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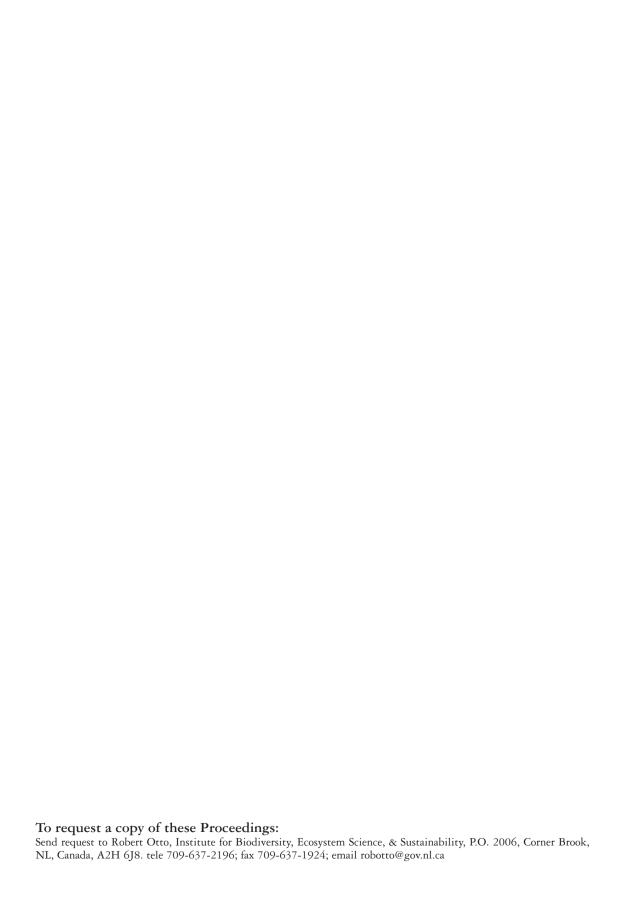
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Preface

Caribou (*Rangifer tarandus*) have been a integral part of the fabric of the cultures of Newfoundland and Labrador for thousands of years; the Maritime Archaic, the Dorset, the Thule, the Beothuk, the Innu, the Inuit, Mik'maq, and decendants of European dispersers. Varied peoples in a varied landscape of rock, forest, bog, mountain and coastline, shaping those that live here, including caribou. It is humbling to recognize that every life history strategy exhibited worldwide by *Rangifer* occurs within Newfoundland and Labrador. The theme of the 12th NACW, Integrating Understanding across Ecotypes, is therefore very topical for this workshop, hosted in Newfoundland and Labrador.

But there are other reasons as well. Dr. A. T. Bergerud, who pioneered the concept of ecotypes, started his career with *Rangifer* while working for the government of Newfoundland and Labrador on the George River herd and the various sedentary populations, and continued his research as the first Chief Biologist working on Newfoundland caribou. His contribution to caribou research and management is formidable and unquestioned.

The North American Caribou Workshop (NACW) is organized every two or three years to bring those interested in *Rangifer* together to discuss research and management issues, human use and impacts, and conservation of caribou, and increasingly, reindeer. The 12th NACW follows a long and impressive list of previously hosted events:

- 1st Whitehorse, Yukon Territory, 28-29 September 1983; Caribou and Human Acitivity
- 2nd Val Morin, Quebec, 17-20 October 1984; Caribou Management Census Techniques Status in Eastern Canada
- 3rd Chena Hot Springs, Alaska, 4-6 November 1987; Reproduction and Calf Survival
- 4th St. John's, Newfoundland, 31 October 3 November 1989
- 5th Yellowknife, Northwest Territories, 19-21 March 1991; Caribou Management in the 1990s: Incorporating Theory into Practise
- 6th Prince George, British Columbia, 1-4 March 1994
- 7th Thunder Bay, Ontario, 19-21 August 1996; Putting Caribou Knowledge into Ecosystem Context
- 8th Whitehorse, Yukon Territory, 20-24 April, 1998; A Future for an Ancient Deer
- 9th Kuujjuaq, Quebec, 23-27 April 2001; Caribou and Man
- 10th Girdwood, Alaska, 4-6 May 2004
- 11th Banff, Alberta, 23-26 April 2006

Planning for the 12th NACW started not long after the conclusion of the event in Banff. An organizing committee was struck, and one of the first decisions was to host the workshop in the central Labrador community of Happy Valley – Goose Bay, providing an opportunity for participants to experience the Labrador portion of the Province, known affectionately as "The Big Land". The province was host to the same event in St. John's in 1989.

Approximately 140 people attended the event, far outpacing the most optimistic expectations of the organizing committee, from Canada, United States, Norway, and Greenland. The 12th NACW included more than 70 oral and poster presentations, including Keynote Addresses by Serge Couturier, Shane Mahoney, John Mameumskum, John Nagy, and Peter Penashue covering a wide spectrum of topics including the latest research from Newfoundland and the Unagava region eastern Canada, caribou of the Northwest Territories, and caribou in the context of aboriginal and treaty rights of the Innu and Naskapi people.

The 12th NACW also provided an opportunity to, sadly, recognize two individuals that made major contributions to the conservation of caribou in Labrador that are no longer with us. Penote (Ben) Michel and Dr. Neal Simon both had significant impacts on my personal perspectives on caribou research, management, and conservation, each from a wide array of philiosophies. I am saddened that I will not have the pleasure and fortune of more conversation with these two thoughtful and committed friends of caribou.

Robert Otto, Chair, Organizing and Scientific Committees 12th NACW

In Memoriam



Penote (Pen) Michel June 24, 1954 – August 1, 2006

Pen (pronounced Ben to an English speaker) was, from an early age starting in the 1970s, heavily involved in assertion of Innu self determination and rights. He was amongst the first to do so after Labrador Innu were forced to establish a more settled life in Sheshashit and Utshimausits/Natuashish. The transition from a formerly nomadic life to a largely sedentary one was, and continues to be, a very trying experience for the Innu. Progress towards recognition of the right to self determination has been painfully slow. Equally slow has been the struggle towards solving socioeconomic issues plaguing the Innu since they began life in permanent settlements starting in the 1960s.

In the field of conservation, Pen was often involved in protest hunts for woodland caribou. The province of Newfoundland and Labrador, in the late 1960s, did not

recognize Innu hunting rights especially for those residing in Sheshashit. Consultation and discussion was not the early provincial approach. People who had spent generations living a nomadic hunting life were expected to suddenly adapt to permits and licenses, quotas and seasons. Given the wide cultural and language divide between the Innu and government, most Innu struggled greatly to make a transition from one world to another. Pen, with a handful of others from his generation, worked tirelessly to stand up for his people in that struggle.

Complicating questions around conservation and Innu traditional ways was a large influx of non-Innu into Innu territory starting in the early 1940s. Flooding of immense areas of habitat in the upper Churchill River basin, a railroad from Quebec, and a road across Labrador combined to give better access to better equipped hunters of all backgrounds. These forces, taken together, have proven to put unsustainable pressure on sedentary woodland caribou. Issues around newly resident moose and associated larger wolf numbers have also put pressure on sedentary woodland caribou. Finally, migration of large numbers of migratory George River caribou into threatened sedentary woodland caribou range and resultant demands by hunters have all conspired to further threaten sedentary woodland caribou.

Pen struggled, time after time, to bridge the divide from the world of his people, who see hunting caribou as a right, and also see population problems with sedentary caribou as problems created by someone else's doing, to the world where the very real peril of Labrador's sedentary caribou has been identified by the Province. Collectively, we still have not resolved those issues, but the two worlds and ways are hopefully closer to coming to a common understanding because of the many times Pen intervened between them, and actively worked, in a respectful and understanding way, to ensure that all points of view were valued whether Innu or non-Innu. For this we deeply appreciate, acknowledge, and miss the efforts of Penote Michel.

In Memoriam



Neal Phillip Perry Simon, PhD December 30, 1973 – September 23, 2006

The late Neal Phillip Perry Simon (1973-2006) passed away suddenly in a tragic boating accident while duck hunting at Gosling Lake, Happy Valley – Goose Bay. Neal was one of the founding members of the Labrador Woodland Caribou Recovery Team (2001) and co-authored a paper on the George River Caribou Herd at the 9th North American Caribou Workshop in Kuujjuaq, Quebec (23-27 April 2001).

Neal was born in Labrador City on Sunday December 30th, 1973. In 1998, he was employed by the Newfoundland and Labrador Department of Natural Resourcesat Happy Valley – Goose Bay in the position of Regional Ecologist of the Labrador portion of the Province. Between 1996 and 1998, Neal worked as a contract biologist for the College of the North Atlantic. He held a B.Sc. (Hons.) from Memorial University of Newfoundland with a major in Ecology and Evolution and a minor in

Statistics, and an M.Sc.F. in Forestry and Environmental Management from the University of New Brunswick. Neal completed his Ph.D. in the faculty of Forestry and Environmental Management at the University of New Brunswick in 2006, and was about to embark on his Post-Doctoral research at the Universite du Quebec a Montreal in the spring of 2007.

Neal's research interests included effects of forest management and changing forest structures on plants and animals, habitat selection, competitive interactions, and evolutionary histories of songbirds. He authored over 20 peer-reviewed journal publications and several internal reports on these topics. Neal also worked with St. Mary's University and the Innu Nation in developing and instructing course modules for the Innu Environmental Guardian Program. Neal was a member of the Society of Conservation Biologists, The Wildlife Society, the Atlantic Regions of the Canadian Climate Impacts and Adaptations Research Network, the Atlantic Cooperative Wildlife Ecology Network, the Labrador Woodland Caribou Recovery Team, the Labrador Wolverine Working Group, and the Committee for the General Status of Wildlife in Newfoundland and Labrador.

The Dr. Neal Simon Memorial Scholarship award was created in 2006 through the many donations of friends, family, and colleagues. The annual scholarship, valued at \$1,000.00, intends on providing financial assistance to residents of Labrador pursuing a post secondary diploma or degree in the natual resources, ecological, biological or environmental fields. The awarding of the scholarship will be based on financial need, community and/or school volunteer activities, academic ability, and environmental conservation interests.

The first Dr. Neal Simon Memorial Scholarship was awarded to Ms. Samantha Joy Irene Churchill of Happy Valley – Goose Bay, Labrador in May 2008. Ms. Churchill, a graduate of Mealy Mountain Collegiate in Happy Valley – Goose Bay, intends on pursuing post secondary studies in biology at the University of New Brunswick (very fitting as Neal completed both his M.Sc. and Ph.D. at UNB).

All proceeds from the Workshop's Silent Auction will be donated to the Dr. Neal Simon Memorial Scholarship in Neal's memory. His friends will best remember Neal as a shining though comedic intellectual, with a love of life and a passion for the outdoors.

Tony E. Chubbs, Chair Dr. Neal Simon Memorial Scholarship Committee The 12th North American Caribou Workshop, Happy Valley/Goose Bay, Labrador, Canada, 4–6 November, 2008.

Historical changes in caribou distribution and land cover in and around Prince Albert National Park: land management implications

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Abstract: In central Saskatchewan, boreal woodland caribou population declines have been documented in the 1940s and again in the 1980s. Although both declines led to a ban in sport hunting, a recovery was only seen in the 1950s and was attributed to wolf control and hunting closure. Recent studies suggest that this time, the population may not be increasing. In order to contribute to the conservation efforts, historical changes in caribou distribution and land cover types in the Prince Albert Greater Ecosystem (PAGE), Saskatchewan, were documented for the period of 1960s to the present. To examine changes in caribou distribution, survey observations, incidental sightings and telemetry data were collated. To quantify landscape changes, land cover maps were created for 1966 and 2006 using current and historic forest resources inventories, fire, logging, and roads data. Results indicate that woodland caribou are still found throughout the study area although their distribution has changed and their use of the National Park is greatly limited. Results of transition probabilities and landscape composition analyses on the 1966 and 2006 land cover maps revealed an aging landscape for both the National Park and provincial crown land portions of the PAGE. In addition, increased logging and the development of extensive road and trail networks on provincial crown land produced significant landscape fragmentation for woodland caribou and reduced functional attributes of habitat patches. Understanding historical landscape changes will assist with ongoing provincial and federal recovery efforts for boreal caribou, forest management planning activities, and landscape restoration efforts within and beyond the Park boundaries.

Key words: boreal forest; caribou distribution; fire management; landscape change; landscape fragmentation; population history; Prince Albert National Park; *Rangifer tarandus caribou*; woodland caribou.

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Introduction

Human land use through settlement, recreation or industrial development may cause habitat fragmentation leading to significant changes in the landscape. Habitat fragmentation is generally defined as "the breaking up of a large habitat into smaller, more isolated, patches" (Andrén, 1994; Fahrig, 1997). Habitat patches are part of the landscape and the use of a patch by wildlife is not only a function of the patch attributes but also of the characteristics of neighboring patches (Andrén, 1994; Fahrig, 1997). In highly fragmented landscapes, the decline of wildlife populations is greater than that expected by habitat loss alone (Andrén, 1994) and ultimately, these changes to

the landscape can isolate groups of animals (Bélisle & Desrochers, 2002). Habitat fragmentation is considered one of the greatest threats to biodiversity making it an important conservation issue (Harris, 1984; Forman & Godron, 1986; Saunders *et al.*, 1991).

In the boreal forest, the main factors leading to habitat loss and habitat fragmentation are: changes in natural and anthropogenic disturbance patterns, increased commercial and industrial activities, increased road access to remote areas and recreational activities (Harris, 1984; Forman & Godron, 1986). Fire is a natural disturbance and has long-term ecological benefits (Bergeron, 1991; Klein, 1992; Johnson *et al.*, 2001). In the boreal mixedwood for-

est of North America, the fire return interval ranges from 30 to 150 years (Johnson, 1992). Changes in fire frequency can be caused by shifts in climate, land use pattern and land management strategies (Clark, 1988; Bergeron, 1991; Johnson & Larsen, 1991; Larsen, 1997). At the time of human settlement, fires were frequent as deliberate burns were set to clear land for agricultural purposes (Williams, 1989; Whitney, 1994; Weir, 1996). After an area is settled, fire frequency tends to decrease as forested areas become fragmented and cannot support the spread of fire (Weir, 1996).

Following settlement of the boreal forest, roads were constructed to provide access for industrial development, primarily forestry (Walker, 1999). Forest harvesting is an important commercial activity across the boreal region and usually targets coniferous stands older than 50 years (Walker, 1999). To be sustainable, logging practices attempt to maintain stands of a variety of ages within a given forest management area (Walker, 1999). In Saskatchewan, fire is suppressed over areas of commercial forest tenures or in proximity to communities; natural forest pattern standards and guidelines for the forest industry aim to produce landscapes and harvest areas that emulate the patterns created by fire (Saskatchewan Environment, 2009). However, occurrence of fire on landscapes where logging activities are prevalent can add a level of complexity and produce a younger stand age structure (Reed & Errico, 1986).

Landscape changes, natural and anthropogenic, can have significant impacts on the boreal population of woodland caribou (Rangifer tarandus caribou), a threatened species under the Species at Risk Act (2004). Boreal caribou are habitat specialists, dependent on old growth forests to survive (Rettie & Messier, 2000; Smith et al., 2000; Mahoney & Virgl, 2003). They avoid logged areas (Cumming & Beange, 1987; Chubbs et al., 1993; Smith et al., 2000; Johnson & Gilligham, 2002; Lander, 2006), areas near roads and trails (Nellemen & Cameron, 1996; Cameron et al., 2005) and recent burns (Schaefer & Pruitt, 1991; Klein, 1992; Thomas & Gray, 2002; Lander, 2006). Caribou also avoid hardwood stands or stands of vounger age classes as these areas often allow for higher densities of other ungulate species (moose, deer and elk) and associated predators. Caribou have persisted in the boreal forest for thousands of years in the presence of fire, provided suitable habitat is available in adjacent areas (Schaefer & Pruitt, 1991; Schaefer, 1996). Logging and road development also often displace caribou (Chubbs et al., 1993; Dyer et al., 2001) and since these activities lead to more permanent landscape changes, they can result in range retraction (Bradshaw *et al.*, 1997; Thomas & Gray, 2002).

The Prince Albert National Park (PANP) and Greater Ecosystem (PAGE) are located in the boreal mixedwood forests of Canada, in the province of Saskatchewan, and part of the Smoothstone-Wapaweka Woodland Caribou Management Unit (SW-WCMU). The fire frequency of this area has decreased following settlement (Johnson, 1992; Weir et al., 2000) and over the past 40 years, significant logging and road development surrounding the Park has occurred. This ecosystem has traditionally been used by a resident population of boreal caribou (Banfield, 1961) but there are concerns over the long-term viability of the population (Arsenault, 2003; Saskatchewan Environment, 2007). In central Saskatchewan, population declines have been documented in the 1940s and again in the 1980s. The first decline led to a ban in sport hunting and an increase in caribou population in the 1950s was attributed to wolf control and hunting closure (Rock, 1988; Rock, 1992). In 1987, another population decline was documented and sport hunting was again banned (Rock, 1988; Rock, 1992). Subsistence harvesting still occurs, although only opportunistically (Trottier, 1988). Work conducted by the University of Saskatchewan (Rettie & Messier, 1998) and more recently through a collaborative effort between Parks Canada, Saskatchewan Environment, the Prince Albert Model Forest, Weyerhaeuser Canada Ltd. and the University of Manitoba (Arsenault & Manseau, 2011) suggests that the population is declining. The Park and surrounding area are managed separately and under different legislations. The management of the National Park centres on the maintenance or restoration of ecological integrity while also providing opportunities for public education and enjoyment (Parks Canada, 1986). Logging has not been permitted within the Park in the past 60 years and fire has been suppressed; however, a prescribed burning program has been put in place to reinstate a natural fire cycle (Prince Albert National Park, 2008). The area outside of the National Park is managed primarily for the forest industry by the Saskatchewan Ministry of Environment (MoE) (Government of Saskatchewan, 2002).

The main objectives of this work were to assess changes in caribou distribution and landscape composition in the PAGE over a period of 40 years, between 1966 and 2006. Since the data sources differed between the crown land and the National Park portion of the PAGE, analyses were done separately for the two areas. Careful attention was given to the production of the historical datasets to allow for a reliable comparison. A better understanding of

historical landscape changes should assist with the recovery efforts for woodland caribou and guide current and future forestry management and land-use planning activities.

Methods

Study area

The Prince Albert Greater Ecosystem (PAGE) is a 13 380 km² area located in central Saskatchewan, Canada (Fig. 1). Prince Albert National Park was established in 1927 to represent the southern boreal forest region of Canada. The portion of the Park within the PAGE is 2688 km². The remaining part of the PAGE is provincial crown land. This includes the communities of Weyakwin and Waskesiu, the reserve community of Montreal Lake First Nation, Ramsey Bay Subdivision on Weyakwin Lake, and a few private properties. The main commercial activities are forestry, trapping and outfitting and significant in vehicular and off-road traffic for recreation (snow mobiles. all-terrain vehicle use, cross-country skiing, hiking, boating, cottages. etc.).

Historically, when fires started in the National Park they were extinguished before much of the landscape burned. In recent years, controlled burns and clearing has been initiated to create a fire barrier along the Park boundaries with the objective of letting non-threatening fires burn in the Park and restoring the natural fire frequency (Prince Albert National Park, 2008). The Saskatchewan Provincial Government manages the area for forestry and produces a 20-year forest management plan which is reviewed every 10 years. The Park produces a park management plan every 5 years. Both planning processes are subject to significant public consultation. The Prince Albert Model Forest was established in 1992, it supports research activities to assist with forest management planning efforts and community sustainability (Prince Albert Model Forest, 2008). Both the Province and the federal government are developing recovery plans for woodland caribou even if the species is not listed in provincial legislation as a species at risk.

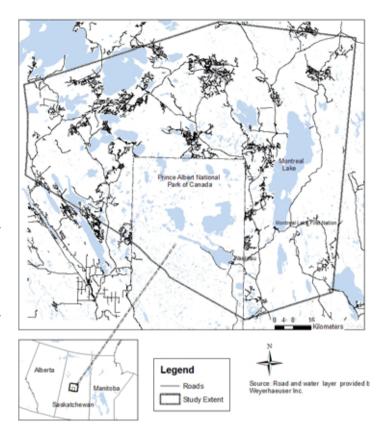


Fig. 1. Prince Albert Greater Ecosystem, Saskatchewan, Canada.

Smoothstone-Wapaweka Woodland Caribou Management Unit

Arsenault (2003, 2005) has defined seven Woodland Caribou Management Units (WCMUs) within the Province based on clusters of caribou observations, areas of similar ecological characteristics (Acton *et al.*, 1998) and peatland distribution. The PAGE is part of the Smoothstone-Wapaweka WCMU and fecal-DNA capture-mark-recapture analysis of population size conducted in 2008 based on two capture events estimated the number of caribou at 128 (95% 116, 145) (Hettinga, unpublished results; Hettinga 2010). This corresponds to a population density of 0.009 caribou/km² when calculated over the entire PAGE study area, and 0.11 caribou/km² when based on MCPs of annual home ranges (Arsenault & Manseau, 2011).

Caribou past and present distribution

In order to examine changes in caribou distribution over time, woodland caribou occurrence data and associated survey efforts were collated for the period of 1950 to present. Data were obtained from Parks Canada and Saskatchewan Ministry of Environment

and primarily consisted of survey observations, incidental sightings and telemetry data.

Landscape reconstruction

Map layers for the National Park and provincial crown land portion of the PAGE were created separately since the type and extent of data available for the two areas differed. Although we tried to create seamless layers for the PAGE area, map resolution issues could not be resolved and prevented us from directly comparing landscape changes between the two areas. For both the Park and the provincial crown land portion of the PAGE, we created map layers for 1966 and 2006 (same resolution) to assess historical landscape changes.

For the National Park area, the map layers consisted of a vegetation layer based on aerial photos taken in the 1960s (Parks Canada, 1986), a road layer and a burn polygon layer produced by Parks Canada, and a time since fire map produced by Weir (1996). Since the time since fire map was based on data collected in the 1990s, 30 years was subtracted from each forest stand to obtain a stand age for the 1966 layer. For the 2006 layer, stand types from the 1966 layer were used (we did not account for forest succession) and 10 years added to the stand ages obtained from Weir (1996) and the time since fire map. To account for natural disturbances that occurred in the past 10 years, after the creation of the time since fire map, the burn polygon layer was used and a burn class was assigned to all forest stands that fell under those polygons.

For the provincial crown land portion of the PAGE, the most recent forest resource inventory (FRI) was used along with a road and a cut block layer developed by Weyerhaeuser Canada Ltd. and a burn layer from the Province. The FRI was based on aerial photos from 2004 and the attributes of each forest stand consisted of cover type (species, height and density), soil type, topography, history of disturbance and stand age. For the current layer, data layers were provided by Weyerhaeuser Canada Ltd. Since a burn class was not available in the FRI, the burn polygon layer was used and a recent burn class assigned to all forest stands that fell under those polygons if the vear of origin corresponded to the vear of the fire ± 5 years. The cut block layer lacked a harvest year or a stand age for a number of polygons. To determine those stand ages, ring counts on tree cores was done on 10% (142 polygons) of the cut block polygons lacking a harvest year (Cook, 1990). Cut block polygons that were not sampled were assigned an age based on proximity to sampled cut block polygons, on the assumption that stands in a general area were harvested at approximately the same time. For the 1966 layer, 40 years was subtracted from the stand age. Since the FRI was current, stand composition and stand age prior to fire was not available. To obtain this information, older provincial FRI and hard copy maps from the 1960s were used. The maps were scanned and georeferenced and the composition and age of forest stands that burned over the last 40 years were entered manually.

To prepare the map layers for analyses, the vegetation layers were reclassified using a simplified classification scheme (Rettie *et al.*, 1997). Vegetation classes of similar composition were combined to produce 7 habitat classes (Table 1). Each map layer was rasterized at a 100 m grid and filtered using Spatially Explicit Landscape Event Simulator (SELES; Fall & Fall, 2001) to remove patches of less than 2 ha. Patches of this size are smaller than the minimum mapping unit and are often artifacts from the vector to raster conversion.

Validation of the 1966 layer

To validate the created 1996 layer, we used the georeferenced Forest Resource Inventory maps from the 1960s and compared the two layers using 7450 points systematically distributed with the Hawth's tools extension (Beyer, 2004) in ArcGIS 9.2 (Environmental Systems Research Institute, 2006). Stand attributes were derived for each point and compared. The results indicated that more than 70% of the points on the 1966 layer corresponded to the classes extracted from the 1960 hard copy maps. This overall accuracy level is above the accepted standard of 70% (Burnside, 2003). Accuracy levels of 72% were obtained for coniferous mature and 84% for coniferous young and recent burns. Some of the differences may be attributed to different classification schemes, differences in map resolution or differences in the boundaries drawn (limits of the polygons) for each forest stands.

Transition probabilities analyses

Transition probabilities measure the likelihood of one habitat type transitioning into another within a given time period (Burnside, 2003). We calculated the transition probability of each habitat class between 1966 and 2006 by quantifying changes of each pixel in the two layers using SELES (A. Fall, unpublished).

Landscape composition and configuration

Landscape metrics are commonly used when assessing fragmentation (e.g. Hargis *et al.*, 1998; Southworth *et al.*, 2002; Burnside *et al.*, 2003; Jackson *et al.*, 2005). Total area, patch number, area-weighted mean patch size, mean nearest neighbor, mean shape index

Table 1. Habitat classes used in the mapping and analyses of the provincial crown land and National Park portion of the PAGE.

Provincial Crown Land	National Park	Habitat Class	Age (years)
Jack Pine Mature	Jack Pine Mature	Mature Coniferous	≥40
Jack Pine/Black Spruce Mature	Jack Pine/Black Spruce Mature	Mature Coniferous	≥40
Black Spruce Mature	Black Spruce Mature	Mature Coniferous	≥40
White Spruce Mature	White Spruce Mature	Mature Coniferous	≥40
Coniferous Mixedwood Mature	Coniferous Mixedwood Mature	Mature Coniferous	≥40
Brushland	Brushland	Treed Muskeg	na
Closed Treed Muskeg	na	Treed Muskeg	na
Black Spruce/Larch	Black Spruce/Larch	Treed Muskeg	All ages
Open Treed Muskeg	na	Treed Muskeg	Na
Open Muskeg	na	Treed Muskeg	Na
Fen, marsh, bog	Meadow, marsh, bog	Treed Muskeg	Na
Hardwood Mixedwood	Hardwood Mixedwood, Aspen Mixedwood	Hardwood Mixedwood	All Ages
Hardwood	Hardwood	Hardwood Mixedwood	All Ages
Coniferous Young	Coniferous Young	Coniferous Young/Recent Burn	<40
Recent Burn	Recent Burn	Coniferous Young/Recent Burn	<40
Recent Logged	na	Recent Logged	<40
Road	Road	Road	na
Water	Water	Water	na

and amount of linear features were computed for each habitat type on the 1966 and 2006 map layers for the National Park and provincial crown land portions of the PAGE using Fragstats (McGarigal & Marks, 1995). Differences in landscape metrics between 1966 and 2006 were tested for statistical significance using t-tests in SAS 9.1 (SAS Institute Inc., 2003).

To further assess changes in landscape configuration, we used results from resource selection function analyses presented in Dyke (2008) which shown a greater selection of mature coniferous and treed muskegs away from avoided habitat types such as hardwood mixedwood. ArcGIS 9.2 was used to measure distances from a source patch, either coniferous mature or treed muskeg, to the nearest hardwood mixedwood patch. Resulting distances were compared using *t*-tests (SAS Institute Inc., 2003).

