *t*-test significance was confirmed by non-parametric Mann-Whitney U tests (C = caribou range; M = moose range, $P< 0.05$*, $P<0.01$**, $P<0.001$***).

Variable	Range	N	Mean	S.E.M.	*t*-value	Significance	MannWU
Sterum Fat (mm)	C	8	7.9	2.0	0.756	0.459	0.585
	M	13	6.1	1.4			
Rump Fat (mm)	C	8	6.4	2.3	0.509	0.616	0.654
	M	14	5.0	1.6			
Back Fat (mm)	C	8	7.3	2.4	0.840	0.411	0.706
	M	14	5.4	1.0			
Inguinal Fat (mm)	C	8	26.6	5.5	1.580	0.077	0.108
	M	14	17.4	2.2			
Mesentary Fat (index)	C	8	2.5	0.4	0.138	0.892	1.000
	M	14	2.4	0.3			
Total External Fat (index)	C	8	1.9	0.5	-0.363	0.720	0.713
	M	14	2.1	0.3			
Total Internal Fat (index)	C	8	2.5	0.4	0.740	0.468	0.570
	M	14	2.1	0.3			
Kidney Fat KFI (index)	C	8	62.3	14.5	0.887	0.385	0.339
	M	14	47.8	9.2			

Discussion

Wolf diet

Wolf diet changed from essentially a 3 prey system (moose, caribou, beaver) in undisturbed boreal forest to a 9+ prey system in ranges 0 to 7 years post-harvest and finally to a moose-specialized system in ranges more than 7 years post-harvest. However, as moose were available within 10 to 60 km from the core caribou wintering area in this study, their presence in the stomachs and scats of wolves in the "no disturbance" area was expected. Lariviere *et al.* (2000) found the highest wolf densities in areas where wolves had access to white-tailed deer and moose and hypothesized that multiple-prey–based ecosystems sustained higher densities of wolves than systems with single prey bases. Empty stomachs were least frequent (6%) in logged habitats 0–7 years post-harvest compared to the other habitats (15%–16%). Fewer empty stomachs suggest an improvement in the availability of prey for wolves in areas with recent disturbance. McKenney *et al.* (1998) found that moose density increased in the province of Ontario from 0.116 per sq. km in 1975–1980 to 0.145, 0.179, and 0.209 per sq. km for the years 1980–1985, 1985–1990, and 1990–1995, respectively. These increases were not uniform and occurred in spite of moose declines in late successional areas, such as Wabakimi Provincial Park and the area north of Lac Seul that lacked substantial timber harvest. Moose are the primary prey of wolves throughout the southern half of Quebec, with a direct exponential relationship between wolf and moose densities, particularly when moose exceeded 0.3 animals/km^2 (Lariviere *et al.,* 2000). Below 0.3 moose/km^2, wolf density remained relatively constant at slightly less than 1 animal/km^2. Analysis of moose densities in Ontario between 1975 and 1995 (McKenney *et al.,* 1998) indicated that initial scattered patches of higher moose density had expanded to cover a vast area across northern Ontario. The boundary separating areas of moose density above and below the provincial average of 0.209/km^2 closely approximates the southern limit of caribou distribution and the northern limit of timber harvest. Caribou continue to exist along the northern limit of timber harvest where moose densities are below 0.209. Zones of lower than average moose density south of the caribou line are separated from caribou ranges by bands of high moose density. Using the regression line of Lariviere *et al.* (2000), the band of high moose density would represent an ecological barrier of elevated wolf density through which caribou would be unable to re-colonize their former range.

A more varied prey base implies that wolves benefit from a more constant food supply (Cumming, 1975). Prey items such as snowshoe hare, small mammals, fish, birds, and vegetation increased from 0 in undisturbed ranges to 28% in areas 0 to 7 years post-harvest to 14% in ranges more than 7 years post-harvest. Increases in diversity during the transitional stage (0 to 7 years post-harvest) can be explained by the presence of species associated with both early and late successional habitat.

Forbes and Theberge (1996) found that beaver acted as a buffer prey species when ungulate densities were low. They noted that the inspection of beaver houses was a common activity among Algonquin Provincial Park wolves. In this study, winter observations of wolf tracks in a caribou wintering area indicated that wolves checked a previously opened beaver house. Tracks indicated that wolves had watched the opened house, suggesting that beaver might continue to use a house previously opened by wolves. Beaver were found in 26% of the scat/stomach samples from undisturbed ranges and in 12% of the samples from ranges more than 7 years post-harvest.