Results

Caribou past and present distribution

Although the survey efforts varied greatly between decades (particularly on provincial crown land), our results indicate that the extent of caribou use of the National Park portion of the PAGE has changed over the last 50 years, with very limited use detected since the 1980s (Fig. 2). Despite multiple surveys conducted throughout the Park in recent years and large radio-collaring programs, only one observation was made over the last 14 years, in 2007. Caribou are still present over most of the provincial crown land portion of the PAGE despite their low density and clustered distribution. A comparison of home range sizes using location data of radio-collared adult females from 1992-1995 (Rettie & Messier, 2001) and 2004-2008 (Arsenault & Manseau, 2011)

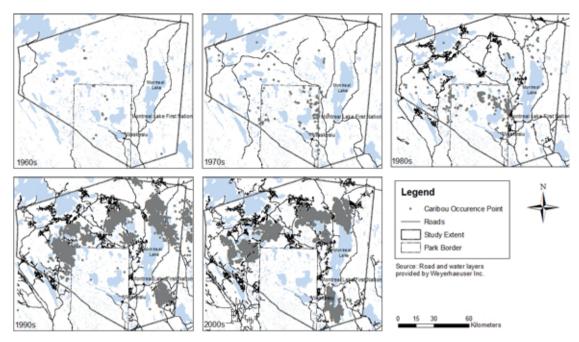


Fig. 2. Compilation of boreal caribou occurrences in the Prince Albert National Park for the period of 1960 to the present.

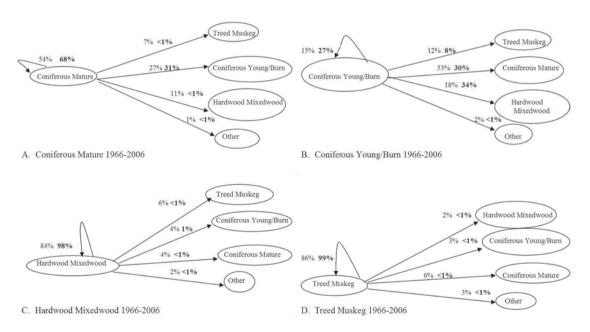


Fig. 3. Habitat transition probabilities between 1966 and 2006 for the Provincial crown land (normal font) and National Park portions (bold font) of the Prince Albert Greater Ecosystem. The main habitat types consisted of coniferous mature (A), coniferous young and burn (B), hardwood mixedwood (C) and treed muskeg (D).

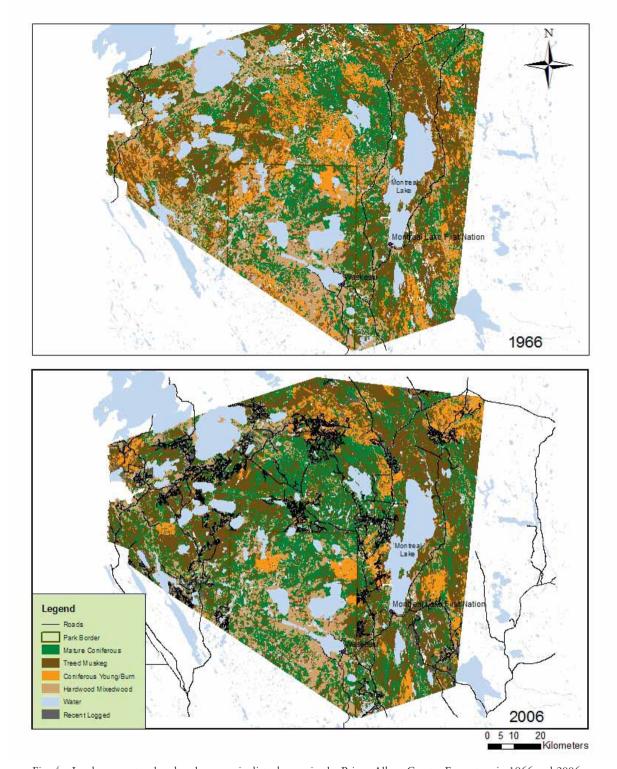


Fig. 4. Landcover, natural and anthropogenic disturbances in the Prince Albert Greater Ecosystem in 1966 and 2006.

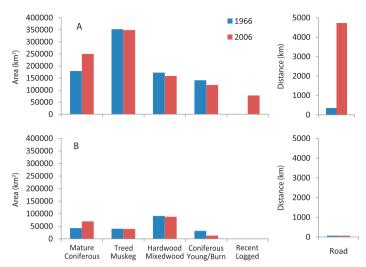


Fig. 5. Area covered by the main habitat types and linear features in 1966 and 2006 on the Provincial Crown Land (A) and National Park (B) portions of the Prince Albert Greater Ecosystem.

Table 2. Changes in habitat patch metrics ($\bar{x} \pm \text{s.e.}$) between 1966 and 2006 for the National Park portion of Prince Albert Greater Ecosystem.

Landscape metrics and habitat types	1966	2006	P	
Area-weighted mean pa	tch size (ha)			
Coniferous Mature	7186 ± 1000	8317 ± 1128	< 0.0001	
Treed Muskeg	647 ± 159	624 ± 155	0.0014	
Hardwood	4895 ± 980	4905 ± 958	0.887	
Coniferous Young/Burn	2010 ± 464	4771 ± 1413	< 0.0001	
Mean nearest neighbour (m)				
Coniferous Mature	225 ± 388	166 ± 192	0.0007	
Treed Muskeg	183 ± 232	188 ± 241	0.6451	
Hardwood	182 ± 176	193 ± 211	0.4499	
Coniferous Young/Burn	258 ± 455	1323 ± 2292	0.0208	
Mean shape index				
Coniferous Mature	1.98 ± 1.64	1.98 ± 1.70	0.898	
Treed Muskeg	1.91 ± 1.03	1.91 ± 1.02	0.9535	
Hardwood	1.97 ± 1.44	1.95 ± 1.40	0.9217	
Coniferous Young/Burn	1.96 ± 1.10	2.11 ± 1.16	0.2536	
Number of patches				
Coniferous Mature	436	544		
Treed Muskeg	954	945		
Hardwood	443	447		
Coniferous Young/Burn	279	28		

showed a significant reduction in areas used from an average minimum convex polygon (MCP) of 441 km² (s.d. = 393, n = 31) in 1992-1995 to 221 km² (s.d. = 145, n = 23) in 2004-2008.

Transition probabilities

Transition probabilities showed similar trends in the National Park and provincial crown land portion of the PAGE. The most notable changes were with forest stands in the coniferous mature and coniferous young/burn classes (Fig. 3A,B). Less than 27% of the coniferous young/ burn class remained in that class. A large portion of these stands aged to coniferous mature or to hardwood mixedwood: the transition to a hardwood mixedwood class being higher for the National Park area. Fifty four percent of National Park land and 68% of provincial crown land remained in the coniferous mature class. A substantial portion of land within the PAGE as a whole also transitioned to coniferous young/ recent burn class. Of all habitat types, hardwood mixedwood and treed muskeg had the highest probability of remaining the same habitat type (Fig. 3C,D). For hardwood mixedwood, 84% on provincial crown land and 98% on National Park land remained in the same class between 1966 and 2006. Similarly, 86% of treed muskegs on provincial crown land and 99% in the Park area remained treed muskegs.

Landscape changes

The predominant change to older stand ages suggests an ageing forest over the PAGE landscape as a whole. The transitioning of large tracts of crown land in the PAGE to coniferous young/burn stands corresponds to an increase in the number of cut blocks and the development of road and trails network (Figs. 4, 5). The first mill was built in 1966 and the amount of area logged increased from 0 ha logged in 1966 to 58211

ha logged in 2006. The road network remained the same in the National Park but increased 14-fold on the provincial crown land portion of the PAGE, from 342 km to 4730 km over the same 40-year period (0.03 to 0.44 km/km²). During that time, major highways were constructed to improve access to the communities of La Ronge, Montreal Lake First Nation, Sled Lake, and Dore Lake. In addition, highways and logging roads were built as travel corridors to the pulp mills in Prince Albert, to the south, and to the saw mills in Big River and Nipawin, to the southwest and southeast, respectively. Finally, land was converted from forest to commercial/residential with the moving of Molanosa residents from the east side to the west side of Montreal Lake and the formation of a new community, Weyakwin. This

change was further augmented with the expansion of residential areas on reserve lands of Montreal Lake First Nation and the Lac La Ronge Indian Band, and with development of the Ramsey Bay subdivision at Weyakwin Lake.

Landscape metrics include various measures of distribution, spacing, types, sizes and shapes of forest stands. The increased amount of mature coniferous stands shown in the previous results (Figs. 3, 4, 5) is further described in the landscape metrics analysis as an increased number of mature coniferous patches, from 436 to 544 in the Park and from 4874 to 5398 on crown land (Table 2, 3). The area-weighted mean patch sizes also increased significantly and the mean nearest neighbor distances decreased significantly indicating larger patches occurring closer together. Mean shape index describes patch shape and complexity and a significant decrease in the mean shape index outside the Park, indicating a drop in shape complexity, which often results from logging activities.

Change in coniferous young/burn stands between 1966 and 2006 also followed a similar trend in both portions of the PAGE, with the exception of area-weighted mean patch size (Table 2, 3). The decreased number of patches between 1966 and 2006 was again likely a reflection

of changes in the amount of young coniferous/burn forest on the landscape. The change in area-weighted mean patch size of coniferous young/burn differs between the Park and provincial crown land; the observed increase in the National Park and decrease on crown land is likely due to natural disturbance in the Park and a combination of natural and anthropogenic disturbance on crown land. An increased mean nearest neighbor distance was also detected for both areas indicating patches of the same cover type occurred farther from one another.

Treed muskeg was the habitat type exhibiting the least amount of change in the PAGE. The area covered by treed muskeg and the number of patches were comparable between 1966 and 2006 in both the Park and on crown land and there were no sig-

Table 3. Changes in habitat patch metrics ($\bar{x} \pm$ s.e.) between 1966 and 2006 for the provincial crown land portion of Prince Albert Greater Ecosystem.

Landscape metrics and habitat types	1966	2006	P
Area-weighted mean p	atch size (ha)		
Coniferous Mature	4013 ± 449	4043 ± 450	< 0.0001
Treed Muskeg	14822 ± 1232	8880 ± 902	< 0.0001
Hardwood	3886 ± 497	340 ± 95	< 0.0001
Coniferous Young/Burn	3353 ± 426	2154 ± 372	< 0.0001
Cutblocks	n/a	121 ± 47	n/a
Mean nearest neighbou	ır (m)		
Coniferous Mature	217 ± 220	184 ± 162	< 0.0001
Treed Muskeg	200 ± 170	196 ± 171	0.3154
Hardwood	265 ± 354	254 ± 354	0.2514
Coniferous Young/Burn	275 ± 392	333 ± 636	0.0015
Cutblocks	n/a	169 ± 295	n/a
Mean shape index			
Coniferous Mature	1.81 ± 1.08	1.77 ± 1.19	0.0453
Treed Muskeg	1.83 ± 1.24	1.79 ± 1.19	0.0697
Hardwood	1.69 ± 1.02	1.79 ± 0.66	0.0991
Coniferous Young/Burn	1.76 ± 1.07	1.79 ± 1	0.6443
Cutblocks	n/a	1.90 ± 1.2	n/a
Number of patches			
Coniferous Mature	4874	5398	
Treed Muskeg	3543	3760	
Hardwood	2830	3845	
Cutblocks	0	2526	

Table 4. Landscape configuration changes. Distance ($\bar{x} \pm \text{s.e.}$) between selected and avoided habitat types in 1966 and 2006 for the provincial crown land and Prince Albert National Park areas of the Prince Albert Greater Ecosystem

2006	P			
283 ± 721	<0.001			
191 ± 620	<0.001			
Prince Albert National Park				
80 ± 330	0.712			
74 ± 237	0.689			
	191 ± 620 80 ± 330			

nificant changes in mean nearest neighbour or mean shape index (Table 2, 3). The only noticeable change in treed muskeg was a significant decrease in areaweighted mean patch size, both in the Park and on the provincial crown land.

Similar to treed muskeg, limited changes were observed for hardwood mixedwood stands between 1966 and 2006. The only changes detected were a decrease in area covered by hardwood mixedwood stands (174643 ha to 108063 ha), an increase in number of patches (Table 2) and a decrease in area-weighted mean patch size, all on the crown land portion of the PAGE. These changes coincided with a history of logging that accelerated over the study period along with the construction of a road network.

Finally, changes in landscape configuration measured through distance metrics were only significant on the provincial crown land portion of the PAGE. Distances between habitat classes selected by boreal caribou (mature coniferous and treed muskeg) and those avoided (hardwood mixedwood) were significantly less on provincial crown land in 2006 when compared to 1966 (Table 4).

Discussion

The historical compilation of caribou observations indicates that the southern boundary of caribou distribution (in central Saskatchewan) has not changed over the last 50 years, although range retraction has occurred in other parts of the Province (Arseanult 2003, 2005; Saskatchewan Environment, 2007). Also, very few caribou observations have been made in the National Park since the 1980s despite signifi-

cant survey and collaring efforts. In 2007, caribou tracks were seen in the northeast sector of the Park, north of Crean Lake, fecal pellets were collected and 3 unique genotypes profiled (unpublished results). Other tracks were seen east of the Park along Highway 2, near Crean River. These results along with habitat modeling work done by Dyke (2008) and Arlt (2009) suggest that the Park area corresponds to only a small portion of the population range, the northern sector of the Park primarily consists of winter habitat and recent landscape changes may be affecting a seasonal range use pattern. Results of Dyke (2008) suggest that calving and summer habitats are primarily found north of the Park boundaries.

with some of the core areas north of Montreal Lake. Reduced movement and a more clustered distribution of adult females were also quantified through telemetry work for the period of 1992-1995 to 2004-2008 (Arsenault & Manseau, 2011).

For both the National Park and the provincial crown land portions of the PAGE, our results showed an ageing landscape which is also reported in other regions of the boreal forest (Johnson et al., 1998, Walker, 1999; Harvey et al., 2002) and most often attributed to changes in fire incidence and fire management strategies (Walker, 1999). As observed in other regions of the boreal forest, anthropogenic activities also increased over the last 40 years and particularly over the last 20 years. As expected, the changes primarily occurred on the provincial crown land portion of the PAGE and are the direct response of commercial logging activities and associated roads and trails network. Interestingly, both the results from the 1992-1995 and the 2004-2009 collaring work showed that animals north of Montreal Lake. west of Bittern Lake and near Weyakwin Lake never crossed Highway 2. Animals west of Lawrence Lake never crossed Highway 922. In both locales, the animals moved within a few meters of the road but did not cross the road.

The National Park was established in 1927 and it is only in the 1960s that major landscape changes occurred with the beginning of commercial forest harvesting, the development of road network and increase infrastructure. The commercial interest in forest timber, the development of roads, cottaging areas and settlements have all contributed to the current fire suppression efforts (Arsenault & Manseau,

2011). In the early 1940s, many fires burned unsuppressed in both the Park and surrounding area (Weir, 1996) as fire prevention and fire suppression were not practiced (R. Davies, pers. comm.). Changes in fire interval following settlement and industrial development have also been observed in other regions including Ontario and Québec (Bergeron, 1991), British Columbia (Johnson & Larsen, 1991), Alberta (Larsen, 1997) and Minnesota (Clark, 1988).

In the Park, fire suppression still occurs to protect residences, neighboring communities, park facilities and adjacent provincial forests (Prince Albert National Park, 2008). Research on fire frequency in Prince Albert National Park documented a fire cycle of 25 years from 1760 to 1890, an increased fire cycle of 75 years from 1890-1945 and 645 years from 1945 to 1995 (Weir, 1996; Weir et al. 2000). They explained that the short fire cycle of the early period coincided with the Little Ice Age, the longer cycle of the early 1900s with the end of the Little Ice Age and a change of climate and the more recent longer fire cycle to be likely due to fire suppression. Extending fire intervals beyond long-term norms is detrimental in the boreal forest because fire is a natural disturbance and essential to maintaining lichen rich coniferous stands (Klein, 1992; Johnson et al., 2001). The National Park recently initiated controlled burns along the Park boundaries in order to create a fire break, enabling them to let wildfires burn in the Park and reestablishing a natural fire frequency (Prince Albert National Park, 2008). Our results clearly showed that increased anthropogenic activities over the last 40 years have led to a different landscape and significant habitat fragmentation. The roads and trails network increased 14-fold on the provincial crown land portion of the PAGE, from 342 km to 4730 km. Fragmentation as characterized by an increased number of patches and mean nearest neighbor distances (Forman & Godron, 1986; Heggm et al., 2000; Turner et al., 2001) was detected for most habitat types except mature coniferous stands. A decrease in mean shape index for the mature coniferous stands suggests a drop in complexity of patch shape which is often associated with logging activities (McGarigal & Marks, 1995). Aside from the development of a road network, the most significant indicators of fragmentation for caribou are the distance metrics which capture the functional attributes of high quality habitat patches. Along with a larger number of patches and larger patch sizes of mature coniferous stands in 2006 (which is favorable to caribou), we observed a greater proximity of habitat classes selected by boreal caribou (mature coniferous and treed muskeg) and those avoided (hardwood

mixedwood) on provincial crown land in 2006 when compared to 1966. The interspersion of avoided habitat types and roads and trails network impacted the functional attributes of selected habitat types for caribou and resulted in reduced habitat connectivity at landscape scales (see Arlt (2009) for more results of landscape connectivity analysis).

Boreal caribou are sensitive to landscape changes and the long-term persistence of local populations is essential for the conservation of this species (Thomas & Gray, 2002, Environment Canada, 2007). The increased abundance of mature forest stands, in both the Park and the provincial crown land of the PAGE. should be favorable to woodland caribou (Hirai, 1998; Brown et al., 2000a; Brown et al., 2000b; Rettie & Messier 2000, Schneider et al., 2000; Thomas & Gray 2002, Mahoney & Virgl, 2003; Lander 2006, O'Brien et al., 2006) however, the increased amount of anthropogenic disturbances and resulting patchwork of selected and avoided habitat types on provincial crown land are potentially counteracting those benefits and reducing the functional values of the mature coniferous stands. O'Brien (2006) showed that woodland caribou select large clusters of high quality habitat patches over the high quality habitat patches themselves. These large clusters of well-connected habitat patches or the resulting habitat mosaic are important in providing food, cover and separation from other ungulate species and associated predators.

Anthropogenic disturbance, such as logging and access development, have detrimental effects on caribou populations (Cumming & Beange, 1987; Rettie & Messier, 1998). Increased number of patches of recently logged areas may attract greater number of other ungulate species such as moose, elk and whitetailed deer (Brown et al., 2000a; James et al., 2004) and subsequently, higher densities of predators such as wolves (Bergerud & Elliot, 1986; Rettie & Messier, 1998). Ultimately, increased area logged can lead to range retraction (Bradshaw et al., 1997) as caribou actively avoid disturbance (Cumming & Beange, 1987; Chubbs et al., 1993; Smith et al., 2000; Johnson & Gilligham, 2002). A developed roads and trails network may also facilitate access to formerly isolated areas increasing mortality, from hunting and predation (Dyer et al., 2001; Whittington et al., 2005) and from caribou-vehicle accidents (Cumming & Beange, 1987). In an attempt to identify landscape disturbance threshold for woodland caribou, Sorensen et al. (2007) examined the relationship between functional habitat loss resulting from cumulative effects of natural and anthropogenic disturbances, and the rate of population change for six populations of boreal caribou in Alberta, Canada. In defining habitat loss

as the percentage area of caribou range within 250 m of anthropogenic footprint and the percentage of caribou range disturbed by wildfire within the last 50 years, they obtained a strong negative correlation between these two variables and population growth rate. They also identified landscape disturbance thresholds above which a population would be declining (λ <1). When applying their equation to the PAGE area, we obtained a λ of 1.06 when the amount of disturbance was calculated as a proportion of the entire PAGE study area, 1.03 when based on a study area excluding PANP and 1.17 when based on the extent of caribou home ranges (Arsenault & Manseau, 2011). This suggests that the amount of disturbance in the PAGE is below the disturbance threshold identified by Sorensen et al. (2007) and the area should support a stable or growing population. Population demographic work done by Rettie & Messier (1998) for the period of 1992-1995 and the PAGE study for 2004-2009 (Arsenault & Manseau, 2011) do not support these results. The characteristics of the PAGE landscape may be different than caribou ranges studied in Alberta and work on landscape changes and disturbance thresholds is ongoing (Environment Canada, 2008).

The PAGE study area has undergone structural changes over the last 40 years from an area that presented a lesser amount of mature coniferous forest and limited access to a working landscape with older forest stands, a well developed roads and trails network and significant human activities. The National Park and provincial crown land portions of the PAGE are managed differently; the provincial crown land being accessible to forestry, offering transport corridors among communities and diverse commercial and recreational activities. The National Park area is protected from industrial activities and as seen in this study, accounts for a small portion of the population range and can only play a minor role in ensuring the long-term viability of boreal caribou. Recovery efforts will therefore require a recognition of the highly dynamic nature of this landscape, the co-occurrence of many ungulate species and their prey, and a recent but well developed access network. Recovery efforts will also require integrated landscape level management strategies (Armstrong et al., 2000; Mosnier et al. 2003), ensuring that sufficient high quality habitat and adequate connectivity within and between clusters of habitat exist and that land use planning (forest harvesting, resource exploration, access development) is done in a way that ultimately allows caribou to move freely throughout their range (for more specific forest management recommendations, see Arsenault & Manseau, 2011).

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Land management strategies for the long-term persistence of boreal woodland caribou in central Saskatchewan

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Abstract: We investigated landscape changes and their potential effects on woodland caribou-boreal ecotype (Rangifer tarandus caribou) within a portion of the Smoothstone-Wapaweka Woodland Caribou Management Unit (SW-WCMU). The SW-WCMU is one of eight areas delineated by the Province of Saskatchewan for potential recovery planning efforts for boreal caribou, and is one of four management units located on the Boreal Plain Ecozone. The Prince Albert Greater Ecosystem (PAGE) study area was selected within the SW-WCMU for intensive study from 2004 – 2008. Studies focused on quantifying a suite of landscape and population parameters. This paper presents a summary of study results to date and recommends land management strategies intended to contribute to the long-term viability of boreal caribou in the central boreal plain ecoregion of Saskatchewan. The PAGE study area has undergone structural changes from an area that historically presented a lesser amount but well connected mature coniferous forest, to a currently larger amount of mature coniferous stands fragmented by a highly developed network of roads and trails. Movement data pointed to highly clustered use of the landscape by small groups of caribou and smaller home ranges when compared to 15 years ago. Calving sites were located within each individual home range in treed peatland and distant from hardwood/mixedwood forest stands, roads and trails access. Adult annual survival rates were low, averaging 73% over the course of the study. In order to ensure a self-sustaining population level, study results clearly point to the need for landscape restoration to reduce the level of anthropogenic disturbances in some key parts of the study area. Key strategies include retention of mature softwood forest interior proximate to local areas of caribou activity, protection of calving habitat, improving structural connectivity, planning disturbances (forest harvesting, fire salvage, resource exploration, access development) in ways to minimize the anthropogenic footprint, and recovery action planning integrated with other land-use planning initiatives.

Key words: boreal woodland caribou; ecological integrity; habitat connectivity; habitat selection; land management strategies; non-invasive genetic sampling; Saskatchewan.

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Introduction

The approach to ecologically-based land management strategies for boreal caribou in Canada are outlined in the national recovery strategy (Environment Canada, 2007). Specifically, each jurisdiction within Canada with boreal caribou agreed that recovery efforts should occur at the range level because caribou populations have broad landscape-level habitat requirements. The range of a given caribou population contains a variety of habitat components that are differentially used, as well as the intervening landscape matrix. Sorensen et al. (2008) demonstrated a strong relationship between population growth rates and the amount of natural and anthropogenic disturbance. They also identified landscape disturbance thresholds above which population growth rate would likely be declining. Numerous documents have been prepared at the provincial/territorial level detailing best management practices, industrial operating guidelines, and landscape management planning processes that will serve as the basis for boreal caribou recovery action planning efforts across the country (Environment Canada, 2007).

Habitat strategies focus on defining the types and amounts of natural and anthropogenic activities that can occur on the landscape to ensure that populations are self-sustaining, or growth rates are either stable or increasing. This entails looking at the habitat quantity, quality and spatial configuration within a range (Environment Canada, 2008), the amount and configuration of selected habitat types in relation to burn areas, younger forests, and industrial development such as linear features which have the potential to reduce caribou population viability and lead to an increased abundance of other cervid species such as white-tailed deer (Odecoileus virginianus), elk (Cervus elaphus) and moose (Alces alces), as well as their associated predators such as grey wolf (Canis lupus) and black bear (Ursus americanus) thereby influencing predator-prey dynamics, resource selection functions, and boreal forest integrity (Cundiff & Gray, 2004; Environment Canada, 2007).

Currently in Saskatchewan there is limited integration between caribou conservation planning and land management processes such as the area specific land-use planning process on sensitive landscapes, project specific environmental assessment, review and screening process (subject to *The Environmental Assessment Act 1980*, best management practices (SMEGAC, 2007), set-back distance recommendations (SKCDC, 2003; Arsenault, 2009), and forest management agreements governing commercial forest harvesting (subject to *The Forest Resources Management Act, 1996*). This is due in part because boreal caribou have not

yet been formally listed in provincial legislation as a species at risk. Saskatchewan Ministry of Environment (2009) is developing natural forest pattern standards and guidelines for the forest industry, which are intended to produce landscapes and harvest areas that look and function like landscapes and disturbance patches created by natural disturbances such as fire. Ultimately, a recovery action plan for the Smoothstone-Wapaweka Woodland Caribou Management Unit (SW-WCMU) must have direct linkage to an effective and integrated decision-making process for land management, subject to the appropriate provincial and federal legislation.

Prince Albert National Park (PANP) land management focuses on maintaining ecological processes and functions within the park, as well as integration of efforts with adjacent land-use activities that potentially impact the park's ecological integrity and native biological diversity. Boreal caribou still reside in the Prince Albert National Park Greater Ecosystem (PAGE), but there is concern that management activities within PANP, and in the adjacent forested landscape surrounding the park, are compromising the ecological integrity of the PAGE landscape and the ability for boreal caribou to persist as a viable component of this portion of the Boreal Plain Ecosystem over the long-term. Consequently, in 2004, the Western and Northern Service Centre of Parks Canada, Prince Albert National Park, Saskatchewan Environment, University of Manitoba Natural Resources Institute, Prince Albert Grand Council, Prince Albert Model Forest, Weyerhaeuser Canada Ltd. and the National Resources DNA Profiling and Forensic Centre at Trent University formed a collaborative research partnership to collect data needed to determine measures of landscape connectivity for appropriate land management planning that would ensure boreal caribou remain a viable component of the PAGE landscape. The PAGE study area is situated within the SW-WCMU. The study focused on obtaining population and landscape parameters. Population parameters were obtained through a collaring program and DNA analysis, and landscape parameters were obtained through mapping and ground truthing activities, which were used to produce decadal landcover maps for the period of 1947-2007, resource selection function models, and predictive habitat maps for both summer and winter. The models were structured around habitat quality attributes (including spatial and temporal anthropogenic and natural disturbance), lichen productivity, optimal foraging strategies, and predator avoidance strategies. Time-series analyses were used to assess landscape changes over time. Spatial graph theory

Table 1. Summary of research projects, primary focus and research lead.

Projects	Authors
Landscape changes and decadal landscape reconstruction.	Arlt, 2009; Arlt & Manseau, 2011
Delineate Saskatchewan caribou range by integrating information sources.	Arsenault, 2003; Saskatchewan Environment, 2007
Telemetry study of movement rate and seasonal habitat use patterns.	Dyke, 2008; Koper & Manseau, 2009
Quantification of range size and distribution changes over the past decade.	Arlt & Manseau, 2011
Changes in landscape connectivity.	Fall et al., 2007; Arlt, 2009; Galpern et al., 2010
Caribou calving site selection.	Dyke, 2008
Population genetic structure and gene flow.	Ball, 2008; Ball et al., 2010
Fecal-DNA based capture-mark – recapture population size estimates.	Hettinga et al., 2010; Hettinga (unpubl. results)

models (Fall & Fall, 2001; O'Brien et al., 2006; Fall et al., 2007; Galpern et al. 2010) were used to assess habitat connectivity and to project future scenarios based on changes to available habitat and landscape connectivity, including the implications to boreal caribou.

A non-invasive DNA sampling technique was furthered by collecting winter caribou fecal samples in the PAGE study area. The purpose of this study was to determine relatedness of caribou populations across broad landscape scales (i.e. landscape connectivity at the SW-WCMU level), to assess genetic diversity at the population level, and to attempt estimation of population size through fecal-DNA based mark-recapture methods (Hettinga *et al.*, 2010) within the PAGE study area.

The PAGE project was multi-faceted, employing multiple methods in related studies with several project objectives. This paper integrates all available information collected in the SW-WCMU, and presents a summary of key results. Table 1 provides a summary of the research projects, primary focus and lead authors. Based on study results, land management strategies are proposed to ensure that sufficient habitat is available for the long-term viability of boreal caribou in central Saskatchewan.

Boreal caribou in Saskatchewan

Arsenault (2003; 2005) compiled a comprehensive geospatial coverage of boreal woodland caribou location data for Saskatchewan dating back to 1950. Data sources included that from Arsenault (1984-present, unpubl. data), Saskatchewan Government histori-

cal survey data and incidental observations, PAGC (2002), Prince Albert National Park (unpubl. historical data), Trottier (1988) and Rettie (1998). The coverage provides context for assessing historical caribou distribution, and was used to delineate local population occurrence (Fig. 1). The information used included documented observations of caribou from aerial surveys, incidental sightings, telemetry data, and local knowledge (Arsenault, 2003; 2005; Saskatchewan Environment, 2007) (Fig. 1). Eight WCMUs (Fig. 1) were then delineated by encompassing clusters of caribou location data and peatland distribution on ecologically similar areas, as defined by Acton et al. (1998). Four of the WCMUs occur on the Boreal Shield Ecozone and four occur on the Boreal Plain Ecozone. Each WCMU represents an ecologically delineated portion of the provincial caribou range for the purpose of monitoring and assessing caribou populations and managing land-use activities impacting them. WCMUs were used as a base for developing directed studies, for recovery and landscape planning in Saskatchewan (Saskatchewan Environment, 2007), and as part of the national recovery strategy development (Environment Canada, 2007).

A local population has been defined as a group of potentially interbreeding individuals at a given locality (Mayr, 1963; Cronin, 2003). A local caribou population in Saskatchewan is defined as a geographically distinct association of potentially interacting and interbreeding individuals occupying a discrete area of suitable habitat, with recurring history of use as demonstrated through the historical location data (Arsenault, 2003; Saskatchewan Environment, 2007) (Fig.1). Environment Canada (2008) describe a local

population as distinguished spatially from areas occupied by other local populations, experience limited exchange of individuals with other local populations such that population dynamics are primarily driven by local factors affecting birth and death rates, rather than immigration and emigration. At the landscape scale, the spatial extent and degree of isolation of local populations affects the WCMU population through the dynamics of its recruitment system, effects on population growth through immigration and emigration, dispersal movement among local populations, influxes from other WCMUs, and distribution pattern on the landscape (Thomas & Kunin, 1999; Steen & Haydon, 2000; Berryman, 2002; Camus & Lima, 2002; Baguette & Stevens, 2003; Schaefer, 2006). As additional work is done in the SW-WCMU and detailed information on population structure becomes available, the current local population boundaries (Fig. 1) may be altered. Environment Canada (2009) has identified potential criteria for subdividing contiguous caribou distribution into local population ranges based on animal movement data and where less than 10% emigration and immigration occurs among groups of animals.

Taiga Shiek Boreal Shield Boreal Plain Carifford Observation Local Populations Prince Albert National Park Prince Albert Greater Ecosystem Ecorones 1. Davy-Athabasca 2 Clearwater 3. Highrook-Key 4. Steephill-Foster Saskatoon 5 Primmose -Cold Lake 6. Smoothstone-Wapaweka 7. Suggi-Amish-Historian 6. Pasquia-Bog

Woodland Caribou Management Units

Fig. 1. PAGE Study Area and woodland caribou management units (WCMU – red), indicating local population ranges and range contraction based on data compiled from 1900 (green), 1950 (purple) to present (red) (source: Arsenault, 2003; Saskatchewan Environment, 2007).

Study area

The PAGE study area (Fig. 2) was 13 381 km² in size, located in the central part of the Boreal Plain Ecoregion within the SW-WCMU (Fig. 1). PANP is central to the PAGE study area and represents a transition zone between the aspen parkland and the boreal forest. This is the only location in Canada where freeranging plains bison occur within their natural range as part of the compliment of endemic cervid species (Arsenault, 2005). Within the SW-WCMU, elk, white-tailed deer and mule deer occur in the highest densities at the interface of the aspen parkland-farmland and the provincial crown forest, diminishing northward. Moose are found at higher densities in proximity to regenerating clear-cuts throughout

the area (Arsenault, 2009). This has implications for the number and distribution of natural predators and for caribou distribution. Within the SW-WCMU, the size and distribution of local caribou populations increases northward.

Caribou populations within the SW-WCMU appear to have fluctuated during the last 60 years. Rock (1992) reported a decline in woodland caribou during the mid-1940s resulting in closure of the hunting season in 1946. This was followed by an increase in the late 1950s attributed to the hunting season closure and a wolf control program (Rock, 1992). Regulated caribou hunting resumed in a portion of the north in 1961, but low harvest levels

resulted in closure of the hunting season in 1987. In PANP, a 1939-1940 census of caribou indicated an overwinter population of 600-700 (Soper, 1951). Banfield later reviewed Soper's data and down-graded the estimate to 200 animals, and estimated the 1951 population to be 50 (Rock, 1992). Over the next 25 years, survey efforts reported 24 caribou in 1970-71, 37 in 1977, and 26 in 1978 (Burles *et al.*, 1978). Very few sightings of caribou have been reported in the park since, despite significant survey and collaring efforts (Arlt & Manseau, 2011).

Wildfires have occurred throughout much of the study area to varying degrees and sizes over recent decades along with fire suppression. Recent burns have occurred in the Bittern Lake area east of PANP and in the northeast section of PANP. Access has dramatically increased in relation to development and forestry, with resultant increases in vehicular and off-road traffic for recreation (snow mobiles. all-terrain vehicle use, cross-country skiing, hiking, boating, cottages, etc.), hunting, fishing, trapping, resource extraction, and travel among communities. Weyakwin, Ramsay Bay on Weyakwin Lake, Timber Bay, reserve

communities of Montreal Lake First Nation and Lac la Ronge Indian Band (Bittern Lake), Waskesiu and seasonal resorts east of PANP are settlements within the PAGE study area. Dore Lake and Sled Lake are additional small settlements adjacent to the PAGE study area. There is significant variation across the SW-WCMU in terms of habitat mosaic, anthropogenic footprint, and species distribution. Therefore, application of landscape management strategies will vary spatially depending on the characteristics of the particular area.

Results

Landscape changes

A land cover map consisting of 20 vegetation classes was developed for the PAGE study area using forest resource inventory data obtained from PANP, Weyerhaeuser Canada Ltd. and the Saskatchewan Government. Using this land cover map, the PAGE landscape was reconstructed for each decade from 1946 – 2006 to document changes in land cover

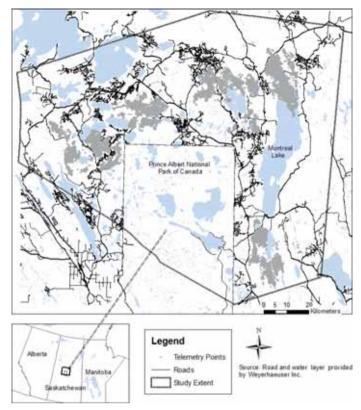


Fig. 2. Map of the Prince Albert Greater Ecosystem highlighting anthropogenic features and telemetry data from 28 female caribou between 2004-2008.

types, the development of linear features, the occurrence of logging activities and wildfire (Arlt, 2009; Arlt & Manseau, 2011). Transition probabilities analyses showed that the PAGE landscape was historically characterized by a high wildfire frequency with a greater proportion of younger aged coniferous stands and marginal access development for forest harvesting activities. The current PAGE landscape has larger proportions of mature coniferous stands because of fire suppression and ecological succession. Many of these stands have been modified outside of PANP primarily by forest harvesting activities, wildfires, wildfire suppression with salvage logging, and linear development (roads, trails, power corridors). The landscape has a high density of linear features with about 20% of the area logged or comprised of hardwood dominated forest stands (Arlt, 2009; Arlt & Manseau, 2011). The cumulative area logged in the PAGE increased from essentially nil between 1956 and 1976 to 58 211 ha (4.4 ha/km²) by 2006. During this same period cumulative permanent road/trail development within the PAGE increased from about

342 km in 1956 to almost 4730 km (0.35 km/km²) by 2006 (Arlt & Manseau, 2011). The PAGE area was assessed using the landscape disturbance threshold equation presented in Sorensen et al. (2008), which calculates population rate of change (λ) in relation to the amount of natural and human disturbance on the landscape. We obtained a λ of 1.06 when the amount of disturbance was calculated as a proportion of the entire PAGE study area, 1.03 when based on a study area excluding PANP and 1.17 when based on the extent of caribou home ranges. This suggests that the PAGE population should be growing, but our study results do not support this.

Caribou distribution

Over the course of the PAGE study, a total of 28 adult female caribou were fitted with #4400 GPS telemetry collars (Lotek Wireless Inc., Newmarket, Ontario) to monitor survival rates, movement and landscape use patterns at fine temporal and spatial scales (3 hr relocation frequency). Flights were conducted periodically to upload location data, to adjust collar data collection schedules, and to monitor mortality. Collars from dead caribou and collars nearing the end of their battery life were retrieved and refurbished annually, and redeployed to attempt to maintain a minimum of 15 collars on females across the PAGE study area. The telemetry data was used to assess caribou distribution, movement rate and seasonal habitat use patterns (Dyke, 2008; Koper & Manseau, 2009; Arlt & Manseau, 2011). Lastly, PAGE telemetry data was compared to that collected in an overlapping area by Rettie (1998) and Rettie & Messier (1998; 2001) in 1992-1995, to quantify changes in range size and distribution over the last decade.

In a previous study within SW-WCMU, Rettie & Messier (1998) reported a spatially disjunct distribution which is consistent with range contraction and local boreal caribou occupancy data reported by Arsenault (2003) and with current telemetry data. Current telemetry data was used to determine minimum convex polygons (MCP) of individual ranges. The analysis revealed that the PAGE animals are sedentary, with individual summer and winter ranges overlapping, with range occupancy being comparable between the two studies, but with individual home range sizes being significantly smaller (t = -2.559, P = 0.013, df = 52) for the 2004-2008 telemetry data (MCP: \bar{x} = 221 km², s.d. = 145, n = 23), compared to the 1992-1995 telemetry data (MCP: $\bar{x} = 441 \text{ km}^2$, s.d. = 393, n = 31).

Telemetry and genetic results from the PAGE study also confirmed that the boreal caribou population has a fragmented distribution with limited use of PANP. Multi-year GPS telemetry data (2004-2008) for the PAGE study demonstrated that animals have a clustered distribution (Fig. 2), small annual home ranges ($\bar{x} = 221 \text{ km}^2$, s.d. = 145), low hourly movement rates ($\bar{x} = 122 \text{ m/hr}$, s.d. = 249) when compared to other caribou studies, no detected movement between groups, and with calving sites located throughout the landscape within each individual home range. This contrasts with other caribou studies where individual home ranges overlap and calving sites are clustered (Dyke, 2008).

Caribou calving sites

Dyke (2008) used fine scale telemetry movement data from the PAGE study to look at the spatial and temporal characteristics of animal movement during the calving period. Dyke (2008) identified calving caribou if they presented a reduction of adult cow movement rates to <50 m/hr for a minimum of a week, which corresponded to a highly defined location during the calving period (treated as a minimal number of animals calving). Dyke (2008) was able to determine a 29 April - 7 June calving season for PAGE caribou with almost 75% of calving completed by mid-May, which was similar to that reported elsewhere (Hirai, 1998; Schaefer et al., 2000; Lantin et al., 2003). Timing of calving is highly dependant on the presence of suitable forage species to ensure sufficient milk production (Rutberg, 1987; Post et al., 2003; Gustine et al., 2006). Dyke (2008) noted the occurrence of late calving could be attributed to fertilization in second estrous.

Animals that presented the calving behavior showed a high degree of spatial separation from conspecifics, which is consistent with that reported elsewhere (Bergerud et al., 1984; Gustine et al., 2006). The spatial clustering of areas used for pre-calving, calving and post-calving in the PAGE area was different from other caribou studies (Dyke, 2008), suggesting that calving site selection may be influenced by disturbances in the surrounding area (Gustine et al., 2006; Dyke, 2008) and predation risk (Post et al., 2003).

Boreal caribou generally show strong selection for black spruce stands within large treed peatlands (Hirai, 1998; Rettie & Messier, 2001; Lantin *et al.*, 2003), which is supported by Dyke's (2008) results. Calving females in the PAGE area demonstrated strong selection for treed peatlands, (particularly those further from mixed hardwood stands), and avoidance of mature jackpine stands, mixed hardwood stands, and roads during the calving period and in the spring – summer seasonal range (Dyke, 2008). However, when habitat was treated as a cat-

egorical variable in the analysis, both treed peatland and jackpine were selected. Habitat selection and avoidance patterns for PAGE caribou were similar to that reported in other boreal caribou populations (Ferguson *et al.*, 1988; Johnson *et al.*, 2003; Mahoney & Virgil, 2003; Brown *et al.*, 2007; Dyke, 2008), and for an earlier study of the PAGE area (Rettie & Messier, 2000). Dyke (2008) attributed the weaker selection of jackpine by PAGE caribou to the highly fragmented nature of jackpine stands and their proximity to hardwood mixedwood stands, young stands and roads.

Genetic structure and gene flow

Genetic diversity allows species to adapt to changing environmental conditions (Reed *et al.*, 1986). Isolation increases the probability of local extinction, reduction of population size, reduction in gene flow, and ultimately a decline in genetic health (loss of rare alleles, reduced heterozygosity, and inbreeding) (Reed *et al.*, 1986; Loew, 2000), which may affect the recovery of small meta-populations (Lacy, 1997; Lande, 2002; Arsenault, 2003).

The inbreeding coefficient (F_{is} value) ranges between -1.000 (outbreeding / heterozygote excess) and 1.000 (inbreeding / heterozygote deficiency). Based on a sample size of 78, the F_{is} was calculated to be 0.061 with an expected heterozygosity ($F_{st EXP}$) of 0.76±0.02 and observed heterozygosity (F_{st OBS}) of 0.71±0.02 for the PAGE population (Ball, 2008; Ball et al., 2010). The genetic diversity of PAGE caribou within the SW-WCMU was similar to that reported in other populations (Côté et al., 2002; McLoughlin et al., 2004), with no apparent inbreeding or outbreeding issues. Isolation can result in disparate levels of genetic diversity that put populations at risk of local extinction if movement of adaptive alleles is not maintained by gene flow (Reed et al., 1986; Lacy, 1997; Ray, 2001; Lande, 2002; McLoughlin et al., 2004).

Population size and mortality rate

The minimum PAGE population based on identification of unique genotypes was 93 caribou, with preliminary results pointing to an estimate of 128 (95% 116, 145) animals (Hettinga, unpubl. results, Hettinga *et al.*, 2010). This yields a population density of 0.009 caribou/km² when calculated over the entire PAGE study area, and 0.11 caribou/km² when based on MCPs of annual home ranges.

Even minor increases in adult and/or calf mortality can cause a trend in population decline (Arsenault, 2003). This is because boreal caribou have a low reproductive rate (twinning is rare; cows commonly do not produce a calf annually) and they breed at relatively older ages compared to other cervids (McDonald & Martell, 1981; Godkin, 1986; Lavigueur & Barrette, 1992). Average annual adult survival rates of boreal caribou have been reported by Rettie & Messier (1998) in Saskatchewan (84%), McLoughlin et al. (2003) in northeast Alberta (83-93%), Brown et al. (2000) in Manitoba (90%), with mortality most common in summer (Rettie & Messier, 1998). Annual adult survival rates of collared PAGE caribou was 71% (2005, n=17), 71% (2006, n=17), 83% (2007, n=12), and 69% (2008, n=13), with a mean of 73% for all years pooled. The majority of mortalities occurred in summer, in June and August. Mortality features would have been more identifiable if the collars were retrieved immediately following receipt of the mortality signal. The high adult mortality rate suggests the population may be declining.

Calf survival to one year is usually low and varies temporally and spatially (Fuller & Keith, 1981; Edmunds, 1988; Adams et al., 1995). Typically only 30-50% of calves survive their first year of life (Thomas & Gray, 2001). We were not able to estimate calf survival. A non-spatial population viability analysis conducted by Arsenault (2007, unpubl. data) for Saskatchewan indicated a minimum recruitment of 31.4 calves/100 adult females (yearlings excluded) was required for a stable population based on mean annual adult female survival of 85% (Saskatchewan Environment, 2007). An independent critical habitat science review led by Environment Canada performed a similar analysis, concluding that a minimum recruitment rate of 28.9 calves/100 females was required (Environment Canada, 2008).

Discussion

Ecological considerations

The boreal forest landscape is naturally dynamic with specific habitat components having a functional role at different spatial and temporal scales which are necessary to assure persistence of local boreal caribou populations (Racey & Arsenault, 2007). In most impacted landscapes, the number, location and size of habitat patches, as well as the demographic parameters of the wildlife populations inhabiting them change temporally and spatially (Schaffer, 1981; Lande, 1988; Akcakaya, 2001; Mitchell, 2005). The influences of natural and anthropogenic landscape alteration and disturbance on caribou range use and occupancy includes documented range shifts following wildfire (Schaefer & Pruit, 1991), logging (Rettie & Messier, 1998; Smith et al., 2000; Lander, 2006; Schaefer & Mahoney, 2007; Vors et al., 2007), and industrial development (Dyer et al., 2001; Nellemann et al., 2003; Weir et al., 2007), barrier and displacement effects of linear features (Rettie & Messier, 1998; Dyer et al., 2002; Schindler et al., 2007), increased predation risk (James, 1999; James & Stuart-Smith, 2000; James et al., 2004), and potentially increased energetic costs (Bradshaw et al., 1998). The degree of response to disturbance depends on the type, magnitude, frequency, and duration of the disturbance (Bradshaw et al., 1998; Arsenault, 2009). The impact of non-lethal human disturbance on the behaviour and reproductive success of animals can have a similar trade-off to predation, resulting in avoidance of perceived risk and other fitness enhancing activities such as feeding, parental care, or mating (Frid & Dill, 2002).

Assessing habitat use in relation to availability determines habitat selection (Bradshaw et al., 1995; Manly et al., 2002; Arsenault, 2003; Koper & Manseau, 2009). Habitat selection occurs at several scales, is variable, and reflects the strategies used by an animal to meet habitat requirements through selection of different environmental features at each level of spatial and temporal scale to optimize biological fitness (Johnson, 1980; Orians & Wittenberger, 1991; Holling, 1992; Bradshaw et al., 1995; Rettie & Messier, 2000; Arsenault, 2003; Johnson et al., 2004; Dussault et al., 2005; Lander, 2006; Dyke, 2008). Distribution and abundance of species-at-risk are adversely affected by changes in the land-use activities that cause habitat loss, habitat fragmentation, and other disturbances (Akcakaya, 2001). Small isolated local populations are subject to sudden extirpation by a stochastic event, or slow extinction due to accumulation of deleterious alleles through inbreeding (Reed et al., 1986). Local extinctions of fragmented populations are common; therefore, recolonization of local extinctions is critical for regional survival of fragmented populations (Fahrig & Merriam, 2002).

Understanding landscape connectivity in terms of habitat configuration and intervening covertypes in determining the degree to which a landscape facilitate or impedes movement among habitat patches is critical for determining ecological integrity, for effective landscape management, and for conservation of species-at-risk (Taylor *et al.*, 1993; Foreman, 1995; Tischendorf & Fahrig, 2000; Fahrig & Merriam, 2002; O'Brien *et al.*, 2006). An animal's ability to utilize a resource patch is dependent on its ability to get there. O'Brien *et al.* (2006) have shown the importance of landscape connectivity for woodland caribou and a strong selection for larger clusters of high quality habitat patches over the selection of a given high quality habitat patch. Habitat fragmenta-

tion isolates habitat patches and reduces patch size, thereby increasing the vulnerability of local populations to environmental and demographic threats (Shaffer, 1981; Lande, 1988). Boreal caribou are wide-ranging with natural occurrence at low population densities typically between 0.03 - 0.05 caribou/ km², and have protracted time lag responses to habitat changes (Tilman et al., 1994; Arsenault, 2003; Schaeffer, 2003; Environment Canada, 2007; Vors et al., 2007; Wilkinson, 2008). Therefore, studies that focus on landscape pattern analysis, as well as structural and functional habitat connectivity, are necessary to determine impact development thresholds, critical habitat, and movement corridors (Manseau et al., 2002; O'Brien et al., 2006; Fall et al., 2007; Racev & Arsenault, 2007; Galpern et al., 2010). Boreal caribou population declines are characterized by a loss of landscape connectivity accompanied by declines in population size and constrictions in local range occupancy, followed by a period of persistence of isolated populations exhibiting a slow decline culminating in local extirpation and range recession (Schaefer, 2003; Wilkinson, 2008).

Predation is the main factor limiting boreal caribou populations. Caribou have historically coexisted with wolves and other predators for thousands of years in a boreal forest ecosystem driven by natural disturbances such as wildfire. Boreal caribou sparsely distribute themselves and spatially separate from other prey species (commonly moose) into areas composed of habitats with very low densities of other prey species, as a predation-limiting strategy (Bergerud *et al.*, 1984; Bergerud, 1992; Seip, 1992).

In the Boreal Plain Ecozone caribou commonly select upland mature and old-growth jackpine and lichen-rich treed peatland complexes interspersed in mature and old growth black spruce forest (Brown et al., 2000b; Rettie & Messier, 2000; Schneider et al., 2000; Arsenault, 2003; Lander, 2006; O'Brien et al., 2006; Dyke, 2008; Koper & Manseau, 2009). These are conifer dominated habitats (>60 yrs old) that generally are not selected by other prey species because they lack sufficient quality and quantity of browse, and therefore typically have lower associated predation risk. Caribou tend to avoid early-succession hardwood-dominated covertypes with high quantities of regenerating browse that are preferred by other prey species and have a higher associated predation risk. However, anthropogenic disturbances tend to occur in mature and old-growth upland forest habitat, including those adjacent to treed peatlands. This has the effect of increasing the population density of other prey species as well as predator numbers and predator access efficiency, which compromises the

functional value of treed peatlands and upland jackpine as refuges from excessive predation by increasing caribou-wolf encounter rates (mortality risk) (James, 1999; James et al. 2004). Messier (1995a) calculated a minimum density of 0.20 moose/km² as required to support a wolf population. The long-term mean (1979-2006) winter moose population density for the PAGE area was 0.15/km², with a low of 0.08/km² in 2005 (Arsenault, 2000; Arsenault, unpubl. data). Winter elk population densities tend to average about 0.28/km² in core range, with herds occurring in a clumped distribution along the forest fringe at the southern boundary of the PAGE area and PANP, in regenerating cut-overs in the Clark Lakes area northwest of the Park, and in the Montreal Lake area along the east side of the Park (Arsenault, 2008; Arsenault, unpublished data). White-tailed deer tend to concentrate in highest densities (2.10 - 2.80/km²) along the forest fringe and occur at lower densities (0.69 - 1.40)km²) northward in suitable habitat (which is limited) with an overall long-term (1984-2003) mean density of 1.18/km2 for the PAGE area (Arsenault, 2005). Mule deer occur within the PAGE area, but in very low densities and in a sporadic occurrence (Arsenault, 2005). Prior to calving, pregnant female caribou disperse from conspecifics to minimize predation risk to their newborn calf. The associated loss of habitat connectivity has the potential to limit the ability for caribou to disperse to safer refuges from predators.

Conservation of boreal woodland caribou requires land management strategies that not only maintain caribou habitat within the landscape mosaic, but also maintains a landscape pattern and structure that ensures structural and functional connectivity among habitats to facilitate movement of caribou throughout the landscape. Henein & Meriam (1990) found that corridors connecting habitat patches influences metapopulation dynamics and persistence based on corridor quality but not quantity. They concluded that meta-populations with habitat patches connected by high quality corridors have a larger population at equilibrium than those connected by >1 low quality corridors and that addition of a habitat patch connected by low quality corridors has a negative effect on overall meta-population size. They also concluded that meta-populations in isolated patches connected by low quality corridors were the most vulnerable to local extinction, but any connection between isolated patches was better than no connection with respect to persistence and population size at equilibrium. The degree to which the intervening landscape between habitat patches facilitates or impedes movement corresponds to the connectivity of the landscape (Taylor et al., 1993; O'Brien et al. 2006; Fall et al., 2007, Galpern et al., 2010). Landscape connectivity influences the ability for caribou to access habitat, avoid predators, move between core portions of their range and between ranges, and contribute to gene flow (Manseau *et al.*, 2008).

The conclusion reached from the PAGE vegetation analysis is that 50 years ago the forest was younger, presenting less, and widely distributed older coniferous stands across the landscape (Arlt & Manseau, 2011). Their results suggest an aging landscape in the present, with a larger amount of old coniferous stands attributed to changes in fire incidence and fire management strategies. But the functional value of the older forest is likely reduced by its proximity to roads, cut blocks and hardwood-mixedwood forest stands (Arlt & Manseau, 2011). The fur harvest data for bears and wolves is inadequate to assess predator population trend in the PAGE because the data lacks information on trapper effort. Licensed harvest of moose and elk in the PAGE area has remained relatively stable from the mid 1980s through mid 2000s (Arsenault, 2000; Arsenault, 2005; Arsenault, 2008). However, the licensed harvest of white-tailed deer increased by almost 200% over the same period, particularly near the southern portions of the PAGE along the forest fringe (Arsenault, unpubl. data).

The effects of diminished habitat connectivity of the PAGE for caribou are potentially manifested through:

- 1. Direct habitat loss from landscape disturbances.
- 2. Functional habitat loss because of displacement, avoidance and barrier effects of disturbances and anthropogenic features.
- Alteration of predator-prey dynamics as a consequence of increases in other cervid species attracted to recent cut-overs and burns, which supports a larger predator base.
- 4. Increased mortality risk to caribou because of increased predator densities, ease of predator access and search efficiency to habitat patches proximate to local caribou populations because of the extensive road/trail network.
- Fragmentation of the PAGE caribou into small, sedentary, highly clustered local populations with limited movement among habitat patches throughout the landscape. Effective habitat connectivity is critical for the long-term persistence of caribou.

Recommended land management strategies

The data used to develop the following land management strategies are by no means perfect, resulting in landscape planning and management within an environment of uncertainty. In some situations the

recommended strategies would apply to local population ranges (including specific habitat types) and in others they would apply at a broader scale (WCMU and beyond). Regardless, application of the strategies should be conducted within an adaptive management framework accompanied by ecological performance measures for monitoring and assessing their effectiveness against established targets and objectives.

Declines in caribou populations and range occupancy are likely to continue in the PAGE area because of the high degree of habitat fragmentation, loss of habitat connectivity, alteration of adjacent forest stands leading to increased numbers of other prey species, and associated increased predation risk. Wolf density for the PAGE area based on a linear regression model using the relationship of wolf density and ungulate biomass (per Keith, 1983; Messier, 1995b; Mech & Boitani, 2003), yields a density of 0.01-0.02 wolves/km². Urton (2004) estimated the wolf density in the PAGE area to be about 0.02/km². There are inadequate data to estimate bear populations for the PAGE area.