While moose were available in remote undisturbed ranges, their densities were low. Dale *et al.* (1995) found that caribou densities below 0.2/km^2 were associated with wolves switching to preying on moose. Messier (1985) found that wolves changed territory boundaries, increased extraterritorial excursions to white-tailed deer areas, and became more susceptible to mortality when moose density was below 0.2/km^2. In this study—during 8 days of observations including 228 km of transects by snowmobile, snowshoe, and aircraft in the caribou wintering area—the only moose sign observed were tracks and pellet groups found in poplar stands >10 km south of the core caribou wintering area. The absence of moose was also noted while making daily observations of caribou totaling 110 individuals. These observations suggest that, historically, woodland caribou ranges had few to no moose present and that wolf density was low (Bergerud, 1990), as the migratory and clumping behaviour of woodland caribou would leave vast tracts of land seasonally devoid of ungulate prey (Cumming, 1975).

The diet analysis indicated that as sampling moved to areas with increased disturbance, moose increased in importance in the diet, wolves had fewer empty stomachs, and prey diversity increased. It was also concluded that increases in moose density associated with disturbance resulted in the increased use of moose by wolves (Messier, 1995). In addition, it was concluded that increased disturbance subjected woodland caribou to increased predation by wolves, contributing to their extirpation from much of their former range. As timber harvest moved northward, there has been a general increase in moose density (Schwartz & Franzmann, 1991; McKenney *et al.,* 1998) coupled with a decline in woodland caribou (Bergerud, 1974; Darby *et al*., 1989; Mallory & Hillis, 1996; McKenney *et al.,* 1998). The decline in caribou and the increase in moose (McKenney *et al.,* 1998) as one moves south was also reflected in the diet of wolves (Fig. 3). Brousseau (1978), using pellet counts, documented a sharp decline in woodland caribou from 0.86/km^2 to 0.00/km^2 within 5 years following the commencement of timber harvest in the Cliff Lake area, northwestern Ontario. Aerial surveys also indicated a 75% decline in the number of caribou using the area during the 11 years of study. Similar to Brousseau (1978) and Kohira & Rexstad (1997), the wolf diet in this study supported the hypothesis that commercial timber harvest changed the predator–prey relationship.

Skull morphology

Adult male moose-wolves had significantly larger values than adult male caribou-wolves in a number of skull measures including: Mandible Width, Length of Premolar ^{4}, Zygomatic Breadth, Cheek T W, and Width across the 1st Molars. The Canonical Discriminant Analysis correctly classified 95.7% of male wolves to their respective ranges using these 5 skull measures. Adult female moose-wolves had larger values than adult female caribou-wolves in two skull measures: Length of Premolar ^{4} and Width between the 2nd Premolars. The Canonical Discriminant Analysis correctly assigned 94.7% of the adult female wolves to their respective ranges with only one of 19 being erroneously classified. The fact that male wolves were more different than female wolves is significant. Similar results were reported by Hillis (1990) for arctic wolves along the west coast of Hudson Bay, Nunavut. In addition, the fact that adult male moose-wolves had significantly larger skull parameter values that are associated with prey capture, supports the conclusion that these differences are directly related to capture of larger, more dangerous prey. Increased width across the Zygomatic Breadth without a correlated increase in the width of the brain case provides space for larger masseter muscles. Thomason (1991) and Wiersma (2001) demonstrated that bite force increased with greater Zygomatic Breadth and Mandible Width. Larger masseters would increase the bite force and should be selected for in predators preying on larger and more dangerous prey (Mallory *et al.,* 1994). The high classification success of the discriminant functions indicated that there are significant morphological differences in male skull parameters between moose- and caribou-wolves. Mallory *et al.* (1994) and Hillis & Mallory (1996) hypothesized that during hunting, adult male wolves usually make first contact with large ungulate prey and are most prominent in the capture and killing of risky prey. This behavior would strongly influence the natural selection for male wolf body size and skull morphology in relation to prey specialization, gender, and sexual dimorphism (Mallory & Hillis, 1995; Hillis & Mallory, 1996) and also influence differences between related species, such as the coyote (*C. latrans*) (Mallory & Edwards, 1996).

Body morphology and condition indices

As diet changed from caribou to moose, the body size of male wolves increased significantly. Male moose-wolves had significantly greater mean neck girth (397.1 mm) than caribou-wolves (344.3 mm) and significantly larger hearts, lungs, livers, and spleen masses. In addition, male moose-wolves had significantly greater body mass (31.6 kg) than male caribou-wolves (24.7 kg), while adult female wolves had few significant differences in body or organ weights. Schmitz & Kolenosky (1985) and Schmitz and Lavigne (1987) found that over a period of 25 years (1959–1984) there was an increase in mean body weight and length of coyotes at the same time as there was a decrease in the mean body length of wolves in south-eastern Ontario. Prior to European settlement, wolves in southeastern Ontario were typically predators of large ungulates like moose (Kolenosky & Stanfield, 1975) and Schmitz & Lavigne (1987) concluded that changes in wolves were correlated with an increase in the use of smaller, more abundant white-tailed deer as primary prey. Increases in body size were observed in coyotes that recently arrived in the Maritimes (wolves had been extirpated since the 1800s) and it has been hypothesized that the size increase was due to specialization on the larger prey such as white-tailed deer (Crete & Desrosiers, 1995).