Landscapes with fragmented caribou populations or clustered distributions require spatially targeted action to protect and manage for preferred habitat (including movement corridors). A common resolution to problems associated with human disturbance impacts on the landscape is to separate human activities from centers of sensitive wildlife activity by use of buffer zones or set-back distances within which human activity is restricted to minimize impacts (Arsenault, 2009). Refugia from human encroachment and landscape disturbance may be vital to retaining range occupancy of PAGE caribou (Schaeffer, 2003; Vors et al., 2007). Effective protection may be possible through establishment of protected areas, landscape planning and management of the amount and type of human developments and natural disturbances to ensure ecological functionality of the boreal landscape. Natural disturbances are integral to molding the structure and function of landscapes, ecosystems and species (Landres et al., 1999; Saskatchewan Ministry of Environment, 2009). Natural variability is defined as spatial and temporal variation in the ecological conditions that are relatively unaffected by humans within a defined geographical area and period of time appropriate to an expressed goal (Landres et al., 1999, Oliver et al., 2007). Failure to consider the occurrence and biological fitness of boreal caribou could result in incorrect assessments of critical habitat importance and ecological integrity to disturbance-generated landscape mosaics, leading to ineffective land management strategies influencing set-back distances or attempts by industry at natural

disturbance emulation (Landres *et al.*, 1999; Laliberte and Ripple, 2004; Arsenault, 2009). Caribou conservation requires land management strategies that maintain caribou habitat, favor habitat connectivity, and supports sustainable caribou populations (O'Brien *et al.*, 2006).

The following land management strategies are recommended as a contribution to the conservation of boreal caribou populations and range over the long term in the Boreal Plain Ecosystem:

- 1. Retain large softwood (black spruce, jackpine, larch tamarack) habitat patches (>60 yrs old), and a large proportion of mature and old growth forest interior within local population ranges. Caribou are at greater predation risk if they have a relatively small proportion of mature and old forest in their individual home ranges and the collective local population range (Wittmer et al., 2007). Larger habitat patches that support larger local populations present a better opportunity to ensure long-term population viability than do small patches with small, highly fragmented, local populations (Barryman, 2002; Baguette & Stevens, 2003).
- 2. Habitat selection (e.g. calving site) occurs at multiple spatial scales, therefore in highly fragmented landscapes it is important to maintain buffer habitat (e.g. lichen-rich conifer stands >60 yrs old) surrounding important habitat patches (e.g. important peatland complexes) and sensitive areas to discourage increases of other prey species in response to landscape alterations, thus minimizing predation risk. Old growth forest associated with treed peatlands within local population ranges that have been significantly impacted by forest harvesting should be highest priority for extended rotation and wildfire suppression. At low population densities, caribou have lower survival probabilities in areas with greater amounts of young hardwood and mixedwood forest (Wittmer et al., 2007). Therefore, the spatial pattern of buffering habitat patches along the margins of preferred caribou habitat within and among local caribou population ranges is important to consider when anthropogenic disturbance is proposed.
- 3. Protect habitat selected for the calving period, particularly treed peatlands within local population ranges, to increase likelihood of calf survival and aid in recovery. There should be no access development or peat and forest harvesting in important peatlands or treed peatland complexes within local population ranges such as those in the Montreal Lake portion of the PAGE area.

- 4. Identify, prioritize, and protect high quality habitat and movement corridors linking habitat patches and clusters using telemetry data and habitat structural connectivity analysis (O'Brien et al., 2006; Fall et al., 2007) to ensure a landscape mosaic that is functional for caribou. Prioritization of corridors for protection and/or restoration should consider caribou distribution, local population range occupancy, movement patterns, size of available corridors, disturbance magnitude, and population viability. Caribou habitat is characterized as high-quality habitat patches embedded within a matrix that facilitates foraging, predator avoidance and protection from human disturbances (Rettie & Messier, 2000; Smith et al., 2000; James et al., 2004; O'Brien et al., 2006). The least-cost paths connecting core habitat clusters can point to movement corridors (Taylor et al., 1993; O'Brien et al., 2006). Landscape conservation and restoration goals should concentrate effort on maintaining high quality linkages between clusters of habitat patches within and among local populations, and ensure that the required connectivity is effectively buffered from anthropogenic disturbance. The connectivity between the remnant habitat patches within and among local populations is essential to animal movement, dispersal ability, gene flow, and ultimately the long-term persistence of local populations, particularly if the WCMU population is small and/or exists at low density (Arsenault, 2003). Recolonization of abandoned habitat is critical for regional survival of fragmented populations (Fahrig & Merriam, 2002). Contiguous habitat promotes more movement of species and links among local populations than fragmented habitat. The greater the distance between ranges, the larger the width of corridor required to facilitate movement between local populations or regional populations.
- 5. Fire salvage should not occur in or adjacent to treed peatlands or peatland complexes within local caribou population ranges. This will help to minimize creation of, or improve, access for predators, to minimize disturbance of impacted habitat, and to avoid creation of movement barriers. This is an important consideration for the Bittern Lake portion of the PAGE area.
- 6. Ecosystem-level disturbance such as developments and resource extraction activities should be planned in a way to minimize habitat fragmentation and/or avoid creation of barriers to movement within and among critical habitats. The scientific literature documents displace-

- ment of caribou from anthropogenic disturbance as far as 1000 m to 1200 m depending on the type, duration, extent, frequency and magnitude (Smith *et al.*, 2000; Dyer *et al.*, 2001). Therefore, identification of critical habitat should occur at the local population scale within each WCMU to ensure it is well distributed and connected at the local population scale and at the WCMU scale. This would ensure the long-term persistence of caribou within each WCMU. It is also important to ensure that industry activity set-back distances are sufficient to effectively buffer local caribou populations and sensitive locations from the disturbance.
- Forest planning and harvest operations within and among local caribou population ranges should ensure that caribou are able to freely move across the forest landscape through time. For example, if caribou habitat is to be logged, it is better to log a few larger patches that more closely emulate the pattern of wildfire. This strategy should minimize the response of other prey species populations to increase, and result in a cut-block that more closely resembles lichen-rich caribou habitat once the cut-block has matured into older aged stands (>60 years old), minimize access development that might improve predator efficiency, and retain higher quality caribou movement corridors through reduced edge effects and fragmentation that would result from multiple smaller cut-blocks.
- 8. Minimize disturbance around sensitive caribou habitat by concentrating disturbances spatially and temporally. This will help minimize the cumulative effects of disturbance in occupied caribou range. Constraints on anthropogenic disturbance should depend on the level of natural disturbance, degree of connectivity within and among core use areas, population viability, and factors limiting to caribou in the planning area. This is an important consideration in the Clarke Lakes portion of the PAGE area which has been significantly impacted by forest harvesting.
- 9. Landscape planning should occur at a WCMU (or comparable) scale over a natural fire cycle. The historical fire cycle for the Boreal Plain Ecozone in Saskatchewan is estimated at 50 150 years (Weir *et al.*, 2000; Li *et al.*, 2005; Saskatchewan Ministry of Environment, 2009).
- 10. Manage fire suppression, forest harvesting and silviculture activities to emulate an appropriate natural disturbance regime that will mimic natural forest patterns to the greatest extent possible for forest habitat renewal. Saskatchewan Ministry

- of Environment (2009) has developed draft natural forest pattern standards and guidelines for the forest industry intended to produce landscapes and harvest areas that look and function like landscapes and disturbance patches created by natural disturbances such as fire.
- 11. Use reclamation prescriptions and silviculture practices within impacted local population ranges that encourage rapid re-establishment of caribou habitat. Such prescriptions and practices will act by decreasing shrub response and early successional hardwoods, and speeding succession to a structural stage preferred by caribou. This should be applied to the Clarke Lakes area and cut-over areas along the north side of PANP.
- 12. Access management for all industries should include reclaiming seasonal roads and trails that are no longer needed, through reforestation, as well as access restrictions and limitations on new access development in proximity (within 1 km) to high quality caribou habitat and movement corridors within and among local population ranges throughout the PAGE area and larger SW-WCMU. This would aid in reducing human disturbance, predation risk, functional habitat loss through displacement caused by disturbance, potential barriers to movement, intrusiveness of the linear feature, as well as limiting further landscape fragmentation.
- 13. Access planning should occur at large spatial (WCMU scale) and broad temporal scales with development focused on shared use. This will help to minimize excessive or unnecessary access development and reclamation when no longer required. Roads should avoid high caribou use areas and clusters of selected habitat types such as jackpine and treed peatland complexes. Use of winter roads in caribou habitat is desirable. because of their short duration of use and minimal footprint. The short-term disturbance during a winter season is preferable to the long-term effect of a permanent road. Predator efficiency is reduced by limiting their line of sight to less than 200m, which is further supported by ungulate selective use of forest openings to forage within 100-200 m of cover (Hamilton & Drysdale, 1975; Rost & Bailey, 1979; Thomas et al., 1979; Dunford et al., 2003; Arsenault, 2009). Linear developments should ensure reduced line-of-sight (<200 m) where it occurs within local population ranges to provide adequate visual and winter escape cover (wildlife blinds), reduce predation risk by minimizing line-of-sight for predators, to and mitigate potential barriers for movement.

- 14. Within local population ranges, maintain appropriate community dynamics, species interactions and functional diversity such as spatial separation from other cervid species and predators. Mortality risk to PAGE caribou from predation could be reduced in areas requiring habitat restoration by aggressively hunting other prey to impede predator numbers, and concurrently allowing post-disturbance vegetative recovery to a state less favorable to other prey species.
- 15. Periodically monitor genetic status within and among WCMU populations. This will help to provide early assessment of impacts on ecological integrity from the cumulative effects of anthropogenic and natural disturbance, vegetation change, and landscape restoration efforts.
- 16. Quantify the current level of human disturbance within a WCMU and use this to stratify into high, medium and low levels to determine risk, to prioritize areas of management concern, and to plan for suitable future caribou habitat.
- 17. Assess WCMUs in relation to development thresholds. This could include quantifying land-scape level development impact thresholds such as linear corridor densities, effective set-back distances to buffer core caribou habitats from various disturbance types, and effective habitat connectivity levels that support caribou range occupancy.

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Use of island and mainland shorelines by woodland caribou during the nursery period in two northern Ontario parks

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Abstract: Predation is considered a primary limiting factor of woodland caribou (Rangifer tarandus caribou) populations across North America. Caribou are especially vulnerable to predation during their first few weeks of life and have evolved space-use strategies to reduce predation risk through habitat selection during the critical calving and nursery period. We assessed landscape-scale physical characteristics and landcover types associated with caribou nursery sites in Wabakimi and Woodland Caribou Provincial Parks in northern Ontario to better understand nursery site selection in relatively undisturbed landscapes. Although free from industrial activity, these protected areas may subject caribou to human recreational disturbance, so our secondary objective was to evaluate female caribou nursery site selection relative to human recreational activities. We determined that parturient caribou selected landscape characteristics at multiple spatial scales that may reduce predation risk during the calving and nursery period. Generally, female caribou in both parks selected larger lakes with larger than average sized islands configured within shorter than average distances to other islands or landforms that might facilitate escape from predators. The majority of caribou nursery areas in both parks occurred on islands rather than the mainland shoreline of lakes that were surveyed. The nearest landform for escape from these nursery sites on islands was typically another island, and most often 2-3 islands, suggesting parturient caribou may choose islands clustered together as part of their escape strategy. In Woodland Caribou Provincial Park, caribou nursery sites occurred more often in coniferous landcover than expected from availability, while in Wabakimi Provincial Park caribou used sparse, mixed and coniferous forests for nursery activity. Caribou cow-calf pairs typically used areas for nursery activity that were 9.1 km (± 1.0 km, range 2.3-20.6 km) in Wabakimi Provincial Park and 10.2 km (± 0.7 km, range 0.7-32.6 km) in Woodland Caribou Provincial Park from any human recreational disturbance. These landscape-scale physical characteristics and landcover types associated with caribou nursery sites may be used to predict locations of potential caribou nursery areas both outside and within protected areas for the provision of adequate protection and to ensure the persistence of this valued species.

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

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Introduction

Woodland caribou (Rangifer tarandus caribou) range in Ontario has steadily receded north since the late 1800s (Racey & Armstrong, 2000). Habitat loss through anthropogenic disturbance is frequently cited as the primary cause of this recession (Schaefer, 2003; Vors et al., 2007), with predation often considered the main proximate factor of population limitation for woodland caribou in Ontario and across North America (Bergerud, 1974; Seip, 1992; Ouellet et al., 1996; Stuart-Smith et al., 1997; Rettie & Messier, 1998). Caribou are particularly vulnerable to predation by wolves (Canis lupus) and black bears (Ursus americanus) in their first few weeks of life (Bergerud & Page, 1987; Ballard, 1994).

Caribou have evolved space-use strategies to reduce predation risk through habitat selection, particularly during the critical calving and nursing stages when calves are too young to outrun predators (Bergerud et al., 1984; Bergerud & Page, 1987; Bergerud et al., 1990; Fitzgibbon, 1990; Rettie & Messier, 2000; Rettie & Messier, 2001). If islands and shorelines are available, female caribou disperse to these relatively safe habitats to calve and nurse (Bergerud, 1985). Female woodland caribou also spatially separate themselves from each other and other ungulates, such as moose, that provide alternate prey for wolves and bears, by using lakeshores and islands (Bergerud, 1985; Cumming & Beange, 1987) or bog complexes (Valkenburg et al., 1996; Stuart-Smith et al., 1997) for calving. Thus, parturient caribou appear to select habitat at different spatial scales to meet their requirements during the calving and post-partum period: at a broad scale they may select landscapes with abundant lakes or bog complexes and within these landscapes they may select shorelines and islands to reduce predation risk.

Female woodland caribou also exhibit fidelity for specific calving and summer ranges that may reduce predation risk to their calves (Brown *et al.*, 1986; Schaefer *et al.*, 2000), but disturbances caused by landscape exploitation (e.g., forestry and mining activities) and human recreational activities (e.g., outpost camps, shore lunch areas, camping) may prevent female caribou from returning to previously used sites. As a result, female caribou may be forced to use less suitable habitats, which can lead to greater predation risk and reduced population viability.

We assessed landscape-scale physical characteristics and landcover types associated with caribou nursery sites in two large protected areas, not directly disturbed by human industrial activity (i.e., forestry or mining), to better understand female caribou nursery site selection at different spatial scales in relatively undisturbed landscapes. Although free from industrial activity, these protected areas may subject caribou to human recreational disturbance, so our secondary objective was to evaluate female caribou nursery site selection relative to human recreational activities.

These analyses provide baseline information that may be used to predict locations of potential caribou nursery sites both within and outside protected area boundaries across northern Ontario. Critical landscape-scale characteristics selected by caribou at nursery sites were hypothesized to primarily reflect predator avoidance strategies, as well as avoidance of human disturbance, and thus appropriate protection of sites with these attributes in future management policies and legislation would likely have the greatest positive impact on population persistence.

Study areas

Wahakimi Provincial Park

Wabakimi Provincial Park is located in northern Ontario about 200 km north of Thunder Bay (Fig. 1). The original boundary of the park was established in 1983 at 155 000 ha, but was greatly expanded in 1997 to roughly 892 000 ha (Duinker et al., 1998). Most of the park has not been harvested, with the exception of a relatively small area in the south that was harvested before the land became part of the park. The average July and January temperatures in Wabakimi Provincial Park are 16 °C and -17 to -20 °C, respectively (Chapman & Thomas, 1968). The forests of the park are typical of the boreal forest, being dominated by white spruce (Picea glauca), black spruce (Picea mariana), jack pine (Pinus banksiana), balsam fir (Abies balsamea), trembling aspen (Populus tremuloides), and white birch (Betula papyrifera) (Harris & Foster, 2005). Mosses are a conspicuous cover over much of the forest floor, while patches of ground lichen (Cladina spp.) are common on jack pinedominated sand flats and under open spruce stands on bedrock (Harris & Foster, 2005; Carr et al., 2007).

Woodland Caribou Provincial Park

Woodland Caribou Provincial Park was regulated in 1983 at 450 000 ha in size and is located along the Manitoba border in northwestern Ontario, about 50 km west of Red Lake (Fig. 1). The average July and January temperatures in Woodland Caribou Provincial Park are 18.4 °C and -20.4 °C, respectively (OMNR, 2004). Forests of the area consist of typical boreal tree species such as jack pine, black spruce, balsam fir, and trembling aspen dominating upland sites, with black spruce and larch (*Larix laricina*)

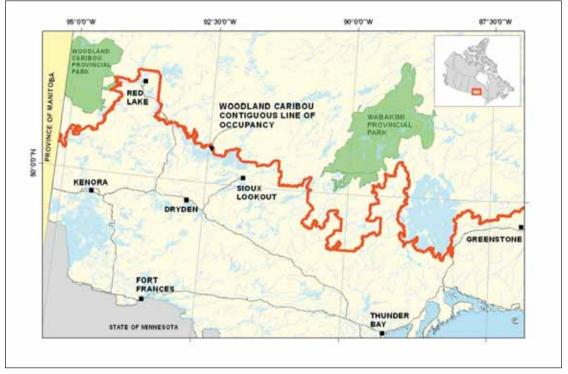


Fig. 1. Locations of Wabakimi and Woodland Caribou Provincial Parks in relation to the southern limit of contiguous range occupancy of woodland caribou (*Rangifer tarandus caribou*) in northern Ontario.

characterizing the wet, organic deposits commonly found in bedrock depressions (OMNR, 2004). The park is situated on a relatively flat plateau and soils are thin when present at all (Brunton, 1986). The slightly elevated position of the park area has resulted in a greater than normal incidence of dry upland forest, so jack pine is more dominant than black spruce (Brunton, 1986). Ground lichen is prevalent in older jack pine forests and a dense ground cover of feather moss is common in black spruce forests (Brunton, 1986). The park is significantly influenced by its proximity to the Prairie Provinces, resulting in a dry, hot growing season creating "boreal prairie" forests that experience a greater frequency of naturally occurring forest fires, in contrast with the more moist boreal forests further east (OMNR, 2004).

Methods

Nursery sites

Caribou calves are generally born between the last week of May and the first week of June in northern Ontario (Bergerud, 1980; Ferguson & Elkie, 2004). To limit the potential effects of human disturbance on the behaviour of calving caribou or physical dis-

ruption of nursery sites (e.g., by walking transects, using motorboats, canoeing), systematic transect surveys started in the middle of June each year (2001-2003), after calving had occurred, and generally finished by the end of July. Study lakes were selected on the basis of their accessibility by ground or water transport and previous knowledge of caribou calving or nursery activity.

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

Along the shorelines of lakes, and islands larger than 500 m in width or length, 100-m transects perpendicular to the shoreline were set every 1-2 km and surveyed for physical evidence (i.e., calf beds, pellets or tracks) of use (Timmermann, 1998). Islands

less than 500 m in width or length were surveyed for nursery sites by walking transects, set perpendicular to the shoreline at 1-km intervals, across the entire island. Island and mainland transects were resurveyed in subsequent years to determine whether or not nursery sites were used in the second and third year of the study. Absence sites were then identified as midpoints of transects that were surveyed in at least two consecutive years without finding any physical evidence of caribou calving or nursery activity.

There were a total of 870 absence sites and 94 caribou nursery sites identified on 83 lakes in Woodland Caribou Provincial Park during the 3 years (2001-2003) of the study. There were a total of 164 absence sites and 39 caribou nursery sites identified on 10 lakes in Wabakimi Provincial Park in the same time period. For comparison of landscape characteristics of surveyed lakes and islands with the general landscape characteristics of each park, the sizes of all lakes, islands, and peninsulas in both parks were measured in ArcMap 8.3 Geographic Information System (Environmental Systems Research Institute, Redlands, California)

GIS analysis

Landcover vegetation classes at sites in both parks were determined from Landcover 2000 (Spectranalysis, 2004). Landcover 2000 is a remotely sensed coverage produced from satellite imagery collected during 1999-2002 to produce a data set composed of 25 m-grid cells, each classified into 1 of 27 different landcover classes consisting of vegetation types (such as forest, wetlands and agricultural crops or pasture) and categories of non-vegetated surface areas (such as water bodies, bedrock outcrops, or settlements). To compare the availability of vegetation landcover classes in areas that were searched for evidence of caribou activity to the availability of these classes at the landscape scale within each park, buffered areas were delineated along the shorelines of lakes and on islands that were surveyed. The buffered areas included the first 100 m of mainland shoreline, all islands less than 500 m either in length or width, as well as the first 100 m of shoreline on all islands over 500 m in length or width. Random points were then created within the buffers of each park (Random Point Generator Version 13; Jenness, 2005). Initially, the number of random points generated was arbitrarily set equal to 5 times the number of absence and caribou nursery sites identified in each park. For each park, we compared the frequency distribution of classified 25-m grid cells in buffered areas with the frequency distribution of random points. If the random points in buffered areas did not represent the

frequency distribution of available Landcover 2000 categories based on 25-m grid cells in the buffers, then more random points were added until there was no statistically significant difference (chi-square) between landcover classes represented by random points in buffered areas and 25-m grid cells within buffered areas. In the end, there were 7935 random points within buffered areas in Woodland Caribou Provincial Park and 3886 random points within buffered areas in Wabakimi Provincial Park.

Geographic co-ordinates of random points within buffered areas, absence sites and caribou nursery sites were imported into ArcMap 8.3 and assigned to landcover classes in Landcover 2000 (Spectranalysis, 2004). Points or sites that fell in the water, timber harvested areas, forest regeneration areas, and categories of non-vegetated surface areas were not included in subsequent analyses. Nursery and absence sites were mostly reduced due to these sites falling on land but being misclassified as water due to their close proximity to water: each grid cell (i.e., pixel) was 25 m by 25 m and a site that fell 15 m from the water's edge was most likely misclassified. This removal left 6002 random points, 24 nursery, and 179 absence sites in Woodland Caribou Provincial Park and 2650 random, 19 nursery, and 69 absence sites in Wabakimi Provincial Park that were classified by vegetation landcover type.

We also classified random points within buffered areas, absence sites and caribou nursery sites according to the landform on which they occurred; island, mainland or peninsula. Because peninsulas may offer caribou cows and their calves greater opportunity than linear shorelines for escape from predators by water, we further categorized points and sites according to their occurrence on peninsulas on the mainland or islands larger than 10 ha in size within the surveyed areas of each park. A peninsula was defined as a landmass that projected from the shore with ≥1 length to 1 width of base ratio. The minimum 1:1 ratio ensured that the landmass was a definite irregular protrusion on the shorelines of the mainland and islands. By including only islands larger than 10 ha in size in our analyses, there were 6380 random points, 81 nursery, and 486 absence sites in Woodland Caribou Provincial Park and 3360 random points, 32 nursery, and 131 absence sites in Wabakimi Provincial Park that were classified by landform type.

A Nearest Feature Tool (Jenness, 2001) in ArcView 3.2 was used to measure minimum distances from the initial points (caribou nursery sites, absence sites, and random points within buffered areas) to the edge of the nearest landform (i.e. island, peninsula, or mainland). If the distance was > 1 km from the

initial point, the distance was not used in further analyses because we assumed that landforms within a 1 km radius of the nursery sites were most important to cow-calf pairs during the nursery period and Ferguson & Elkie (2004) found that female caribou in north-western Ontario did not move more than approximately 1 km a day during the summer season. This constraint left 5214 random points, 94 nursery, and 837 absence sites in Woodland Caribou Provincial Park and 1972 random points, 39 nursery, and 158 absence sites in Wabakimi Provincial Park for measurement. Minimum distances were also measured 3 times from each initial point, regardless if it was a random point in a buffered area or a caribou nursery or absence site, to establish the first 3 minimum escape distances and 3 closest landform types. After removal of distances > 1 km from the initial point, 3484 random points, 89 nursery, and 650 absence sites were available for these distance measurements in Woodland Caribou Provincial Park and 1573 random points, 39 nursery, and 127 absence sites were measured in Wabakimi Provincial Park. The distance to the first landform and the average of the first 3 distances from each point were used in the statistical analyses.

To examine the potential effects of human activity on calving caribou, the closest distance, to a maximum of 35 km, was measured from nursery, absence, and random points within the buffered areas to the closest fly-in fishing outpost in each park, regardless of whether the outpost occurred on the same lake as the nursery and absence sites. The study lakes were much smaller in size in Woodland Caribou Provincial Park in comparison to Wabakimi Provincial Park (Table 1), necessitating a maximum distance of 35 km for comparing the closest fishing outpost between parks. This restriction left 7907 random, 93 nursery, and 870 absence points in Woodland Caribou Provincial Park and 3880 random, 39 nursery, and 164 absence points in Wabakimi Provincial Park.

Statistical analyses

Use-availability study designs are fraught with difficulties (Garshelis, 2000). In particular, comparisons between used and unused sites can be problematic if unused sites are misclassified (i.e., "nonobservation of use may not mean nonuse"; Garshelis, 2000). In our study we could not be certain that absence sites were never used by female caribou for calving or nursery activity so we chose to make comparisons among nursery sites, absence sites and random points within buffered areas along the shorelines of lakes and on islands that were surveyed in each park.

All Landcover 2000 measurements produced nominal data that were compiled into frequency distributions. We compared the frequency distributions among Landcover 2000 categories of random points within buffered areas, absence sites, and caribou nursery sites using a chi-square statistical analysis. Nominal data occurring with expected frequencies < 2 were combined into a single category (Zar, 1999).

A chi-square test was also used to compare the frequency of landform types used by calving caribou at nursery sites with absence sites and random points within the buffered areas in each park.

We tested the assumption of normality of all interval scale data. Log, square root, and arcsine transformations were performed when these data were not normally distributed. All tests were completed using the Statistical Package for the Social Sciences (Version 14.0, SPSS Inc., Chicago, Illinois).

The average of the nearest 3 distances and the nearest landform distance alone were compared among absence, nursery, and random points within the buffered areas in separate t-tests; mean distances from caribou nursery and absence sites were compared to the mean distance from random points in each park with 1-sample *t*-tests and comparisons between nursery and absence sites were made with 2-sample *t*-tests.

Distances to fly-in outpost camps from all nursery, absence, and random points within the buffered areas were first examined using a non-parametric Kolmogorov-Smirnov test of normality and Levene's test for homeogeniety of variance. The data violated both of these assumptions required for ANOVA, even after data transformation, so we chose a non-parametric Kruskal-Wallis test to analyze the untransformed fly-in outpost distance data, followed by a Mann-Whitney *U*-test to compare each pair of conditions in a non-parametric post hoc procedure: nursery versus random sites, nursery versus absence sites, and absence versus random sites.

Results

General landscape characteristics

Differences in the sizes of islands used for calving and nursery activity, as well as distances to the nearest landforms that might be used for escape by caribou cow-calf pairs, may be related to the general land-scape characteristics found in each of the two parks that were studied. There was a great deal of variability in the sizes of lakes in the two parks, ranging from 0.01 to 11 049.70 ha in Wabakimi Provincial Park and 0.02 to 3160.80 ha in Woodland Caribou Provincial Park, yet the average sizes of lakes were

quite similar (Table 1). Lakes that were surveyed and showed signs of caribou nursery activity in the two parks, on the other hand, were much larger than the average sizes, and were an order of magnitude greater in Wabakimi (4822 ha) than Woodland Caribou Provincial Park (488 ha). The average sizes of islands on lakes with caribou nursery activity were twice as large as the averages for all islands in each park (Table 1) and islands with nursery activity in Wabakimi (8.2 ha) were almost twice the size of those in Woodland Caribou Provincial Park (4.6 ha). The average sizes of peninsulas on lakes with caribou nursery activity (Table 1) in Wabakimi Provincial Park (6.0 ha) were smaller than those in Woodland Caribou Provincial Park (8.5 ha).

Vegetation landcover classes

In both parks, absence sites were distributed among vegetation landcover classes similarly to what was randomly available in each landscape (χ^2 = 3.521, 4 d.f., P = 0.475 in Wabakimi Provincial Park and χ^2 = 5.298, 4 d.f., P = 0.258 in Woodland Caribou Provincial Park). Thus, landcover types at caribou nursery sites could be compared to either random points in buffered areas or absence sites in each park to determine whether or not certain landcover types were selected more often by female caribou for nursery activity.

In Wabakimi Provincial Park, there was not a significant difference in the distributions of random points and caribou nursery sites among landcover classes ($\chi^2 = 1.087$, 2 d.f., P = 0.581) or nursery and absence sites (Fig. 2A; $\chi^2 = 1.540$, 1 d.f., P = 0.163). In Woodland Caribou Provincial Park, on the other

hand, there was a higher percentage of caribou nursery sites (63%) in the coniferous landcover category than random points (40%) and a lower percentage of nursery sites than random points in the deciduous (0% and 12%, respectively) or sparse-mixed categories (37% and 48%, respectively) (χ^2 = 6.476, 2 d.f., P = 0.039). There were also more caribou nursery sites (63%) in the coniferous landcover category than absence sites (35%), which were more common in the sparse-mixed (47%) and deciduous (18%) landcover classes than nursery sites (37% and 0%, respectively) (Fig. 2B; χ^2 = 8.991, 2 d.f., P = 0.01).

Landform types

Neither caribou nursery sites or absence sites were distributed among landform types similarly to what was randomly found on the landscape in either Wabakimi (nursery sites vs. random points, $\chi^2 = 57.573$, 2 d.f., P < 0.001; absence sites vs. random points, $\chi^2 = 16.763$, 2 d.f., P < 0.001) or Woodland Caribou (nursery sites vs. random points, $\chi^2 = 362.783$, 2 d.f., P < 0.001; absence sites vs. random points, χ^2 = 793.596, 3 d.f., P < 0.001) Provincial Park (Fig. 3). This suggests that absence sites did not represent the availability of landforms on the study lakes for comparisons with nursery sites. Consequently, caribou nursery sites were compared to both random points in buffered areas and absence sites in each park to determine whether or not certain landcover types were selected more often by female caribou for nursery activity.

In both parks, caribou nursery sites were found more often on islands than expected from the random availability of islands on the landscape (Fig. 3);

Table 1. The average (± s.e.) sizes in hectares (ha) of lakes, islands and peninsulas in Wabakimi and Woodland Caribou Provincial Parks and those showing evidence of caribou nursery activity in each park that were used in this study.

	Study Area (ha)					
Landscape Characteristic	Wabakimi Provincial Park	Woodland Caribou Provincial Park				
Size of Lakes						
Entire Park	$60.0 \pm 4.3 (n = 1787)$	$56.6 \pm 4.0 (n = 1515)$				
Nursery Lakes	$4822.0 \pm 1526.0 (n=10)$	$488.0 \pm 53.6 (n = 83)$				
Island Size						
Entire Park	$4.0 \pm 1.4 (n = 5138)$	$2.2 \pm 0.2 (n = 1952)$				
Nursery Lakes	$8.2 \pm 4.6 (n = 1326)$	$4.6 \pm 0.6 (n = 622)$				
Peninsula Size						
Nursery Lakes	$6.0 \pm 0.4 (n = 684)$	$8.5 \pm 0.6 (n = 862)$				

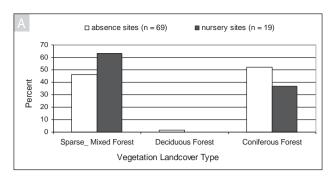
59 vs. 23% in Wabakimi and 77 vs. 11% in Woodland Caribou Provincial Park. Nursery sites were also found more often on peninsulas on the mainland and islands relative to their availability on the landscape in both Wabakimi (19 vs. 4%) and Woodland Caribou Provincial Park (11 vs. 3%). Conversely, nursery sites occurred much less on the mainland than expected from the numbers of random points classified as mainland; 22 vs. 73% in Wabakimi and 12 vs. 86% in Woodland Caribou Provincial Park.

Similar to the broad landscape scale comparisons, caribou nursery sites occurred more frequently on islands and peninsulas and less frequently on the mainland than absence sites within study lakes surveyed in Wabakimi Provincial Park (Fig. 3A; χ^2 = 57.573, 2 d.f., P < 0.001). In Woodland Caribou Provincial Park, caribou nursery sites were also found more often on islands and less often on the mainland than absence sites within surveyed lakes (Fig. 3B; χ^2 = 22.420, 3 d.f., P < 0.001); differences with respect to peninsulas were minor.

Nearest landform types

The nearest landform types to caribou nursery sites or absence sites did not reflect the relative availability of landform types near random points on the landscape in either Wabakimi (nursery sites vs. random points, $\chi^2 = 28.412$, 2 d.f., P < 0.001; absence sites vs. random points, $\chi^2 = 96.912$, 3 d.f., P < 0.001) or Woodland Caribou (nursery sites vs. random points, $\chi^2 = 48.849$, 2 d.f., P < 0.001; absence sites vs. random points, $\chi^2 = 464.110$, 3 d.f., P < 0.001) Provincial Park (Fig. 4). Since absence sites did not represent the availability of nearest landform types on the study lakes for comparisons with nursery sites, nursery sites were compared to both random points in buffered areas and absence sites in each park.

Caribou nursery sites were found more often near islands than were random points in buffered areas in both parks (Fig. 4); 59 vs. 53% in Wabakimi and 48 vs. 37% in Woodland Caribou Provincial Park. Nursery sites were also found more often near the mainland than were random points (21 vs. 4% in Wabakimi and 36 vs. 15% in Woodland Caribou Provincial Park), which were found more often near peninsulas than were



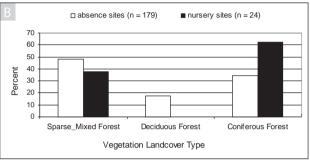
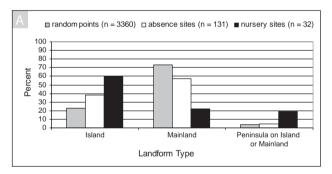


Fig. 2. Proportions of absence sites and caribou nursery sites classified by vegetation landcover types in (A) Wabakimi Provincial Park and (B) Woodland Caribou Provincial Park.



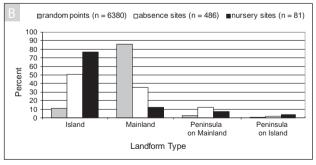
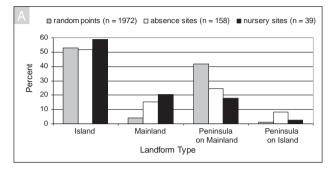


Fig. 3. Proportions of random points, absence sites, and caribou nursery sites classified by landform types in (A) Wabakimi Provincial Park and (B) Woodland Caribou Provincial Park.

nursery sites (43 vs. 21% in Wabakimi and 48 vs. 16% in Woodland Caribou Provincial Park).

Although caribou nursery sites were found more often near islands and the mainland than absence sites on the study lakes in Wabakimi Provincial Park (Fig. 4A), there was no statistical difference in landform types that were nearest to nursery sites or absence sites ($\chi^2 = 2.859$, 3 d.f., P = 0.414). At



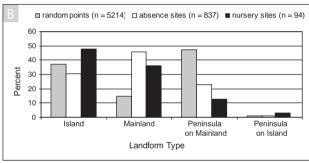


Fig. 4. Proportions of landform types nearest to random points, absence sites, and caribou nursery sites in (A) Wabakimi Provincial Park and (B) Woodland Caribou Provincial Park.

39 nursery sites where measurements were made in Wabakimi Provincial Park, the nearest 3 landforms to 30 (77%) of the sites included 2-3 islands. In Woodland Caribou Provincial Park, nursery sites were found more often near islands and less often near the mainland or peninsulas than absence sites (Fig. 4B; $\chi^2 = 16.074$, 3 d.f., P < 0.001). The nearest 3 landform types to 42 of 89 (47%) nursery sites in

Woodland Caribou Provincial Park included 2-3 islands.

Minimum escape distances

The mean distance from caribou nursery sites or absence sites to the next nearest landform was less than the mean distance from random points in buffered areas in both parks (Table 2); in Wabakimi Provincial Park, nursery sites vs. random points t = -3.140, d.f. = 38, P = 0.003, absence sites vs. random points t = -4.386, d.f. = 157, P < 0.001, and in Woodland Caribou Provincial Park, nursery sites vs. random points t = -10.120, d.f. = 93, P < 0.001, absence sites vs. random points t = -28.397, d.f. = 836, P < 0.001. There were no differences between the mean distances from caribou nursery sites or absence sites to the next nearest landform in either park; t = -0.27, d.f. = 92, P = 0.79 in Wabakimi and t = -1.0, d.f. = 929, P = 0.319 in Woodland Caribou Provincial Park. In Wabakimi Provincial Park, nursery sites were 117 m closer on average than random points to the next nearest landform, and in Woodland Caribou Provincial Park, nursery sites were

Table 2. Mean distances (m) ± s.e. (sample size in parentheses) from random points, absence sites and caribou nursery sites to the nearest landform and nearest three landforms in Wabakimi and Woodland Caribou Provincial Parks.

	Study Area							
	Waba	kimi Provincia	ıl Park	Woodland	Woodland Caribou Provincial Park			
	Random Absence Nursery Random Points Sites Sites Points					Nursery Sites		
Mean distance (m) \pm s.e. (n) to nearest landform	336 ± 5	270 ± 18	219 ± 22	381 ± 3	179 ± 6	173 ± 15		
	(1972)	(158)	(39)	(5214)	(837)	(94)		
Mean distance (m) \pm s.e. (n) to nearest 3 landforms	429 ±4	355 ± 17	311 ± 23	466 ± 3	290 ± 6	265 ± 19		
	(1573)	(127)	(39)	(3484)	(650)	(89)		

208 m closer on average than random points to the next nearest landform.

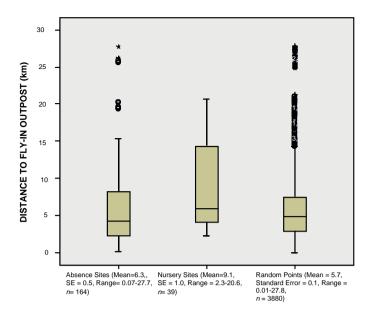
Mean distances to the nearest three landforms from caribou nursery sites or absence sites were not statistically different from the mean distance from random points in Wabakimi Provincial Park (Table 2); nursery sites vs. random points t = -0.158, d.f. = 38, P = 0.875 and absence sites vs. random points t = 0.905, d.f. = 126, P = 0.367. In Woodland Caribou Provincial Park, both caribou nursery sites and absence sites were closer to the nearest three landforms than were random points; nursery sites vs. random points t = -4.867, d.f. =88, P < 0.001and absence sites vs. random points t = -9.018, d.f. = 649, P < 0.001. There were no differences between caribou nursery sites and absence sites in the mean distances to the nearest three landforms in either park; t = 0.57, d.f. = 164, P = 0.57 in Wabakimi and t = 1.82, d.f. = 737, P = 0.07 in Woodland Caribou Provincial Park, In Wabakimi, nursery sites were 118 m closer on average than random points to the nearest three landforms, and in Woodland Caribou Provincial Park, nursery sites were 201 m closer on average than random points to the nearest three landforms.

Distance to nearest fly-in outpost

In Wabakimi Provincial Park, caribou nursery sites were on average over 2.7 km further from the nearest flyin outpost than the mean distance from absence sites or random points (Fig. 5A); nursery sites vs. absence sites U = 2190, P = 0.002 and nursery sites vs. random points U = 53 541, P = 0.002. On average, nursery sites were 9.1 km from the nearest fly-in

outpost while absence sites and random points were not significantly different (U = 303 938, P = 0.332) at mean distances of 6.3 km and 5.7 km from the nearest fly-in outpost, respectively.

Although not statistically different from absence sites or random points (H = 4.38, P = 0.112), the mean distance from caribou nursery sites to the nearest fly-in outpost in Woodland Caribou Provincial Park was just over 10.2 km (Fig. 5B), which is similar



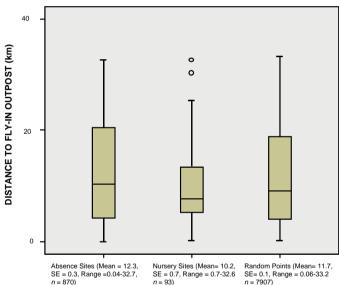


Fig. 5. Standard boxplots of distances (km) to the nearest fly-in outposts from absence sites, nursery sites, and random points in (A) Wabakimi Provincial Park and (B) Woodland Caribou Provincial Park.

to the mean distance from caribou nursery sites to the nearest fly-in outpost in Wabakimi Provincial Park.

Discussion

Parturient caribou select landscape characteristics at multiple spatial scales that reduce predation risk during the calving and nursery period. Comparisons of random points in Wabakimi and Woodland Caribou Provincial Parks with nursery sites and absence sites on surveyed lakes in each park indicated that female caribou selected particular vegetation land-cover classes within certain landform types for calving and nursery activity. Regardless of variability in the sizes of lakes used within and between parks, female caribou selected larger lakes with larger than average sized islands configured within shorter than average distances to other islands or landforms, facilitating escape from predators while meeting the foraging requirements of cow-calf pairs through the postpartum period.

Although the proportions of sparse (approximately 33%) and coniferous forests (about 39%) available along shorelines were similar in the two parks, caribou nursery sites in Woodland Caribou Provincial Park occurred more often than expected in the coniferous landcover type, while nursery sites were used in proportion to the availability of both vegetation landcover types in Wabakimi Provincial Park. In fact, the combination of sparse and mixed forests was used more often than coniferous forests for nursery activity by caribou in Wabakimi Provincial Park. However, Carr et al. (2007) found that these same nursery sites in Wabakimi Provincial Park were typically in old-growth (> 60 yrs) areas of spruce. The densities of mature trees were higher and densities of shrubs were lower at nursery sites than unused absence sites in both parks (Carr et al., 2007). Vegetative groundcover, including greater lichen abundance, was also higher at nursery sites than absence sites in both parks. Thus, regardless of landcover type, calving caribou in both parks selected nursery sites with finescale characteristics that may reduce predation risk while providing necessary forage (Rettie & Messier, 2000; Carr et al., 2007). Broad classification systems, such as Landcover 2000 used in this study, may be inadequate to capture these fine-scale vegetation characteristics and may only be useful for preliminary identification of potentially important caribou nursery areas.

The selection of caribou calving sites is most likely related to many factors such as past experiences, individual behaviour patterns, age and predator avoidance strategies. At both the site-specific (Carr et al., 2007) and landscape scales, caribou apparently seek nursery areas with anti-predator features, such as islands, to avoid bears and wolves (Bergerud et al., 1984; Cumming & Beange, 1987). Our study indicated that a significant majority (60 – 80%) of caribou nursery areas in Wabakimi and Woodland Caribou Provincial Parks occurred on islands rather than the mainland shoreline of lakes that were surveyed. The mean island sizes used for nursery activ-

ity in Wabakimi and Woodland Caribou Provincial Parks (8.2 ha and 4.6 ha, respectively) were within the much broader range reported by Cumming & Beange (1987), who found female caribou used islands in the summer that were from 0.5 to 1,550 ha in size in the Lake Nipigon and Wabakimi Provincial Park area. Our results also agree with Ferguson and Elkie (2005) who reported that female caribou used islands 10 – 100 ha in size in the landscape between Wabakimi and Woodland Caribou Provincial Parks. In both parks, the islands that were used were, on average, twice the mean size of available islands, suggesting some minimum island size may be required for predator detection and avoidance, as well as supporting the food requirements of adult female caribou through the initial post-partum period. In addition to being an important anti-predator tactic, seclusion allows control of social interactions and the formation of strong bonds between cow and calf (Lent, 1974).

Cumming & Beange (1987) found caribou sign on Lake Nipigon showed more clumping of island use than would be expected by chance and suggested calving caribou chose islands clustered together as an escape strategy; caribou are good swimmers and could retreat to a neighbouring island fairly quickly if a predator was encountered. In both Wabakimi and Woodland Caribou Provincial Parks, we found caribou most often selected nursery sites on islands where the closest landform for escape was another island or the mainland. Minimum escape distances from nursery sites on these islands to the next nearest landform were similar in the two parks and, on average, were less than the minimum distance between random points or sites that were not used and other landforms on lakes that were surveyed. Likewise, average distances from nursery sites on islands to the nearest three landforms were less than the average three distances between random points or absence sites and landform types on surveyed lakes in both parks. Similar to Cumming & Beange (1987), we found nursery sites in Wabakimi Provincial Park were most often located on islands where 2-3 islands were the nearest landforms. Although not as prevalent as in Wabakimi, almost half of the nursery sites examined in Woodland Caribou Provincial Park were also located on islands where 2-3 islands were the nearest landforms. Taken together, these results suggest calving caribou may choose clusters of islands as part of their escape strategy, but there is some limitation on distances between islands in a cluster or other landforms. Addison et al. (1990) suggested moose calves may have difficulty swimming more than about 200 m after a period of running on land. Similarly, our

results may indicate a maximum escape distance of 200 – 300 m that is related to the endurance of caribou calves while swimming between nursery areas on islands and other landform types to escape predators.

Human activities within caribou range, which do not necessarily destroy habitat, may still result in a functional loss of usable space because of disturbance and the resulting displacement of caribou (Webster, 1997). Nellemann et al. (2000) determined that maternal wild reindeer (R. t. tarandus) avoided a 10 km zone around a high-altitude tourist resort near Rondane National Park in Norway, which is remarkably similar to the average 9.1 km distance to the nearest fly-in outpost from caribou nursery sites that we measured in Wabakimi Provincial Park and the 10.2 km distance in Woodland Caribou Provincial Park. These values also approximate the average 9.2 km distance of female caribou from active logging in late spring and summer as determined by Schaefer and Mahoney (2007) in central Newfoundland and the tolerance threshold of 13 km to nearest cutover suggested by Vors et al. (2007) for caribou in northern Ontario. Together, these studies suggest a critical threshold for parturient caribou of 10-15 km from disturbance.

Further studies should focus on substantiating these potential ecological thresholds for both recreational and forestry activities within and outside protected area boundaries. It is extremely difficult to identify abrupt ecological threshold break points, even with good quality data (Huggett, 2005), and there needs to be further development of statistically rigorous methods, as well as non-parametric approaches such as those recently proposed by Sonderegger et al. (2009), to identify thresholds. Moreover, there are potentially a wide range of different threshold responses to the same disturbance or land use changes that ecological processes can exhibit (Huggett, 2005) and the confounding effect of multiple variables interacting to produce a complex threshold response makes it difficult to identify a single casual factor (Bennett & Radford, 2003). Nonetheless, given the threatened status of woodland caribou, we believe these studies need to be attempted.

In the meantime, the landscape-scale physical characteristics and landcover types associated with caribou nursery sites that we measured in this study, combined with fine-scale characteristics measured previously (Carr et al., 2007), could provide baseline information that may be used to predict locations of potential caribou nursery sites at multiple spatial scales both outside and within protected area boundaries across northern Ontario. To ensure caribou persistence across northern Ontario it is critical

to identify currently used and potential nursery areas and make sure that adequate protection is given to these sites (Morrill et al., 2005; Carr et al., 2007). Large protection zones should be considered in areas with high use by parturient caribou and sufficient buffers to protect these areas from recreational use and logging activity should be established. Based on the results of this and previous studies, a sufficient buffer would approximate the critical threshold for parturient caribou of 10-15 km from human disturbance. In caribou nursery areas, activities that likely disturb nursing caribou (e.g., recreational watercrafts, air-traffic, camping) should be limited or restricted, especially during the critical calving and nursing period from May to August. To minimize stress by human disturbance, park users in caribou areas should be educated to stay an appropriate distance away from caribou so that they are not alarmed or disturbed. Further facility development on or near caribou nursery sites should be prevented. Although fidelity to calving areas has been noted in several studies (Brown et al., 1986; Edmonds, 1988; Seip, 1992; Brown et al., 2000; Schaefer et al., 2000), disturbances caused by landscape exploitation and human recreational activities, both outside and within protected area boundaries, may prevent female caribou from returning to previously used calving sites, so continued monitoring of potential nursery areas on lakes is necessary to ensure that policy and management can adapt to these changes. More studies should inventory and monitor fen habitat as well; Ontario Parks' research has found high use of remote fens by calving caribou in Wabakimi Provincial Park (Morrill et al., 2005). Most importantly, education of park users must be enhanced with regard to caribou and their lifecycle.

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Movements of boreal caribou in the James Bay lowlands

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Abstract: Little is known about the movements and home range of boreal woodland caribou (Rangifer tarandus) in the James Bay lowlands, northern Ontario. Our preliminary study involves the use of GPS collars with Argos satellite system uplink to monitor movements of caribou and 10 animals were collared in December 2004. Animals appeared to have reduced rates of daily movement starting approximately in mid to late December and stretching until late February. Similarly, most animals appeared to have very reduced rates of movement from the beginning of May to the end of June indicating that this is their calving period (includes both parturition as well as the period immediately after parturition). Thus the over-wintering range was assumed to be where the animals were from mid-December to late February and the calving range was defined as the area they were in from the beginning of May to the end of June. Individual home-ranges were typically large, the mean 90% kernel home range for 2004 – 2007 was 41 579 km². Over wintering areas and calving areas were small when compared to annual home-range size and reflect the reduced rates of movement during these time periods. Female caribou show site fidelity to calving grounds, using the same core areas year after year. However, the same level of site fidelity was not observed in over-wintering areas. The caribou in the James Bay lowlands display behaviours that are characteristic of both the forest-tundra and forest-forest ecotypes which may warrant the reconsideration of the validity of proposed ecotypes with respect to protection under species-at-risk legislation.

Key words: behavior, calving areas, home range, James Bay lowlands, movement, over-wintering areas, site fidelity, *Rangifer tarandus*, woodland caribou.

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Introduction

Movement and behavioural plasticity is a distinguishing feature in the ecology of caribou. Previous studies have identified 3 distinct ecotypes associated with movement behaviour, sedentary boreal forest (woodland), migratory tundra and migratory mountain (Bergerud, 1988, 1996). Caribou ecotypes are similar in their use of movement as a strategy to minimize

the risk of predation and maximize forage efficiency. During the calving season, the migratory ecotypes aggregate on calving grounds away from predator concentrations while sedentary ecotypes space out and use muskegs or islands as safe havens (Bergerud, 1988, 1996; Stuart-Smith *et al.*, 1997; Harris, 1999; Hummel & Ray, 2008). Thus, knowledge of movement behaviour is valuable to understand the

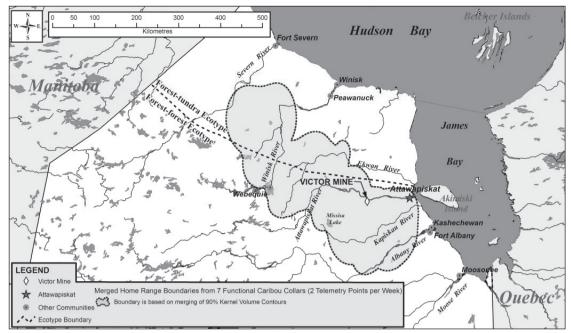


Fig. 1. The study area with regions of forest-forest and forest-tundra woodland caribou ecotypes delineated (Ontario Woodland Recovery Team, 2008) and the combined home ranges of 6 caribou between Dec 2004 and Feb 2007 using the 90% kernels.

distribution and abundance of caribou populations and the effects of factors such as predation (Bergerud, 1988; Seip, 1992; Stuart Smith *et al.*, 1997; Schaefer *et al.* 2000; James *et al.* 2004).

Woodland caribou range across much of northern Ontario with isolated populations as far south as Lake Superior (Ontario Woodland Recovery Team, 2008). The Ontario provincial recovery team recognizes 2 types of boreal or woodland caribou, the "foresttundra" and "forest-forest" ecotypes (Fig. 1; Ontario Woodland Recovery Team, 2008). Caribou belonging to the forest-forest ecotype are currently listed both provincially and federally as threatened and as such are protected under both the federal Species at Risk Act (SARA) 2002 and provincial Endangered Species Act (ESA) 2007. Caribou in the James Bay Lowlands are considered as forest-forest ecotypes and are protected under SARA 2002 and ESA 2007. However, Hummel & Ray (2008) show the Pen Island caribou as being migratory caribou and their range extending as far south as Akimiski Island and including much of the range of the caribou studied in this project. Although studies examining the spatial behaviour of caribou have been undertaken in many parts of Ontario, few studies have examined the distribution and size of home ranges for caribou in the James Bay lowlands and the information about their distribution and numbers is limited (Simkin, 1965; Ahti &

Hepburn, 1967; Gray, 1978; Thompson, 1984; Lytwyn, 2002; Magoun *et al.*, 2005). Boreal caribou in other parts of Ontario, Manitoba and Saskatchewan appear to be quite sedentary ranging from 1.25 km² to 13 030 km² (Table 1). As such, caribou homeranges appear to be context dependent and extrapolation of estimates from different ecosystems may not be applicable to the James Bay lowlands.

Our study was initiated as part of the environmental assessment process for a diamond mine, located near Attawapiskat, Ontario (Fig. 1, AMEC Earth and Environmental, 2004). There were concerns that the mine may effect local boreal caribou population (TEK Working Group, 2004). In response, we initiated a long-term monitoring program to assess the likelihood of any effects. As this study is the first in the region to provide detailed movement behaviour of caribou in the James Bay lowlands, the initial goal was to obtain basic information on the ranging behaviour of these animals as it is likely that information and management practices utilized elsewhere in Ontario may not be applicable for these animals. This is particularly important with respect to the Recovery Strategy for boreal caribou which provides the boundary line between forest-forest and foresttundra caribou (Fig. 1); only animals considered part of the forest-forest population are protected by legislation.

Table 1. Existing annual and seasonal home range estimates in Ontario, Manitoba and Saskatchewan.

Location	Size	Reference
Northern Ontario	 Home range = 3000 km² – 5000 km² Distance between summer and winter ranges = 34 km - 53 km 	Brown, 2005
Northern Ontario	 Home range = 1.25 km² - 13 030 km² Median home range size = 137 km² 	Ferguson & Elkie, 2005
Eastern Manitoba	• Home range = 2471 km ²	Schindler, 2005
West Central Manitoba	 Summer range = 162 km² Winter range = 856 km² 	Metsaranta, 2002
Central Saskatchewan	 Home range = 221 km² - 1240 km² Females without calves had larger home ranges than those with calves. 	Rettie & Messier, 2001

The specific objectives of this study were to examine seasonality in annual movement patterns, the distribution and size of home-ranges as well site fidelity to calving and over-wintering areas of caribou in the James Bay Lowlands. The analysis was multi-tiered; and used changes in movement patterns to characterize the time periods for calving and over-wintering. These ranges can be compared from year to year and for individual caribou. Specifically we hypothesized that; (1) annual and seasonal home range sizes and movement behaviour will be similar to those observed in other boreal caribou populations in Ontario; (2) these caribou will display two types of movement behaviour, encampment in the summer and winter where animals exhibit lower daily movement rates and a more migratory type of movement in spring and fall where animals have increased movement rates and move directly between areas and; (3) caribou will show site fidelity to overwintering and calving areas.

Methods

Study area

The study area covers a range of habitat types from the coastal marshes, through extensive fens covered in stunted tamarack to forested eskers, old beach ridges and extensive upland bogs. The area is drained by the Attawapiskat and Ekwan Rivers and is dotted with numerous lakes, the largest one being Misissa Lake on the southwestern margin of the study area. Attawapiskat (Fig. 1) is the only permanent community within the study area and is approximately 5 km inland from James Bay on the north side of the Attawapiskat River. The study area is dominated

by treed fens and bogs with stunted black spruce (*Picea mariana*) and tamarack (*Larix laricina*) as the major tree species and a shrub layer of ericaceous shrubs and an herbaceous layer dominated by sedges (*Scirpus* spp.), cotton grasses (*Eriophorum* spp), mosses and lichens. The river edges that are well drained are dominated with balsam fir (*Abies balsamifera*), white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). Some of the areas are characterized by many small shallow ponds (flarks), while other areas are essentially treeless and are raised bogs dominated by sedges and sphagnum (Riley, 2003).