Hillis & Mallory (1996) found that the greatest sexual dimorphism in wolves (n = 425) from Nunavut was in body and visceral organ masses, particularly of the heart, lungs, liver, and spleen. They attributed these differences to the division of labor between the sexes, with males being highly specialized for capturing and killing large ungulate prey. In this study, we found that male moose-wolves were larger than male caribou-wolves for the same set of organ measurements and concluded that the differences were due to specialization for capturing larger prey. Thicker necks in moose-wolves would assist in pulling prey down and the increase in bite force due to wider zygomatic arches (Thomason, 1991; Wiersma, 2001) and larger masseter muscles would complement increased neck girth. Larger hearts and lungs would increase the cardiovascular fitness in moose-wolves, and the larger spleen—a blood reservoir—would release more erythrocytes in response to drops in blood oxygen or blood pressure (Walker and Liem, 1994).

The fact that condition indices did not differ between moose- and caribou-wolves suggests that the body size and pack size of each wolf type adjusted to the nutritional input available from their primary prey. Although no significant differences occurred in condition indices, moose-wolves consistently had higher levels of adipose tissue. Hall (1989), working on arctic fox (*Alopex lagopus*), found larger litter sizes when adipose reserves increased due to an abundance of small mammals. The greater amount of adipose reserves also resulted in higher ovulation rates and we expect a similar relationship in wolves, which would affect wolf pack size.

The results from this study support the conclusion that the greater adult skull and body size of moose-wolves relative to caribou-wolves was related to specialization on larger prey. The data also support the conclusion that wolves adapted to larger prey would be more efficient at capturing smaller ungulate prey and impact these populations negatively. Gates & Larter (1996) observed that after wood bison (*Bison bison athabascae*) were introduced to the MacKenzie Wood Bison Reserve, moose and caribou populations in that region declined, which likely reflects the same shift in the predator–prey system as described in this study on moose and woodland caribou in Ontario.

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Appendix 1. Cranial, mandibular and dental measurements (*n* = 45) taken from *C. lupus* skulls.

No.	Abbrev.	Description
1	Condy L	Condylobasal length (from premaxilla to occipital condyle)
2	I^1-SagC	Maximum length from premaxilla to sagittal crest posterior
3	Nasal L	Maximum length of nasals
4	I^1-Palat	Palatal length from alveolar of I^1
5	I^2-Palat	Palatal length from alveolar of I^2
6	PosPal	Post palatal length
7	C^1 to M^2	Crown length of upper cheek teeth from C to M^2
8	W to C^1	Maximum anterior-posterior width of upper canine at base
9	W to P^4	Maximum buccolingual width of P^4 at enamel line
10	L of P^4	Maximum anterior-posterior length of P^4 at enamel line
11	W of M^1	Buccolingual width of M^1 at enamel line (at major cusp)
12	L of M^1	Maximum anterior-posterior length of M^1 at enamel line
13	W of M^2	Crown width of M^2
14	I^3 to I^3	Crown width across upper incisors
15	P^1 to P^1	Minimum width between alveoli of P^1
16	P^2 to P^2	Palatal width inside the second upper premolars (at hollow)
17	C^1 to C^1	Width of skull across outside of upper canines
18	M^1 to M^1	Palatal width outside the first upper molars
19	Cheek T W	Maximum crown width across upper cheek teeth
20	Pos For W	Width between the postglenoid foramina
21	Aud Bul W	Width between the auditory bullae
22	Occ Cre W	Maximum width of skull at lateral borders of occipital crest
23	Condyl W	Maximum width of long axis of left condyle
24	Condyl L	Maximum width of short axis of left condyle
25	Occ Con W	Total width across both occipital condyles
26	InterOr W	Minimum interorbital width
27	Postorb W	Width at postorbital processes
28	Tem Fos W	Minimum cranial width at temporal fossa
29	Pari - Temp	Maximum breadth of brain case at parietotemporal suture
30	Zygom W	Maximum zygomatic width
31	M^1 to Orb	Minimum distance from alveolar margin of M^1 to orbit
32	Jugal H	Minimum height of jugal at right angles to axis of bone
33	SagC - AudB	Height of skull from auditory bulla to sagittal crest
34	Sym - AngPr	Maximum length from symphysis to angular process
35	Sym - Condy	Maximum length from symphysis to condyle
36	C^1 to M^3	Maximum crown length from C^1 anterior to M^3
37	W of P^4	Buccolingual width of P^4
38	L of P^4	Anterior-posterior length of P^4
39	W of M^1	Buccolingual width of M^1
40	L of M^1	Anterior-posterior length of M^1
41	Mandib W	Width of mandible at P^4
42	Art Con W	Maximum width of long axis of articular condyle
43	Art Con L	Maximum width of short axis of articular condyle
44	H of Ramus	Maximum height of ramus between P^4 and M^1
45	AngP - CorP	Distance from angular process to top of coronoid process

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