Data collection

GPS Collars (Telonics TGW-3600 GPS/ARGOS) with programmed release mechanisms were fitted to 10 adult female caribou in December 2004. Animal locations were obtained twice a day at 8 am and 8 pm. Poor quality GPS fixes were removed from the data set based on signal quality class and the number of signals received from the satellites. We used the Position Dilution of Precision (PDOP) measure, which was indicated in the raw downloaded collar data, to filter out the inaccurate data. PDOP is a combination value of the Horizontal and Vertical Position Dilution of Precision (HDOP and VDOP). Only fixes with PDOP values less than 6 were used in the analysis.

Analysis

Seasonal Patterns of Movement

In order to accurately delineate the boundaries of calving and wintering ranges as well as identify periods of migration, the dynamics of annual movements (movement rates and turn angles (Turchin, 1998) were assessed to demark these distinct time periods. Daily movement rates were calculated based on consecutive fixes 24 hours apart and calculated as the average number of kilometres traveled per day per month per caribou. Turn angles are the measured change in direction from one successive location to another (Turchin, 1998) and were calculated between subsequent successive positions for each caribou and plotted.

It is expected that animals would be turning more frequently during calving and over-wintering periods of the year to stay in these more localized areas; thus variance in the distribution of turn angles would be high. It is also expected that lower movement rates would occur during these periods of higher turn angles; caribou may travel at the same rates during the calving and over-wintering periods except that they exhibit more tortuous movement paths (zigzagging and backtracking) which reduces the level of spatial displacement, though movement speed may remain the same. Conversely variance in the distribution of turn angles during the migratory spring and fall periods are expected to be much lower as animals would move more directly between ranges. During these periods higher movement rates are expected as animals are presumed to move with a straighter movement trajectory, maximizing spatial displacement over time to get to calving or over-wintering ranges. An assessment of movement rates (isolating turn effects) would require GPS fix rates that are much higher than once or twice a day.

A long fix interval creates uncertainty about an animal's activity in the intervening period between GPS fixes and has been shown to underestimate the actual distance travelled (Pepin *et al.*, 2004) and prediction errors (Swain *et al.*, 2008). The current data has a relatively long interval between fixes (2 fixes a day, 12 hours apart); as such the current estimates of movement rate may be underestimated.

Mean vector length (r) varies inversely with the amount of dispersion in the data. It is a measure of directionality of the movement path based on the distribution of turn angles, and ranges from 0 for meandering trails to 1.0 for linear movement in one direction (Batschelet, 1981). Circular variance was calculated by taking the inverse of the mean vector lengths (Batschelet 1981).

Home-range size and distribution

We calculated both adaptive kernels (90% occupancy for annual home range and 70% occupancy for the seasonal ranges of calving and over-wintering). We used a smoothing factor (h), which defines the spread of the probability kernel generated for each observa-

tion point, of 0.4. For wintering and calving ranges, the data were delineated into groups based on patterns observed in cumulative movement rates (see Results). Each individual data set (comprised of fixes with PDOP values < 6) was evaluated for consistency in fix rate over the 3 year period (see Results).

Site fidelity

The over- wintering and calving areas were compared from year to year to assess the degree to which females return to calving and over-wintering areas. Schaefer *et al.* (2000) discusses the difficulties in avoiding arbitrary designations of how close an individual must be to its previous location to be considered displaying fidelity. Our analysis of fidelity is preliminary and simply evaluates the extent to which animals return to a previous year's site location. This philopatric estimate was obtained by calculating the area (in km²) a caribou occupied during the calving periods in 2005 and 2006 dividing these areas by the "overlap" area in ArcView 9.2.

Results

Between January 2005 and March 2007, 12 043 locations were obtained for 10 female caribou fitted with GPS satellite collars. Two of the animals collared in 2004 were shot by First Nations' hunters, one in April 2005 and one in February 2007. GPS fix rates ranged from 62.9% to 97.6%. Of the 10 original animals; 6 had complete data sets with a minimum of 2 fixes a week 3 days apart for 3 years; 9 had complete data sets with a single fix a day from May – June (calving period) for both 2005 and 2006; 9 had complete data sets with a single fix a day from December to February (over-wintering period) in 2005 and 6 had complete sets for the same over-wintering period in 2006. These were the complete data sets used in the home and seasonal range analysis.

Home-ranges

Collared caribou ranged within the James Bay peatlands generally moving from the south- east region in the summer months to the north-west region in the winter months (Fig. 1). Individual home-ranges were typically large, but with great variance (Table 2). The James Bay Lowland caribou have home ranges of approximately 15 000 to 75 000 km² with distances between summer and winter ranges ranging from 31 km to 384 km (Table 3). Over wintering areas and calving areas were small when compared to annual home-range size and reflect the reduced rates of movement during these time periods (Table 4, Table 5, Table 6).

Table 2. Annual home range size estimates of 6 caribou with 90% kernel estimates for 2005 and 2006.

	Compiled Home range (90% kernel km²) December 2004 to February 2007	Annual Home range (90% kernel km²) January to December	Annual Home range (90% kernel km²) January to December
Caribou #	2004 - 2007	2005	2006
46262	31 195	20 352	22 744
46267	27 542	4920	20 044
46268	23 624	16 632	24 798
46269	41 812	16 697	51 878
46270	34 719	20 346	21 885
46271	15 732	9689	13 022
46272	74 847	28 114	87 012
Mean +/- 1 SD	41 579 +/- 19 158	19 458 +/- 7581	36 440 +/- 28 144

Table 3. Distance between calving and over-wintering ranges.

Caribou #	Distance between calving range 2005 and winter range 2005/2006 (km)	Distance between calving range 2006 and winter range 2006/2007 (km)
46262	183	88
46267	95	102
46268	160	62
46269	336	31
46270	256	158
46271	186	140
46272	384	62
Mean +/- 1 SD	228.57 +/- 102.37	91.85 +/- 45.27

Table 4. Size of core over-wintering areas for 8 caribou in 2005, 2006 & 2007.

Caribou #	December 2004 to February December 2005 to February 2005 (70% kernel km²) 2006 (70% kernel km²)		December 2006 to February 2007 (70% kernel km²)		
46261	323	7557	not available		
46262	198	687	1565		
46266	173	4472	not available		
46267	577	547	9741		
46268	207	641	8286		
46269	222	2533	880		
46270	473	604	9665		
46271	274	281	154		
46272	447	23 818	not available		
Mean +/- 1 SD	321.5 +/- 144.28	4571.11 +/- 7618.97	5048.51 +/- 4632.06		

Note: 46261, 46266 and 46272 did not have complete data sets for the winter of 2006 - 2007 (due to collar malfunction and/or mortality).

Table 5. Size of core calving areas for 9 caribou in 2005 and 2006 with estimates of site fidelity (philopatric index).

Caribou #	2005 (May - June, 70% kernel km²)	2006 (May - June, 70% kernel km²)	Overlap Areas 2005 - 2006 km²)	Philopatric Index
46261	42	21	11	32.7%
46262	9	1	7	66.0%
46266	387	254	95	29.6%
46267	33	9	7	34.3%
46268	24	104	7	10.0%
46269	19	6	0	0.0%
46270	27	288	22	13.9%
46271	84	479	0	0.0%
46272	71	72	71	17.7%
Mean +/- 1 SD	77.3 +/- 118.6	210.6 +/- 253.1	24.3 +/- 34	22.7 +/- 20.8

Table 6. Average daily movement rates (km) from 2005 to 2006.

					Caribou #					
Month	46261	46262	46266	46267	46268	46269	46270	46271	46272	Average
January	2.93	2.21	3.17	2.81	4.46	2.0	3.58	4.50	2.08	3.08
February	1.53	1.75	0.54	1.78	1.61	1.74	1.15	1.36	0.59	1.34
March	1.76	1.09	0.19	1.46	1.10	1.51	1.56	3.95	0.64	1.47
April	6.03	11.13	12.27	3.35	12.17	3.48	5.47	5.95	6.57	7.38
May	2.13	2.72	2.39	0.61	2.44	0.59	1.25	3.02	2.22	1.93
June	2.93	1.81	3.65	2.90	3.80	2.87	3.02	3.11	3.12	3.02
July	1.96	2.09	1.25	3.19	2.93	1.79	2.42	2.46	3.18	2.36
August	2.93	2.40	1.62	5.39	5.28	2.74	3.49	4.57	2.33	3.42
September	2.38	2.87	6.95	2.75	2.92	3.19	2.70	1.99	1.98	3.08
October	3.05	2.87	6.43	3.68	7.22	6.08	4.70	2.91	36.90	8.20
November	16.25	9.70	13.36	6.12	10.52	12.90	11.23	9.95	8.23	10.92
December	9.66	6.67	11.14	5.39	8.84	5.50	8.0	7.88	5.41	7.61

Seasonality

Collared caribou alternated between bouts of migratory movement characterized by increased rates of direct movement and bouts of encamped movement characterized by decreased rates of movement and frequent turns. Increases in movement rate typically started in late March or early April when animals moved from their winter range to their summer range and then again in late October to mid November when they moved to a winter range (Table 6). Periods of spatial encampment typically occur during the

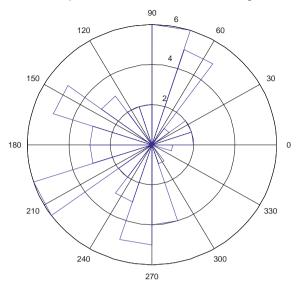
calving months of May and June, as well as from late December to March (Table 6). Migratory periods occur from November to December when the caribou are moving to the over-wintering grounds and in April when females are moving to calving areas. The encampment period during summer and winter months is reflected in the distribution of turn angles. The variance in turn angles observed when the animals were encamped on their winter and calving ranges was high compared to that observed when they were moving between ranges (Fig. 2),

indicating that they were turning more frequently and reversing direction to stay in these localized areas (i.e. many turn angles were close to 180 degrees). Conversely, the distribution of turn angles was narrow during the time period when they were moving between ranges indicating more direct, linear movement. Overall the caribou displayed greater absolute changes in direction during the calving and over-wintering periods (mean angle = $61^{\circ} + 0.82$) than while moving between these seasonal ranges in the spring and fall (mean turn angle = $22^{\circ} + 0.43$).

Animals appear to exhibit site fidelity to calving areas, repeatedly using the same general area in 2005 and 2006 for calving and for some individuals there was a very distinct overlap in the area used for calving between vears (collar 46262, 46261, 46266, 46267, 46272, Fig. 3, Table 5). In some cases (collar 46269 and 46271) there was no overlap of calving areas between the two years. But vet, the calving areas were relatively close together (within 20 km), so in spite of a philopatric index of zero, there is obviously a return to a geographic region that is familiar to the animal.

There is considerable variation from year to year in both the size and location of area used during the winter (Fig. 4, Table 4). While it appeared that there was a general trend for the caribou to move to the north-west in winter to the same general region, it was not observed in all collared caribou.

Encamped Movement Mode - Calving Period



Migratory Movement Mode – Moving from Over-wintering to Calving Area

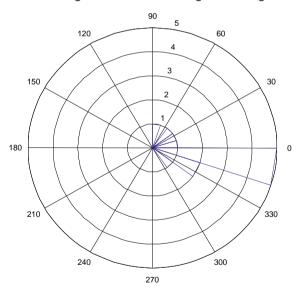


Fig. 2. A comparison of the turning angles of encamped movement behaviour versus migratory movement behaviour. During periods of encampment when animals are staying within the calving or over-wintering areas they are making large turns, frequent reversals (i.e. turning 180 degrees) to stay in localized areas; whereas during periods of more nomadic movement in the spring and fall they are moving more directly rarely turning.

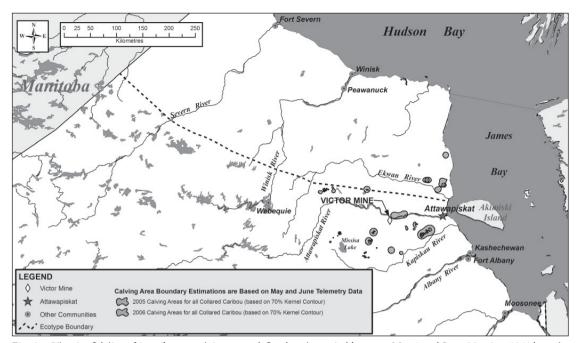


Fig. 3. The site fidelity of 9 caribou to calving areas defined as the period between May 1 and June 30 using 70% kernels.

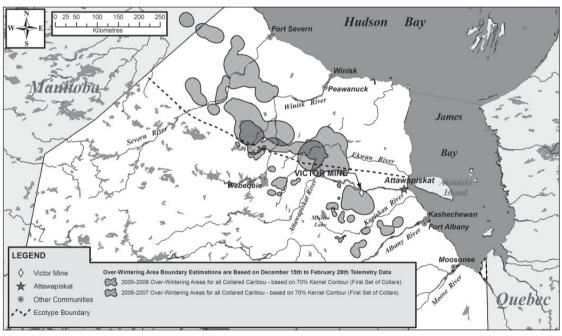


Fig. 4. Over wintering areas of 8 caribou from 2005 to 2007 using 70% kernels.

Discussion

Our preliminary analyses suggest that the movements of the James Bay Lowland caribou are much more extensive than other woodland caribou in northern Ontario and other parts of Canada (Table 1). Woodland caribou in northeastern Ontario typically have home ranges of about 3000 to 5000 km² with the mean distance between summer and winter ranges ranging from 34 to 53 km (Brown, 2005). In contrast, the James Bay Lowland caribou have home ranges of approximately 15 000 to 75 000 km² with a mean distance between summer and winter ranges ranging from 31 km to 384 km (Table 3). The maximum rates of travel for the James Bay lowland caribou in early winter were also much faster (8-10 km/day) than those recorded for woodland caribou in northwestern Ontario (2.5 km/day), during the same time period (Ferguson & Elkie, 2004).

Though size of home-range observed was much larger than that observed in other parts of Ontario, seasonality of range use was comparable to other studies (Brown et al., 2003; Ferguson & Elkie, 2004). Defining animal seasons based on when animals move will invariably vary from year to year because of weather and a variety of other factors confounding direct comparisons among years (Rettie & Messier, 2001; Ferguson & Elkie, 2004) thus many studies have used set time frames (Brown, 2005; Schindler, 2005). However, using set time frames may mask some interesting dynamics that would explain why caribou change their behaviour from year to year and prevent understanding of the mechanistic underpinnings of this behaviour. Theory predicts that movements characterized by straighter paths should increase the likelihood of success of moving between preferred patches (Zollner & Lima, 1999). It is a strategy that is used by many species at multiple scales for reducing the time spent in sub-optimal habitat, and/or the successful movement to high quality habitats (Lima & Zollner, 1996; Duvall & Schuett, 1997). Other studies have found that caribou periodically employed, long distance, direct moves between encamped sites at larger scales (Bergman et al., 2000). Similarly, in this study, collared animals switched from one movement mode to the next by reducing the rate at which they moved and turning more frequently during the calving and over-wintering periods and increasing their rate of movement and moving directly during times of migration in late winter and early winter.

As animals move into novel environments they can potentially experience reduced fitness, thus fidelity to a particular area has been proposed to confer benefits such as knowledge and avoidance of predators and familiarity of resources (Greenwood, 1980). Similar to previous studies (Brown & Theberge, 1985; Gunn & Miller, 1986; Fancy & Whitten, 1991; Schaefer et al., 2000), the majority of the collared caribou exhibited some level of site fidelity to calving areas. In some cases the overlap in seasonal ranges during this time period was found to be greater than 30% (Table 5). In contrast, we did not find that all our animals were repeatedly using the same local areas from year to year during the winter months. None of the winter ranges overlapped between animals from 2005 to 2006. However they did tend to move north-west and in both years there were animals over-wintering along the Ekwan River, north of Webequie (Figure 4); an area that loosely corresponds to an identified lichen belt (Ahti & Hepburn, 1967). This area along the Ekwan River was also identified in Magoun et al. (2005) as an area with a high relative abundance of caribou in winter. Thus it appears as though they may exhibit some fidelity to a general region for over-wintering but not necessarily to more specific local sites.

The caribou in the James Bay lowlands display behaviours that are characteristic of both the foresttundra and forest-forest ecotypes. Individuals displayed characteristics of boreal caribou in that they appear to have isolated calving areas and live in small groups (or are solitary) but their movement behaviour is more similar to the forest-tundra ecotype in that they have large home-ranges and move large distances between summer and winter ranges. Thus, the movement dynamics of this James Bay population appear to almost be intermediate between the sedentary caribou to the south in the Moosonee/ Cochrane area and some of the migratory ecotypes in the north, such as the Pen Islands herd (Abraham & Thompson, 1998; Harris, 1999). Many of the collared animals moved several hundred kilometres northwest into areas currently considered forest-tundra ecotype territory (Fig. 1), thus as more information on the James Bay lowland caribou is collected, the validity of proposed ecotypes with respect to protection under species-at-risk legislation may need to be reconsidered.

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Modeling influences on winter distribution of caribou in northwestern Alaska through use of satellite telemetry

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Abstract: I hypothesize that the distribution of barren-ground caribou (Rangifer tarandus granti) is affected by multiple, interrelated factors. These factors include, but are not limited to, terrain and snow characteristics as well as predation pressure and habitat. To test this hypothesis, I attributed caribou locations derived from satellite telemetry over a 6 year period with terrain (elevation, slope, aspect, and ruggedness), habitat characteristics, and moose density – potentially an index of wolf predation pressure. These locations were compared to random locations, attributed using the same data layers, using logistic regression techniques to develop resource selection functions (RSFs). I found that caribou moved significantly less during mid-winter than early- or late-winter and that cows moved significantly more in April than bulls due to their earlier departure on their spring migration. Distribution was different between cows and bulls. Terrain variables were important factors but were scale-dependent. Cows avoided forested areas, highlighting the importance of tundra habitats, and selected for dwarf shrub, with relatively high lichen cover, and sedge habitat types. Bulls selected for dryas, coniferous forest and dwarf shrub habitats but against lowland sedge, upland shrub and burned tundra. Cow distribution was negatively correlated with moose density at the scale of the Seward Peninsula. My results support the hypothesis that caribou distribution during winter in northwest Alaska is affected by multiple, interrelated factors. These results may be useful for researchers to track and/or model changes in future patterns of range use over winter.

Key words: Alaska; caribou distribution; habitat; lichens; predation; *Rangifer tarandus granti*; resource selection function; satellite telemetry; terrain; Western Arctic Herd; winter range.

Rangifer, Special Issue No. 19: 75–85

Introduction

I hypothesize that the distribution of Western Arctic Herd (WAH) caribou (*Rangifer tarandus granti*) is affected by terrain and snow characteristics, as well as habitat and predation pressure. Looking across the northern landscape, caribou ecotype and disturbance (e.g., wildfire and/or industrial development) are also likely to be important factors in determining distri-

bution (Mallory & Hillis, 1998; Johnson et al., 2005; Joly et al., 2007a). The importance of each factor is likely to depend on the scale of the analysis (Wiens, 1989; Rettie & Messier, 2000; Johnson et al., 2004; Gustine et al., 2006; Mayor et al., 2007). Terrain, snow conditions, habitat characteristics and predation pressure are all interrelated to some degree. High elevation, steep slopes and open habitats often have

less snow due to wind scouring than do protected valleys or forested habitats. Lichen biomass is typically greater in areas that have a protective snow cover as lichens are susceptible to desiccation and wind abrasion (Holt et al., 2008). Terrain is an important factor in determining winter distribution because certain conditions may be correlated with preferred habitats, as noted above, or may provide improved sightability of predators. Snow characteristics are important because movement can be impeded by deep snow, while foraging efficiency can be reduced by either deep or crusted snow (Skogland, 1978; Fancy & White, 1985; Fancy & White, 1987; Collins & Smith, 1991; Joly et al., 2011). Habitat is an important factor because lichens comprise the majority of the winter diet of WAH caribou (Saperstein, 1996; Joly et al., 2007b). Pregnant caribou should be the most reliant on high quality habitat during the winter months as their energetic demands are

relatively higher than other classes of caribou (Cameron *et al.*, 1993; Barboza & Parker, 2008). Different habitat types may also offer varying levels of predation pressure. Similarly, different snow conditions can change the relatively vulnerability of caribou to predation (Telfer & Kelsall, 1984). Predation pressure is an important factor, as caribou not judging this risk correctly will be killed. However, if a caribou is weakened from poor nutrition and killed by a predator, the ultimate factor in its death is habitat quality - predation would be its proximate cause. Too often, this distinction is not made.

The WAH experienced a population crash in the 1970s, rapidly declining from approximately 242 000 individuals in 1970 to 75 000 individuals in 1976 (Dau, 2007). The herd rebounded, reaching a population apex of approximately 490 000 individuals in 2003 (Dau, 2007). At this height, the density of caribou was 1.35/km², which prompted concern about

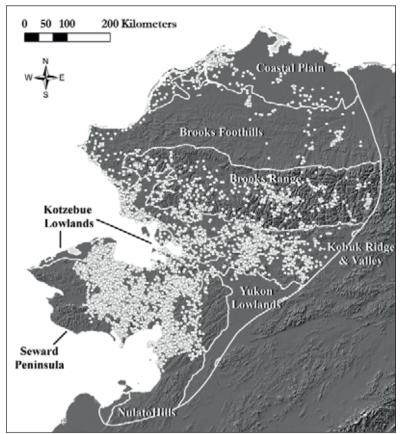


Fig. 1. Distribution of Western Arctic Herd caribou, 1999 – 2005, during winter (October through April), northwest Alaska. Caribou locations acquired by satellite telemetry from 63 cows and 7 bulls are represented by light-colored dots. The ecoregions covering the range of the herd are labeled and outlined in light gray.

overgrazing (Joly et al., 2007c). The 2007 photo-estimate revealed a 23% decline to 377 000 individuals – though the cause of the decline is unknown at this time (Dau, 2007). Significant declines in lichen cover within the core winter range (Joly et al., 2007c) and/or severe winter events (Dau, 2005; 2007) are potential causes. Understanding the drivers of population changes in this herd is important because it serves as a subsistence resource for scores of villages that harvest more than 10 000 caribou annually from this 1 herd (Dau, 2007).

My goals were to 1) document winter distribution of caribou during the period of peak population and 2) determine factors that help explain why caribou go where they do during winter in northwestern Alaska. This information will provide valuable insight into the factors that shape caribou distribution as a basis for predictions of potential changes in caribou distribution if the population continues to decline and

to model how the suitability of winter range may change for caribou under different climate-change scenarios.

Material and methods

Study area

The study area is the range of the WAH, which covers the entire 363 000 km² of northwestern Alaska (63° to 71°N and from 148° to 166°W; Dau, 2007) and contains 8 major ecoregions (Fig. 1, Nowacki et al., 2001). The region transitions from treeless arctic tundra in the north and west to black spruce (Picea mariana) stands and eventually to boreal deciduous forests in the south and east. At the northern extreme of the study area, the Coastal Plain is primarily a flat, poorly drained wetland that is underlain by continuous permafrost. The ground of the Brooks Foothills, to the south, is composed of thick continuous permafrost and supports no trees. Low shrubs, sedges, and tussock tundra dominate this region but extensive willow thickets line the many braided rivers and streams (Nowacki et al., 2001). The steep angular peaks of the Brooks Range are largely barren, while alpine vegetation can be found at lower elevations (Nowacki et al., 2001). Forests and woodlands dominate much of the Kobuk Ridge and Valley ecoregion on the southern flanks of the Brooks Range (Nowacki et al., 2001). The Kotzebue Lowlands lie to the west of the Kobuk Ridge and Valley ecoregion and is dominated by tundra and coastal ecosystems. The Seward Peninsula ecoregion is a mosaic of extensive hills, coastal lowlands and isolated rugged mountain complexes (Nowacki et al., 2001). The moist polar climate supports tundra, dryas, and shrub communities (Nowacki et al., 2001). To the east is the Nulato Hills, an ecoregion dominated by low but often rugged hills. Vegetation varies widely with elevation, from well-forested areas in the river valleys to shrubs on side slopes and alpine communities on the ridges and summits (Nowacki et al., 2001). The Yukon Lowlands is dominated by the confluence of the Yukon and Koyukuk Rivers which forms an expansive wetland system complex of deciduous and coniferous forests, tall shrub and muskeg communities (Nowacki et al., 2001).

Caribou can be found throughout their annual range during winter, though use is more concentrated on the Nulato Hills, upper Kobuk River and eastern Seward Peninsula (Joly et al., 2007a). These regions are diverse, with extensive areas of treeless tussock tundra (Eriophorum vaginatum, Carex spp.), rugged but low elevation (< 1100 m) mountains, and shrub-lined (Salix spp., Alnus crispa) riparian corridors. Lichens

(Cladina spp., Cetraria spp.), mosses (Sphagnum spp., Polytrichum spp.) and shrubs (Betula nana, Empetrum nigrum, Ledum palustre, Vaccinium uliginosum and V. vitis-idaea) are important components in tundra habitats (Joly et al., 2007c). Mean annual precipitation for the region is about 300 mm. Snow cover occurs throughout the winter (October through April), though some areas may be snow free due to wind scouring or uncommon weather events that bring above freezing temperatures and rain. Although average daily temperatures can drop to – 45 °C during winter, the average daily temperature for the winter months is -3.3 °C. Mean temperatures have risen significantly over the study period in this region, especially during the winter (Stafford et al., 2000).

Data acquisition and derivation

Caribou were captured as they swam across the Kobuk River at Onion Portage, located within Kobuk Valley National Park, using motorboats. A total of 70 caribou (63 cows and 7 bulls) were instrumented with satellite telemetry collars. Caribou location data were not used for a year after deployment to ensure adequate mixing with the entire herd (Dau, 2007). A total of 7048 locations from the beginning of October through the end of April were collected from 1999-2005. A total of 20 000 random locations were developed using ArcGIS within the range of the herd. Both the satellite and random locations were attributed with the following data that had potential to affect caribou distribution. Elevation was directly obtained from a Digital Elevation Model (DEM). Slope, aspect and terrain ruggedness indices were derived from the DEM using ArcGIS (ESRI, 2006) tools. I converted aspect from degrees into a categorical variable covering the 8 cardinal directions. I created 2 terrain ruggedness coverages, 1 at a relatively fine scale (180 m cell-size) and the other at a relatively coarse scale (1 km cell-size), using a Vector Ruggedness Measure (VRM) developed by Sappington et al. (2007). This measure incorporates variability in both the aspect and gradient components of slope so that steep, broken terrain can be distinguished from steep, even terrain (Sappington et al., 2007).

I obtained habitat classification data at 2 scales. The National Land Cover Database of 2001 (NLCD; data available from the Multi-Resolution Land Characteristics Consortium, www.mrlc.gov, accessed November 13, 2008) covers the entire study area with 30 m resolution. The development of this dataset relied heavily on remotely sensed data. The study area was covered by the following broad habitat categories; deciduous forest, coniferous forest, mixed forest,

scrub, shrub, sedge, woody wetlands, herbaceous wetlands, bare ground and open water. Forested areas were defined as having > 20% vegetation cover of trees > 5 m high. If there was > 75% of 1 type (not species) of tree it was defined as that type of forest, if neither deciduous nor coniferous trees dominated, then it was defined as mixed. Scrub habitats generally had > 20% cover of low (< 20 cm high) shrubs and were "often co-associated with grasses, sedges, herbs, and non-vascular vegetation". Shrub habitats were dominated by shrubs between 20 cm and 5 m high such as Vaccinium uliginosum, Betula nana, and Salix glauca but could include early successional or trees stunted by environmental conditions (e.g., mesic black spruce stands overlaying permafrost). Sedge habitats were dominated (> 80% cover) by sedges, grasses and forbs. This class included tussock tundra. Woody wetlands were areas of forest or shrubland whose soils were periodically saturated with water. Herbaceous wetlands were dominated by herbs (> 80% cover) and had their soils periodically saturated with water.

The second coverage was a highly detailed habitat vector map, developed by the Soil Conservation Service (SCS; Swanson et al., 1985), was based on extensive ground surveys and low-level photography of the entire Seward Peninsula. This coverage was utilized only when I was performing analyses dealing solely with the Seward Peninsula and represents a fundamentally different dataset and classification system. The SCS delineated over 150 different habitat types within the region. With assistance of local vegetation experts, I aggregated these types into 12 categories; dryas (Dryas spp.; 35 to 65% cover), lowland sedge, lowland low shrub, tussock tundra, lichen (> 24% cover), upland low shrub, tall shrub, forest, mountain meadow, burned tundra, burned forest and miscellaneous un-vegetated areas. Mountain meadow had > 30% graminoid cover whereas upland low shrub had < 25% graminoid cover. The lowland low shrub, mountain meadow, and tussock tundra can have a strong lichen component, with up to 25% cover. These data were from the 1980s, so burned areas are > 25 years old and did not include recent burns.

Data on wolf densities were specious or nearly 20 years old in the study area and so were not analyzed. Existing data for moose density was much more comprehensive, collected annually concurrent with the study period, and may be an index of wolf density (Bergerud, 2007). I also calculated, using the Hawth's Analysis Tools (Beyer, 2006) ArcGIS extension, the distance from every satellite collar location and every random location to the nearest of the 44 villages within the study area.

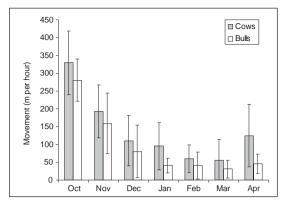


Fig. 2. Winter time movement rates of satellite collared Western Arctic Herd caribou from 1999-2005, northwest Alaska.

Statistical analysis

I used Analysis of Variance (ANOVA) to detect differences among months, between sexes in movement rates, and between satellite location and random points. I employed a logistic regression - resource selection function (RSF) approach to assess factors that influence caribou distribution during winter (Manley et al., 2002). I selected Thomas and Taylor's (1990) Design II, where the locations of individually marked animals are pooled to study population level patterns. Selection or avoidance by caribou was relative to the random locations. Using an information theoretic approach, the best models were determined using Akaike's Information Criteria (AIC.) for small sample sizes to determine the most parsimonious models (Burnham & Anderson, 2002). The full model was compared to the full model minus 1 factor using ANOVA techniques to determine significance of individual model parameters. Using the results of these analyses, I developed a resource suitability map. Significant factors were multiplied by beta coefficients derived from the best model, summed and the exponential was taken of the resultant. The final number represents the relative probability of selecting a given location as determined by the RSF (Manley et al., 2002).

Results

Cows moved significantly more than bulls throughout the winter (140 m/hour versus 97 m/hr, respectively; $F_{1,472} = 6.42$, P = 0.01; Fig. 2). Movement rates declined, for both cows and bulls, from October to December ($F_{1,424} = 112.56$, P < 0.01, $F_{1,42} = 21.65$, P < 0.01, respectively). Movement rates were lowest during mid to late winter. Cow movement rates (124 m/hr) were significantly greater than bulls (45

m/hr) during the month of April ($F_{1,63} = 5.61$, P = 0.02). Cows were found at lower elevations (298 m) and gentler slopes (18°) than bulls (365 m, 23°), but due to low sample sizes these differences were not significant ($F_{1,68} = 2.06$, P = 0.16, $F_{1,68} = 3.33$, P = 0.07, respectively). Because of these differences, I analyzed resource selection separately for bulls and cows.

The best resource selection function model for WAH cow distribution over the entire winter range incorporated slope, aspect, elevation, fine scale (180 m cell-size) terrain ruggedness, habitat and moose density (Table 1a). Cow distribution was positively correlated with slope and fine scale terrain ruggedness but negatively with elevation (Table 2a). Correlation with moose density was not significant. Aspect and habitat were significantly correlated with cow distribution as well (Table 2a). Cows significantly selected southwest to northwest aspects over others and avoided flat (no aspect) terrain (Table 2a).

Scrub, shrub and sedge habitats were significantly preferred, while deciduous and mixed forests and perennial snowfields were used significantly less than expected. The resource suitability map, depicted in Fig. 3, reveals extensive areas of relatively high quality winter habitat in the western (Seward Peninsula ecoregion) and southern Nulato Hills. Areas with lower probability of use include the central Brooks Range and the Yukon Lowlands.

Limiting the analysis to the Seward Peninsula, and using the more detailed SCS habitat map, the best model for cow winter distribution incorporated aspect, elevation, fine scale (180 m cell-size) terrain ruggedness, coarse scale (1 km cell-size) terrain ruggedness, habitat, and moose density (Table 1b). Cow distribution was positively associated with elevation but negatively with coarse scale terrain ruggedness and moose density (Table 2b). Aspect and habitat

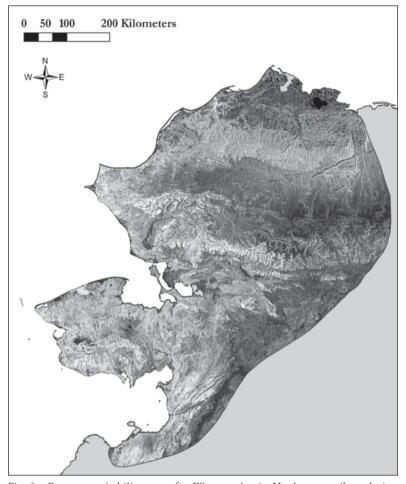


Fig. 3. Resource suitability map for Western Arctic Herd cow caribou during the winters (October through April) from 1999-2005, northwest Alaska. Lighter shades represent greater suitability (relative probability of selection).

were significantly correlated with cow distribution (Table 2b). Cows significantly preferred northeastern aspects. Cows used lowland low shrub, tussock tundra, and mountain meadow habitats preferentially.

The differences between the analysis of the distribution of cows for the entire range and that focusing on the Seward Peninsula included: a change in the correlation with elevation from positive to negative, and negative correlations with moose density and coarse scale terrain ruggedness on the Seward Peninsula. By conducting a second analysis utilizing the range-wide (NLCD) vegetation classification, I was able to directly compare habitat selection for the entire winter and the Seward Peninsula. Selection was very similar for both regions. Cows significantly preferred dwarf scrub and sedge habitats and avoided coniferous forests in both regions. Correlations with deciduous forest (-), mixed forest (-) and dwarf shrub

Table 1. Model selection for Western Arctic Herd caribou distribution during winter (October through April) from 1999-2005, northwest Alaska. Analyses were conducted for cows and bulls for the entire winter range and just the Seward Peninsula.

A) Cows throughout the winter range

Model Parameters	df	AIC	$_{\scriptscriptstyle \Delta}\! AIC$
Aspect, Slope, Elevation, Ruggedness (180 m), Habitat, Moose	25	28687.83	-
Aspect, Slope, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	26	28688.09	0.26
Aspect, Slope, Elevation, Ruggedness (180 m), Habitat,	24	28688.09	0.26
Aspect, Slope, Elevation, Ruggedness (180 m and 1 km), Habitat	25	28688.31	0.48
Aspect, Slope, Elevation, Ruggedness (1 km), Habitat, Moose	25	28699.45	11.62

B) Cows on the Seward Peninsula

Model Parameters	df	AIC	$_{\scriptscriptstyle \Delta}\! AIC$
Aspect, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	24	8093.46	-
Aspect, Slope, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	25	8094.55	1.09
Aspect, Slope, Elevation, Ruggedness (1 km), Habitat, Moose	24	8094.69	1.23
Aspect, Slope, Elevation, Ruggedness (180 m and 1 km), Habitat	24	8096.75	3.29
Slope, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	17	8099.63	6.18

C) Bulls throughout the winter range

Model Parameters	df	AIC	ΔAIC
Slope, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	18	4329.08	-
Aspect, Slope, Elevation, Ruggedness (180 m and 1 km), Habitat	25	4330.56	1.48
Aspect, Slope, Elevation, Ruggedness (1 km), Habitat, Moose	25	4330.92	1.84
Aspect, Slope, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	26	4332.02	2.94
Aspect, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	25	4340.28	11.20

D) Bulls on the Seward Peninsula

Model Parameters	df	AIC	$_{\scriptscriptstyle \Delta}\!AIC$
Slope, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	17	1309.64	-
Aspect, Slope, Elevation, Ruggedness (180 m and 1 km), Habitat	24	1317.40	7.76
Aspect, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	24	1317.70	8.06
Aspect, Slope, Elevation, Ruggedness (180 m and 1 km), Habitat, Moose	25	1319.36	9.71
Aspect, Slope, Elevation, Ruggedness (1 km), Habitat, Moose	24	1319.43	9.79

Table 2. Comparison of coefficients of selection (βi) and standard errors (SE) of factors in the best models describing Western Arctic Herd caribou distribution in winter from 1999-2005, northwest Alaska. (+) indicates a positive correlation while (-) a negative one.

A) Entire winter range

	Cows (n	= 63)	Bulls (<i>i</i> = 7)
Factors	βi	SE	βi	SE
Aspect - SW	0.154 *	0.060		
Aspect - W	0.269 **	0.057		
Aspect - NW	0.145 *	0.058		
Aspect - Flat	-0.581 **	0.090		
Slope	0.021 **	0.001	0.016 **	0.004
Elevation	-0.001 **	0.001	-0.004**	0.001
Ruggedness 180m	3.318 **	0.641		
Ruggedness 1km			4.044 **	0.870
Perennial snow	-2.890 **	1.010		
Deciduous forest	-0.717 **	0.220		
Coniferous forest			0.938*	0.413
Mixed forest	-1.187 **	0.243		
Dwarf scrub	0.727 **	0.109	0.946*	0.394
Shrub/scrub	0.436 **	0.112	0.813 *	0.400
Sedge	0.615 **	0.109		
Woody wetlands	0.269 *	0.136		

^{*} P < 0.05, ** $\overline{P < 0.01}$

B) Seward Peninsula

	Cows (n	Cows (n = 63)		e = 7)
Factors	βi	SE	βi	SE
Aspect - NE	0.239 *	0.109		
Elevation	0.001 **	0.001	0.001 **	0.001
Ruggedness 1km	-5.670 **	0.780	-8.169 **	2.861
Burned tundra			-1.320 *	0.560
Dryas			0.817 *	0.365
Lowland low shrub	1.016 *	0.516		
Lowland sedge			-1.327 **	0.408
Tussock tundra	1.276 *	0.507		
Upland low shrub			-1.148 *	0.481
Moose density	-0.273 *	0.134		

^{*}P < 0.05, **P < 0.01

(+) were not significant for the Seward Peninsula, but showed the same tendency as the correlations did for the entire winter range.

Analyses of bull distribution should be viewed with caution due to limited sample size (n = 7). The best resource selection function model for bull distribution over the entire winter range incorporated slope, elevation, fine and coarse scale (180 m and 1 km cellsize) terrain ruggedness, habitat, and moose density (Table 1c). Bull distribution was positively correlated with slope and coarse scale terrain ruggedness, but negatively correlated with elevation (Table 2a). Habitat was significantly correlated with bull distribution (Table 2a). Bulls selected scrub and coniferous forest habitats. Bull distribution differed from cows in that they were 1) positively associated with coarse scale, not fine scale, terrain ruggedness, and 2) did not show avoidance of deciduous forests and 3) associated with fewer habitat classes.

Limiting the analysis to the Seward Peninsula and the SCS habitat map, the best model for bull distribution incorporated slope, elevation, fine and coarse scale (180 m and 1 km cell-size) terrain ruggedness, habitat, and moose density (Table 1d). Bull distribution was positively correlated with elevation but negatively with coarse scale terrain ruggedness (Table 2b). Bulls showed significant preference for dryas communities, while avoiding burned tundra, lowland sedge, and upland low shrub communities (Table 2b). Similar to cows, the range-wide analysis for bulls revealed a negative correlation between distribution and elevation whereas on the Seward Peninsula the correlation was positive. Also, the correlation with coarse scale terrain ruggedness changed from positive to negative moving from the range-wide to Seward Peninsula analyses. Caribou locations (49.7 km \pm 0.5 km) were significantly closer to villages than random locations (68.6 km \pm 0.3 km) within the study area ($F_{1.27047} = 1272.25$, P < 0.01).

Discussion

A complex interaction of multiple, interrelated factors drive the winter distribution of WAH caribou. My results suggest that studies that focus on a single factor as the presumed determinant of caribou population distribution or dynamics may fail to capture the full, actual situation except under rare cases. The relative importance of predators, habitat, and other factors will be very case specific (Skogland, 1991). For the WAH, all 3 general factors I analyzed (terrain, habitat and predation pressure) were correlated with caribou distribution in winter. Other factors, such as disturbance from wildfire (Joly et al., 2007c; Joly et al., 2010) and industrial development (Vistnes & Nellemann, 2008), which I did not analyze, might also be important for the WAH and other northern caribou herds. By analyzing multiple factors, researchers also garner insight into the cumulative effects these factors may have on caribou (see also Nellemann & Cameron, 1998; Johnson et al., 2005).

The nature and relative importance of terrain features on WAH caribou distribution depended on scale - both of the landscape features themselves and of the extent of the study area. Caribou preferred relatively lower elevations across their winter range but relatively higher elevations on the Seward Peninsula. Average elevation was significantly higher on the winter range outside the Seward Peninsula than within it. Thus selection or avoidance of certain terrain features depends on the landscape available to WAH caribou. Two factors that may help explain these results are vegetation and snow, which are related to both elevation and differ between the entire range and just the Seward Peninsula. Higher terrain is common throughout the herd's range (e.g., the Brooks Range) and is associated with sparsely or non-vegetated areas; providing little forage and thus caribou would utilize relatively low terrain. Relatively high terrain is much more limited on the Seward Peninsula. Furthermore, the Seward Peninsula is a maritime climate and receives more snow on average than most of the range which experiences climate conditions more typical of continental areas. Deep snows accumulate in the lowlands of the Seward Peninsula and would explain caribou preference for relatively higher elevations there as ridges tend to be more windswept and have lower snow depths in general. Ridges with low snow accumulation tend to enhance the predictability of winter range use (Russell *et al.*, 1993). A similar, but opposite, relationship was found with coarse scale terrain ruggedness between these regions. This suggests that there may be threshold values of terrain features where caribou usage will be greatest. WAH cows showed a positive relationship with fine scale terrain ruggedness over the entire winter range. This uneven terrain may provide a diversity of habitats for foraging and softer snow conditions that allow access.

Cow distribution on the Seward Peninsula was negatively correlated with moose density. This result may seem intuitive as caribou tend to avoid habitat that has recently burned (Joly et al., 2007a; Joly et al., 2010), whereas moose select for it (Maier et al., 2005). Furthermore, high moose densities could support high wolf densities which would reduce its suitability for caribou (Bergerud, 2007). However, moose density was not well correlated with cow distribution throughout the winter range or bull distribution at either scale, and these relationships were positive in nature. A positive correlation between caribou and wolf density could develop if wolves were successful in areas that had consistently high caribou densities during winter. Thus the lack of significant correlations among moose density and cow (entire winter range) and bull (both over the entire winter range and the Seward Peninsula) distribution may indicate that moose density may not be an adequate index of wolf density and/or the effects of predator densities on caribou distribution is more complicated than simple selection or avoidance.

WAH cows avoided forested areas across the winter range and preferred scrub, shrub and sedge habitats, highlighting the long-known importance of tundra habitats (Murie, 1935; Skoog, 1968). I found a strong agreement between the habitat associations throughout the winter range and those found on the Seward Peninsula for WAH cows. These habitat types typically have relatively high lichen cover (Swanson et al., 1985). Lichens are an important component of the winter diet of WAH caribou, making up a majority of their forage (Saperstein, 1996; Joly et al., 2007b). Concurrent with major declines in lichen cover within the core winter range of the WAH (Joly et al., 2007c) and the percentage of lichens in their winter diet (Joly et al., 2007b), the size of the WAH peaked and has declined for the first time in 30 years. Though only anecdotal, this evidence supports the theory (Klein, 1991) that lichens may be a critical component of the winter diet of large migratory herds in North America (see also Holleman et al., 1979). This does not, however, refute the importance of predators on Rangifer population dynamics, especially

at lower densities. Nor does it preclude the possibility that other factors, such as severe winter weather (Dau, 2007; Joly *et al.*, 2011), are the major driver or have had additive effects.

The distribution of bulls differed from that of cows. Preference of habitat types was muted in comparison to cows, though bulls avoided lowland sedge habitats. Bulls were found at higher elevations and steeper slopes than cows. These conditions are often associated with more open habitats, as was seen with the affinity for dryas community types on the Seward Peninsula by bulls. Also, bull distribution was not correlated with fine scale terrain ruggedness, as cow distribution was. These differences in distribution point to the use of alternative overwintering strategies between the sexes.

Though hampered by low sample sizes, my analyses suggest that bulls may be adopting an energy conservation strategy that favors reducing exposure to predation, whereas cows are sacrificing exposure to predators in return for maximizing energy intake by utilizing habitats with greater lichen forage. Higher movement rates by WAH cows, as compared to bulls, throughout the winter months supports this theory of differing overwintering strategies (Roby & Thing, 1985). Vigilance alone does not explain these differences as bulls found in higher, open habitat could identify approaching predators at a greater distance than foraging cows but the large group sizes of cow and young caribou would improve vigilance relative to the smaller bull groups. The smaller group sizes would allow bulls to utilize smaller patches and exert less grazing pressure within an area. Cows, which retain their antlers over the winter, would also have a competitive advantage in maintaining and/or usurping optimal foraging locations and feeding craters (see Holand et al., 2004).

Ultimately, the trade-offs between predatory exposure and forage intake are likely due to differing energetic demands. A vast majority of cows are pregnant during the winter months; this extra energetic demand may induce cows to try to maximize energy intake through foraging rather than adopting an energy conservation strategy utilized by bulls. These strategies may be reversed in spring when cows head towards calving grounds with lower predator densities and bulls lag behind consuming emergent green vegetation high in protein content (Heard *et al.*, 1996).

The RSF map (Fig. 3) reveals higher probability of use in the Nulato Hills and Seward Peninsula. Use of the northern Brooks Foothills by WAH caribou has been limited despite moderately high probability of use as determined by the RSF (Fig. 1, Fig. 3). This

lends further support to the argument that lichens are an important winter forage for WAH caribou, as forage lichen abundance is very low in this ecoregion but snow depths and wolf densities are favorable (both low) for caribou compared to other portions of the winter range. However, limitations in the RSF cannot be ruled out as an explanation for this discrepancy. Expansion of the winter range to the southeast, into the Yukon Lowlands ecoregion seems unlikely as the probability of use as determined by the RSF was quite low. Furthermore, this area already supports high wolf densities without having regular or extensive usage by the WAH, more wildfire, and lower biomass of lichens (Joly et al., 2010). The western reaches of the Seward Peninsula have not been extensively used by the herd, had high probability of use and thus represent an area that has potential as an area for the herd to expand its winter range. This portion of the Seward Peninsula includes the largest towns and remaining reindeer (Rangifer tarandus tarandus) herds in the region, which could present problems if the herd did expand its range there (Dau, 2000).

Management implications

In order to better understand caribou distribution in winter, better information on predator densities, habitat, snow conditions, and weather should be collected. While efforts are currently underway to improve our understanding of most of these factors, it cannot be said for predator densities. To better understand caribou distribution and population dynamics in northwest Alaska, improved information is needed on predator distribution, predator abundance, predation rates and the factors that regulate them. A transition from traditional satellite collars to GPS-satellite collars will improve researchers' ability to analyze caribou movements, distribution and habitat use within the region (Joly, 2005; Joly et al., 2010). Dramatic changes are taking place rapidly in the Arctic and on the winter range of the WAH specifically (ACIA, 2005; Joly et al., 2007c). The analyses presented here provide a useful foundation for modeling the effects of future potential climate regimes on the abundance and quality of caribou winter range in northwest Alaska.

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Female site fidelity of the Mealy Mountain caribou herd (Rangifer tarandus caribou) in Labrador

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Abstract: The Mealy Mountain caribou population of southeastern Labrador is listed as threatened. Site fidelity - the philopatric tendency of an animal to remain in or return to the same site - has often been suspected in sedentary caribou like the Mealy Mountain, but rarely has been examined. Philopatric behaviours are important because fidelity sites may then receive priority protection from human disturbance. To describe and document site fidelity for the Mealy Mountain herd, satellite telemetry data from 12 collared adult females during three years was examined. The mean distance between locations in consecutive years of tracking the individual caribou was calculated and an annual profile of site fidelity generated. This profile illustrated that the lowest inter-year distances occurred during calving, when caribou returned to within 3.9 km (2005-06) and 11.5 km (2006-07) of the previous year's location, and during post-calving, when the mean distance was 7.7 km (2005-06). Spring snow depths were substantially greater in 2007 and appeared to weaken calving site fidelity. This spatial information may serve as a basis for detecting anthropogenic effects on woodland caribou.

Key words: anthropogenic effects; calving; Labrador; philopatry; snow.

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Introduction

The Mealy Mountain Caribou Herd (MMCH) is a woodland caribou (*Rangifer tarandus caribou*) population inhabiting 24 000 km² in southeastern Labrador (Otto, 2002), an example of the forest-dwelling, sedentary ecotype. Like other woodland caribou populations, they migrate short distances of only 50-150 km; females "space out" at calving time; and they are either solitary, or form small groups, depending

on the season (Seip, 1992; Mallory & Hillis, 1998). They are late-successional specialists of the boreal forest and are generally found in mature coniferous forests of North America (Miller, 1982; Ahiti & Hepburn, 1967). Since the 1800s, their numbers have greatly declined and their range in North America has diminished, leaving them confined to even more northerly portions of their range (Bergerud, 1974a; Miller, 1982). Many forest-dwelling populations,

along with the MMCH, are listed as threatened by the Committee on the Status of the Endangered Wildlife in Canada (COSEWIC) due to predation, disease, and habitat loss that is potentially caused by forest fires, the expansion of human settlements, and land development (Armitage & Stopp, 2003; Schaefer & Pruitt, 1991; Seip, 1992; Thomas & Gray, 2002). Although the MMCH population has fluctuated in the past (Bergerud, 1967), recently it has been stable or slightly increasing to approximately 2600 caribou (Otto, 2002; Schmelzer et al., 2004). The most significant threats to the caribou herds in Labrador, including the MMCH, are thought to be illegal hunting and developments such as hydroelectric, commercial forestry, highways and snowmobile trails (Roberts et al., 2006). Development increases human access and disturbance and may fragment the landscape.

Due to the threatened status of forest-dwelling MMCH caribou, it is of the utmost importance to understand the ecological processes and patterns that can assist in devising management strategies to promote their survival and recovery. Site fidelity is the tendency of an animal to remain in or return to the same site. If site fidelity is displayed by individual caribou, those sites, or habitats selected for comprising those sites, may be of particular importance to protect from human access and disturbances. Site fidelity is known to occur in a number of birds and mammals, including caribou (Ferguson & Elkie, 2004; Greenwood, 1980; Metsaranta, 2002; Schaefer et al., 2000; Schieck & Hannon, 1989). It is most common in polygamous mammals where breeding dispersal is male-biased. Adult males gain little from being philopatric so they are more likely to disperse (Greenwood, 1980). It has been suggested that female philopatry has evolved mainly to enhance the cooperative potential among breeding individuals within social groups to eliminate female dispersal cost (Chesser & Ryman, 1986).

Caribou are most commonly faithful to their calving grounds, although some herds have been known to return to the same post-calving, breeding and wintering grounds (Brown & Theberge, 1985; Gunn & Miller, 1986; Ferguson & Elkie, 2004; Schaefer et al., 2000). Along with habitat selection, site selection implies that an animal evaluates available habitats and chooses the one with the highest quality and stability (Switzer, 1993). This selection is viewed as hierarchical process in which an organism first chooses a general place to live (a home range) and then makes subsequent decisions about the use of different patches, the search modes it employs, and its responses to specific objects that it encounters (Johnson, 1980). By being philopatric, the animal

may gain benefits such as a familiarity with resources and a reduction in predation risk (Greenwood, 1980; Schaefer *et al.*, 2000; Rettie & Messier, 1998).

Although fidelity is poorly understood in the MMCH, studies in an adjacent Labrador woodland caribou herd, the Red Wine Mountains caribou, found adult females were highly philopatric to calving and especially post-calving sites (Brown & Theberge, 1985; Schaefer *et al.*, 2000). This knowledge is important because those sites and seasons are now recognized and might be used to protect the herd from human disturbance. Further, since female caribou are highly sensitive and avoid human disturbance (Armitage & Stopp, 2003; Banfield, 1974; Cameron *et al.*, 1979; Chubbs & Keith, 1992; Cowan, 1974; Miller & Broughton, 1974; Harrington & Veitch, 1992), changes in site fidelity might be useful to gauge human disturbance and habitat changes.

Satellite telemetry was used to document site fidelity of adult female Mealy Mountain caribou. It was predicted that site fidelity would be displayed by the MMCH and would be most prominent during calving and post-calving seasons, that the degree of fidelity would differ between years, and that this difference may be governed by annual variation in snow cover.

In order to test these hypotheses, 12 female caribou from the MMCH were collared and satellite telemetry was used to pinpoint their locations on 4-day cycles. Because it has been suggested that the MMCH is divided into a mainland subpopulation and an island subpopulation in which individuals are thought to only inhabit George Island, a 12 km2 island located 9 km offshore from the herd's range (Jeffery et al. 2007), the telemetry data from both of these putative subpopulations were examined closely. To quantify fidelity inter-year distances between previous year locations were computed to examine annual profiles of the tendency to return to the same site (Schaefer et al., 2000). Snow cover data were used to relate the strength of fidelity to snow accumulation, a major influence on the year-to-year patterns of range use by caribou (Bergerud, 1967; Eastland et al., 1989). Home range size and travel rates were also quantified in order to test for correlations with site fidelity.

Materials and methods

Study area

Labrador is a relatively undeveloped landmass consisting of boreal and subarctic ecozones. The study area was comprised of approximately 60% forest, 30% tundra, soil and rock barrens, and 3.5% peatlands (Roberts *et al.*, 2006). Black spruce (*Picea mari*-

ana) was the most common tree species, while other softwoods included white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*), and hardwoods included white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), many willow (*Salix*) species, which together made a total of 150 species of shrubs and trees (Ryan, 1978). There are 610 species of lichen known to Labrador (Ahiti, 1983). Moose and wolves were present in the study area (Roberts *et al.*, 2006).

Typical total mean annual precipitation in the southern regions of Labrador is 1300 mm, and normal mean temperature, 0 °C (Banfield, 1981; Peach, 1984), with an annual mean snowfall of 300-400 cm (Roberts *et al.*, 2006).

Data collection

On 18 April 2005, 12 female caribou, 8 from the mainland and 4 from George Island, both from the Mealy Mountain herd, were captured using a Coda net gun with 5-m x 5-m nets. The net gun was fired from an A-Star Helicopter that flew in a systematic flight pattern across the herd's range. GPS satellite hybrid collars (Telonics, Mesa, Arizona, USA) with a lifespan of three years were then fitted onto the animals. Location data via satellite were determined at 4-day intervals from CLS America supplier from 18 April 2005 to 25 June 2007.

Six seasons were established: Winter -4 December to 3 April, Spring Migration -4 April to 31 May, Calving -1 June to 3 July, Post-Calving -4 July to 7 September, Pre-Breeding -8 September to 27 October, and Fall Migration -28 October to 3 December.

Data analysis

All statistical analyses were undertaken using Statistica v.9. One-sample Kolmogorov Smirnov tests were performed in order to confirm normality. All figures were created using Statistica v.9 or Microsoft Excel 2007.

Site fidelity

Longitude and latitude coordinates were converted into radian longitude and latitudes in order to allow for distance between years in kilometres to be calculated. For each individual, the radian location data were paired for every four-day location according to Julian day between consecutive years (2005-2006 and 2006-2007). Locations that were not matched with a consecutive-year location were removed. The distance between consecutive-year locations according to the following formula:

Distance=ABS(ACOS(((COS(Rla1)*COS(Rlo1)) *(COS(Rla2)*COS(Rlo2)))+((COS(Rla1)*SIN(Rlo

1))*(COS(Rla2)*SIN(Rlo2)))+((SIN(Rla1))*(SIN(Rla2))))*6370)

Where Rlo1 was the radian longitude of the later year, Rlo1 was the radian latitude of the later year and Rlo2 and Rlo2 were the radian longitude and latitude of the previous year, respectively.

For every 4-day cycle, the mean inter-year distance was calculated for the group of 8 'mainland' females as well as separately for the 4 'island' females from George Island and was used to generate profiles from 18 April to 28 December (2005-06) and 4 January to 25 June (2006-07). Repeated Measures ANOVA's were performed on the mainland female inter-year distance means for the 2005-06 and 2006-07 year sets. Fisher LSD tests were used to determine where the inter-year distance means for the mainland females differed between months.

Home range size and site fidelity

The annual home ranges size of each of the 8 mainland individuals from 1 June 2005 to 31 May 2006 and 1 June 2006 to 31 May 2007 were calculated by plotting all telemetry locations onto ArcGIS v.9.2. Locations were converted from latitude and longitude (WGS 1984) into UTM (Universal Transverse Mercator; NAD 1927, Zone 21) coordinates. Hawth's Analysis Tools extension was used to calculate a minimum convex polygon (MCP) for each individual. The MCP areas were plotted against the mean intervear distances during the calving seasons (1 June to 3 July), 2005-06 and 2006-07, to examine the relationship between home range size and fidelity.

Home range variation between years

The mean home range size for the 8 mainland females from 1 June to 31 May, 2005-06 and 2006-07 was calculated and a paired *t*-test was performed to determine if there was a significant difference in home range size between years.

Rate of travel

The mean daily rate of travel was calculated for the 8 mainland females from 1 June to 31 May, 2005-06 and 2006-07. A paired *t*-test was performed to determine if there was a significant difference in the distance travelled per day between years.

Snow cover

Snow cover data for the nearby communities of Happy Valley-Goose Bay and Cartwright were obtained from Environment Canada (Environment Canada, 2008) for April to June, 2006 and 2007. The mean depth of snow-on-the-ground for each month during each year was calculated.

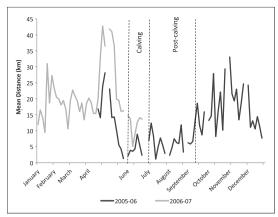


Fig.1. Site fidelty, expressed as mean inter-year distances, 2005-06 (black) and 2006-07 (grey), of mainland adult female caribou of the MMCH.

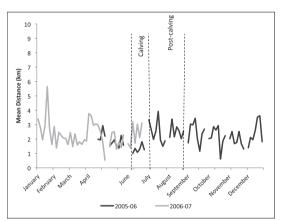


Fig. 2. Site fidelty, expressed as mean inter-year distances, 2005-06 (black) and 2006-07 (grey), of island adult female caribou of the MMCH.

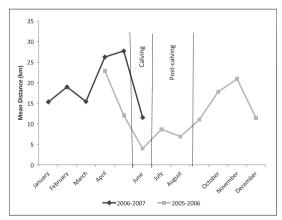
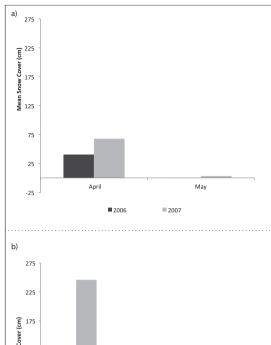
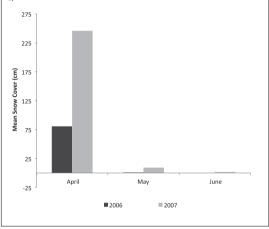


Fig. 3. Annual differences in site fidelity of mainland females, expressed as mean inter-year distance per month during 2005-06 (black) and 2006-07 (grey) of adult female caribou of the MMCH.





Figs. 4a, 4b. Mean snow cover in April, May and June in (a) Happy Valley-Goose Bay and (b) Cartwright, Labrador.

Results

The partial year-long profiles of female caribou fidelity, expressed as the distance between consecutiveyear locations between 2005-06 and 2006-07, for the mainland (Fig. 1) and island (Fig. 2) groups, showed that fidelity was greatest during calving and post-calving for the mainland group, but did not appear to be displayed at a seasonal scale in the island group. Therefore the focus was on the mainland group exclusively for all subsequent analyses. During calving, the inter-year distance was only 3.9 km during 2005-06 and 11.5 km during 2006-07. During post-calving the mean inter-year distance was 7.7 km (2005-06). In contrast, fidelity was lowest during winter. Female caribou were, on average, 17.1 km and 19.0 km, in 2005-06 and 2006-07 respectively, from their previous year's location.

Table 1. Mean inter-year distance between month p-values as resulting from Fisher LSD test (2005-06). * represents significant pairwise differences.

Month	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
April		0.027*	0.003*	0.006*	0.014*	0.058	0.749	0.960	0.120
May	0.027*		0.345	0.510	0.768	0.726	0.054	0.025*	0.467
June	0.003*	0.345		0.771	0.513	0.200	0.006*	0.003*	0.102
July	0.006*	0.510	0.771		0.715	0.316	0.013*	0.005*	0.172
August	0.014*	0.768	0.513	0.715		0.519	0.029*	0.013*	0.309
September	0.058	0.726	0.200	0.316	0.519		0.108	0.052	0.704
October	0.749	0.054	0.006*	0.013*	0.029*	0.108		0.712	0.210
November	0.960	0.025*	0.003*	0.005*	0.013*	0.052	0.712		0.110
December	0.120	0.467	0.102	0.172	0.309	0.704	0.210	0.110	

There was a significant difference in mean interyear distances of mainland females between months in 2005-06 ($F_{8, 24} = 3.4$, P = 0.009) and 2006-07 ($F_{5, 35} = 3.5$, P = 0.012). Fidelity at calving (June) tended to be significantly different than in fall and early spring (April, October, November, sometimes May) but not post-calving (July, August, September; Tables 1 and 2).

The correlation between the mean inter-year calving distances (km) and the annual home range sizes (km²) was weak for both 2005-06 ($r^2 = 0.123$) and 2006-07 ($r^2 = 0.250$).

Strength of fidelty differed between years. The 2006-07 distances were greater than the 2005-06

distances during the overlapping months of April to June (Fig. 3). In April, caribou in 2005-06 were 3.4 km closer to their previous year site than they were in 2006-07 (Table 3); in May, they were 15.7 km closer in 2005-06 than in 2006-07, and in June, were 7.6 km closer in 2005-06 than 2006-07. These distances were significantly different for May and June, but not April.

The snow depth in Happy Valley-Goose Bay (Fig. 4a) was 67% greater in April and May 2007 than in

Table 2. Differences among monthly mean inter-year distances (km) of adult female caribou, 2006-07. * represents significant pairwise differences (Fisher LSD test).

Month	Jan	Feb	Mar	Apr	May	Jun
January		0.462	0.983	0.033*	0.017*	0.450
February	0.462		0.475	0.149	0.085	0.141
March	0.983	0.475		0.035*	0.018*	0.437
April	0.033*	0.149	0.035*		0.768	0.005*
May	0.017*	0.085	0.018	0.768		0.002*
June	0.450	0.141	0.437	0.005*	0.002*	

Table 3. Mean calving site fidelity (inter-year distances) for female MMCH caribou during 2005-06 and 2006-07. Paired t-test results indicated significant differences in May and June (n=8).

	Mean Distance 2005-06 (km)	Mean Distance 2006-07 (km)	Difference (km)	P-value
April	22.9	26.3	3.4	0.58
May	12.0	27.8	15.7	0.0001
June	3.9	11.5	7.6	0.04

2006, i.e., mean snow depth was 40.5 cm in 2006 but 67.7 cm in 2007. Meanwhile, in Cartwright (Fig. 4b) snow depth increased by 204% over the same period. In April of 2006, the mean snow ground cover was 80.8 cm, whereas in 2007 the mean was 245.8 cm. In June, there was no snow in 2006, but in 2007 there was a mean of 1.7 cm. Caribou experienced both greater depth and duration of snow cover during spring 2007.

Discussion

The degree of fidelity may vary due to the analytical effects of scale (Schaefer et al., 2000). For example, caribou on a large scale may display fidelity to a region, such as an island, and on a finer scale, display fidelity to seasonal calving grounds. Mealy Mountain mainland and island female caribou displayed differences in site fidelity. George Island has an area of 12 km² and is located 9 km off the coast of Labrador, to the east of the herd's range. It has been suggested that females of the George Island population do not leave the island (Jefferey et al., 2007). Although strongly philopatric at the scale of the whole island, these island females appeared to display an absence of seasonal site fidelity, likely because of the island's small size. The Mealy Mountain mainland females displayed the expected patterns of fidelity, specifically to calving and post-calving sites. Although caribou have been known to display fidelity to many seasonal sites (Metsaranta, 2002; Schaefer et al., 2000), the most pronounced fidelity for females, including the adjacent Red Wine Mountains Caribou Herd, are to calving and post-calving sites (Brown & Theberge, 1985; Ferguson & Elkie 2004; Schaefer et al., 2000). It has been suggested that site fidelity is beneficial because there is an acquired familiarity with resources and an increase in avoidance of predators (Greenwood, 1980). An animal should respond positively to an environment in which its survival chances and reproductive success increase, such as to a familiar site with a decreased risk of predation (Levins, 1968).

The reproductive success of females in many polygamous ungulates, such as woodland caribou, is limited by their ability to acquire adequate food resources for lactation and calf development (Brown & Mallory, 2007) and minimize the risk of predation (Rettie & Messier, 2000). In Alaskan migratory caribou, the progression of the calving season is highly synchronized with forage plant phenology to ensure sufficient food resources, reducing the energetic burden of lactation (Post *et al.*, 2003). During post-calving seasons, doe milk production, fawn survival, and production rates are highly correlated with midsummer habitat (White, 1983). Thus, forage supply likely influences both the sites selected for calving and post-calving and female fidelity to those sites.

Since predation is considered the most important proximal factor limiting caribou populations (Brown & Mallory, 2007), and caribou often avoid habitats with increased predation risk (Rettie & Messier, 2000; Bergerud & Page, 1987), suitable habitat not only includes an abundance of forage, but also a reduction in predation. Caribou are most sensitive to harassment by predators and humans during the

calving season (Armitage & Stopp, 2003) and most calf mortality occurs during the first six weeks of life (Mahoney et al., 1990). To compensate, females may return year after year to a calving site associated with low predator risk, and some authors have suggested that fidelity occurs as an anti-predator tactic (Rettie & Messier, 1998; Bergerud et al., 1983). Another behaviour exhibited by sedentary woodland caribou, including the MMCH, is that females become solitary during calving, often dispersing along lake shores and on islands in open bogs. This behaviour, too, is considered an anti-predator strategy, as the caribou are 'spacing out', i.e., making themselves rare in the midst of predators (Bergerud, 1985; Bergerud & Ballard, 1988). Caribou may be returning to previous year's sites for the added benefit of predator avoidance. Overall, if a site is recognized to have an adequate forage supply as well as a potential decreased risk of predation, it would seem sensible for an animal to return to such a site, enhancing reproductive success. To date, however, studies have failed to uncover a difference in site fidelity for female caribou with calves versus those without calves, owing perhaps to small sample sizes (Schaefer et al., 2000).

Fidelity may vary due not only to the analytical effects of scale (Schaefer *et al.*, 2000) but also to environmental effects of snow cover (Bergerud 1967). The months of April, May and June displayed differences in which 2005-06 had a stronger degree of fidelity than did 2006-07, although only the months of May and June had differences that were significant.

Habitat selection and fidelity to a particular site may change from year to year depending on many factors such as forage supply, predation, alternative prey abundance, habitat alteration, and other environmental factors (Klein, 1970; Bergerud et al., 1983; Mahoney & Schaefer, 2002; Miller et al., 1985; Ion & Kershaw, 1989). Snow cover is a particularly important factor in the winter ecology of Rangifer (Pruitt, 1959; Bergerud, 1967). Two towns in the vicinity of the herd's range, Happy Valley-Goose Bay and Cartwright, provided snow depth data for the months leading up to calving (April and May, as well as during the calving season, June). There was substantially less snow in 2006 than in 2007. This coincided with greater calving site fidelity in 2006 and weaker fidelity in 2007, and suggests that snow cover acts as an important environmental component affecting the animal's return to the same site (Eastland et al., 1989; Bergerud, 1967).

In contrast, home range size and rate of travel did not differ significantly between 2005-06 and 2006-07. This suggests that in response to the increase in snow cover, the MMCH did not respond with respect

to these two features, but possibly instead moved to regions with less snow accumulation. When snow accumulation is great, caribou often display increased inter-year distances from previous locations (Wittmer et al., 2006). Bergerud (1967) discovered that the winter distribution of the MMCH varied between years in relation to snow cover. In years with greater snow accumulation, caribou moved north onto the Mealy Mountains where there was less snow, and moved south in years with little snow. In a separate study, Bergerud & Page (1987) found that just prior to calving; female woodland caribou in British Columbia moved to high elevations, apparently to avoid predators during spring in years when snow accumulation was greater.

Snow cover has been shown to be associated with movement, and has been correlated with predation rates, as well as forage abundance. Deep snow can restrict caribou movements causing an increase in energy expenditure (Wilson & Klein, 1991; Cumming, 1992). In migratory herds, this may prevent cows from reaching calving grounds (Bergerud & Ballard, 1988). Although caribou may have restricted movement in deep snow, their wolf predators may be able to travel on top of the snow crust as they have a lighter foot loading, thus allowing kill rates of other prey such as white-tailed deer to increase (Mech & Frenzel, 1971; Nelson & Mech, 1986). In deep snow years, not only does predation increase, but forage supply may decrease, causing caribou to move to areas with less snow in order to gain access to forage that is more easily available (Wilson, 2000; Bergerud, 1974b; Bergerud & Nolan, 1970; LaPerriere & Lent, 1977; Pruitt, 1979). Habitats selected in deep snow years may change to more closed canopy and irregular terrain (with varying wind speeds) that result in shallower snow depths (Bergerud, 1974b; Brown, 2005).

The findings of this study generate conservation possibilities for the MMCH. With knowledge of site fidelity, which is a predictable year-to-year behaviour, one can adopt strategies to protect sites, or habitats comprising those sites, selected during high fidelity seasons, such as the calving and post-calving. Anthropomorphic habitat disturbances such as roads, seismic lines, and forest harvesting, have been demonstrated to have negative impacts on caribou abundance, distribution, and potentially survival and reproduction (Vistnes & Nellemann, 2008; Lessard, 2005). Caribou are the least tolerant of all ungulates to human disturbances (Mallory & Hillis, 1998). Females and calves are highly vulnerable to disturbance during calving as stillbirths, injuries, cow-calf separation, and physiological depression of lactation

can result (Armitage & Stopp, 2003; Banfield, 1974; Cowan, 1974; Miller & Broughton, 1974; Harrington & Veitch, 1992). For example, females are known to be found 2-3 times farther away from clearcuts than males, and are generally more influenced by disturbance than males (Cameron et al., 1979; Chubbs & Keith, 1992). These examples display the vulnerability of caribou during calving and post-calving seasons, suggesting that when they have found a site allowing increased reproductive and survival success, the locations should be protected from anthropomorphic disturbances and development. Because the MMCH and other sedentary herds space out during calving and post-calving seasons as an anti-predator strategy, communal calving grounds do not exist. In order to accommodate protection of sites high in fidelity, an approach that identifies the habitats selected for is ideal. Once identified, habitats associated with high fidelity located in proximity to the home ranges of all individuals, rather than the individual sites themselves, should be protected.

Detecting anthropogenic impacts on caribou is complicated by their longevity and wide-range habitats. Human development and infrastructure will likely increase across the range of the MMCH, and will be associated with a rise in human access to region. It is suggested that site fidelity offers a predictable pattern, which, in light of the probable link to reproductive success, can serve as a sensitive gauge of anthropogenic disturbances. Given the baseline fidelity data, a decrease in the strength of fidelity, specifically by females during calving or post-calving, may be a valuable indicator of the negative effects of disturbance, both natural and human mediated. Evidence of severely weakened fidelity may be associated with compromised reproductive success and have negative consequences for this threatened herd. Conservation actions appropriate to promote the continued existence of the MMCH could be justified based on weakened fidelity. Gathering baseline understanding, as it was done here, is the first step to such conservation actions. Future monitoring of inter-year distances, which may indicate changes in the degree of site fidelity, is recommended.

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Little Smoky Woodland Caribou Calf Survival Enhancement Project

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Abstract: The Little Smoky woodland caribou (Rangifer tarandus) herd is a boreal ecotype located in west central Alberta, Canada. This herd has declined steadily over the past decade and is currently thought to number approximately 80 animals. Factors contributing to the herds' decline appear related to elevated predator-caused mortality rates resulting from industrial caused landscape change. At current rates of decline, the herd is at risk of extirpation. A calf survival enhancement project was initiated in the first half of 2006 as a means of enhancing recruitment while other longer-term approaches were implemented. A total of 10 pregnant females were captured in early March and held in captivity until all calves were at least 3 weeks old. Before release, calves were radiocollared with expandable drop-off collars. Following release, survival of mother and offspring were tracked at intervals until the fall rut. Survival of penned calves was compared to "wild-born" calves at heel of non captive radiocollared females. This approach is compared to other techniques designed to increase recruitment in caribou.

Key words: Alberta caribou; increased recruitment; maternal penning; mitigation of industrial activity.

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Introduction

The Little Smoky caribou herd (LSM) is a small (~ 80 individuals) isolated herd of woodland caribou (Rangifer tarandus) located in west central Alberta. The herd is a boreal ecotype and poor recruitment (averaging 11% of the population) has resulted in a steadily declining population (Fig. 1). The impact of human activities (i.e., oil and gas exploration and development, and timber harvest) on the Little Smoky caribou range has been extensive and is long-term in nature. This alteration to caribou habitat has

been linked to increased predation rates of caribou in Alberta (James, 1999; Dyer, 1999; Dyer et al., 2001; Oberg, 2001; Smith, 2004; Neufeld, 2006). Factors contributing to the LSM herd's decline appear related to elevated predator-caused mortality rates driven by changes in land use. At current rates of decline, the herd is at risk of extirpation, potentially within the next 10 years. The Little Smoky Caribou Calf Project (LSCCP) was proposed by Suncor Energy Inc. as part of a program designed to mitigate the impact of a 100 km pipeline through the LSM range. The

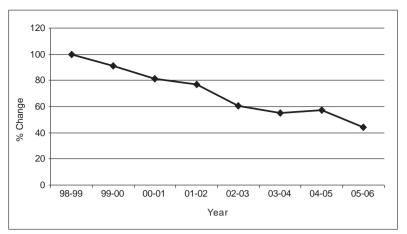


Fig. 1. Cumulative change in the adult female population size (%) of the Little Smoky woodland caribou herd, Alberta (1998 - 2006).

goal was to have an immediate positive impact on calf survival by capturing pregnant females in their last trimester of pregnancy and holding them in a predator-free pen until all calves were at least 3 weeks old. In the long-term, this program was expected to contribute to a broad-based program of intervention and landscape management designed to allow the Little Smoky caribou herd to increase and ultimately be self sustaining within its traditional range.

Methods

The LSM range is located in the upper foothills ecoregion of west central Alberta, Canada (54°N, 119°W). The study area is characterized by an overstory of lodgepole pine (Pinus contorta) and white spruce (Picea glauca) on upland sites and black spruce (Picea mariana) and open muskegs on poorly drained sites. The area has been described in more detail previously (Smith, 2004; Neufeld, 2006). The pen was located within the range of the LSM herd and it included dense, coniferous forest with some terrestrial lichen on elevated well-drained pine sites, arboreal lichens on wetter black spruce sites, an open muskeg and an old trail that bisected the northern half of the enclosure. It was approximately 4.0 ha in size and it was relatively remote from any regular, heavy industrial traffic. A Government of Alberta Ministerial Order was placed on Sections 21, 22, 27 and 28 of Twp. 59, Rge. 26 W5M as provided for under Section 128(1) of Alberta's Wildlife Act. The Ministerial Order excluded non-sanctioned human access and other land uses within the enclosure and the surrounding area between February 15 and July 15, 2006.

The methods guiding the project were mainly based on those developed and successfully imple-

mented for the Chisana caribou herd in the Yukon (http://www.environmentyukon.gov.yk.ca/wildlifebiodiversity/chisanarecovery. php). A geo-textile fence was constructed in late February to early March 2006 by stretching 2 small diameter cables between trees at a height of 2 m and along the ground. Geo-textile fabric was fastened to the cable by overlapping it and stitching it in place with 9 cm nails. An 8 strand, 2 m high electric fence was installed approximately 5 m out from

the geo-textile fence to discourage predators. Additional technical detail on the geo-textile and electric fences can be obtained from the authors.

Adult female woodland caribou were net gunned from a Hughes 500 helicopter and then restrained by the capture team. The caribou were examined by transrectal ultrasonography to determine pregnancy by a veterinarian. Physical parameters were measured, blood samples were drawn and non-pregnant females were collared prior to being released without sedation. Caribou that were pregnant received 100 mg of xylazine plus 1 mg of butorphanol intra-nasally via a 14 cm tomcat catheter. The tomcat catheter was modified for this purpose. After sedation, caribou were placed in specially designed bags for transport in a second (A-star) helicopter. Once in the helicopter, an intranasal oxygen line was placed and the oxygen was set to flow at 5 L/minute.

A staging area was located approximately 500 m from the enclosure to prevent disturbance to caribou already captured and within the enclosure. Ground crews at the staging area transferred the caribou from the helicopter to a sled. The sled was then pulled into the enclosure via a snowmobile. Inside the enclosure the oxygen line, transport bag and hobbles were removed. A reversal of 35 mg of atipamezole was given intramuscularly.

Once all female caribou were captured, field staff remained onsite full-time to manage the daily care of the caribou. This included daily feeding and monitoring, as well as patrolling the enclosure fence perimeter twice daily or more to check the integrity of the geotextile and electric fence, as well as to note any evidence of predator activity. Caribou were fed from troughs. Both lichens collected in the Yukon and commercial pellet rations were used. Feed-

ing began with about 75% lichens and 25% commercial feed, then was slowly switched to 75% commercial feed and 25% lichens. This was reversed a few weeks prior to release, with no commercial feed provided in the last week in order to allow the animals gut flora to once again adapt to native forage. A short (3 m) observation platform was built adjacent to the feed troughs to record daily food intake, behaviour and interactions between animals.

Once calves were born, they were captured within the pen and outfitted with an expandable radio collar (Telonics, Mesa, Arizona). Standard measurements, hair samples and weights were recorded. When the youngest calf was 19 days old, the geo-textile fence was taken down in one section of approximately 100 meters to facilitate release.

Once released, radio-collared caribou were located from the air weekly for the first 2 weeks and then monthly until initiation of the rut. An additional flight was conducted on March 13, 2007 to determine survival to 10 months.

Results

The capture of caribou was delayed in February 2006 due to unseasonably warm weather that presented unsuitable conditions for capture (*i.e.*, +5 °C to +10 °C). A period of colder weather (-15 °C) and precipitation in early March 2006 provided the necessary conditions for capture. Ten pregnant females were successfully captured March 10-12, 2006 and transported to the pen without incident. An additional 2 females were captured and released immediately after collaring. A "wild" sample of adult female woodland caribou had been captured for monitoring purposes in previous winters.

Daily care of the captive caribou began on March 10, 2006. Within 2 days, all animals were approaching and feeding on lichens provided in feed troughs. Within 6 days, pelleted rations were provided along with lichens. Caribou often approached the feed troughs at the sound of the snowmobile or quad used to transport feed. Caribou consumed in the range of 25 to 32 kgs of commercial ration/day (2.5 to 3.2 kgs/animal/day). Caribou also fed upon vegetation within the pen and their reliance on pellets was reduced with spring green-up. Water was available in the muskeg area once temperatures warmed above freezing (no alternative water source was provided). No preda-

 Date of birth and sex of woodland caribou calves born in the Little Smoky Caribou Calf Project enclosure, Alberta 2006.

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Calf ID	Female ID	Calf Birth Date	Calf Sex
C10	F579	May 14, 2006	unknown
C 7	F580	May 27, 2006	F
C6	F583	May 23, 2006	M
C2	F584	May 17, 2006	M
C9	F585	June 1, 2006	F
C4	F586	May 15, 2006	F
C8	F588	May 28, 2006	F
C1	F589	May 22, 2006	M
C3	F587	May 18, 2006	F
C5	F590	May 13, 2006	M

tors approached the fence and the 2 m electric fence functioned well.

Caribou calves were born between May 13 and June 1, 2006. All calves appeared healthy. Collaring of calves was conducted during the period of May 23 and June 3, 2006. During the May 23rd capture attempt one of the oldest calves was not collared because it was too mobile at 10 days of age. Of the nine captured calves, 5 were female and 4 were male (Table 1).

A calf died within the enclosure on June 17, 2006 two days prior to release. The calf was transported to the Calgary Zoo where an autopsy was conducted. Results indicated the cause of death was related to myocardial degeneration and necrosis of the heart (*i.e.*, hemopericardium - an effusion of blood within the sac enclosing the heart) (S. Black, Calgary Zoo, pers. comm.).

The caribou were released from the enclosure on June 19, 2006. The youngest calf was 19 days old. Prior to release, a 5 km wide search was conducted with a helicopter to ensure no predators were within the immediate area (none were observed). The caribou (10 cows and 9 calves) left the enclosure without incident. Staff remained onsite to remove the electric and geo-textile fence and close-up camp.

Aerial telemetry flights were conducted on June 27, July 5, August 25 and September 22, 2006. The cows dispersed well away from the enclosure post-release (up to 20 km). Data from the aerial monitoring surveys recorded two calf mortalities by bear predation (*Ursus* sp.) in the vicinity of the pen near the Little Smoky River (July 7 and August 25, 2006)

Table 2. A comparison of calf survival between penned and "wild born" calves in the Little Smoky woodland caribou range, Alberta, May to September, 2006.

		Calves Al	ive/Dead	
ID # Cow	ID # Calf	May 29, 2006	Sept. 22, 2006	Comments
Pen				
F583	C6	Alive	Alive	
F584	C2	Alive	Alive	
F580	C 7	Alive	Alive	
F586	C4	Alive	Alive	
F585	C9	Born June 1	Alive	
F588	C8	Alive	Dead	Mortality by July 7, 2006. Bear mortality.
F587	C3	Alive	Dead	Died in enclosure on June 16, 2006.
F590	C5	Alive	Dead	Mortality by September 22, 2006. Cause of death unknown.
F589	C1	Alive	Dead	Mortality by August 25, 2006. Bear mortality.
F579	C10 -not collared	Alive	Dead	Mortality by September 22, 2006. Cause of death unknown.
Wild				
F578	N/A	Alive	Alive	
F575	N/A	Alive	Alive	
F581	N/A	Alive	Alive	
F519	N/A	Alive	Alive	
F543	N/A	Alive	Alive	
F576	N/A	Dead	Dead	Calf assumed to have died before May 29, 2006 or female not pregnant.
F554	N/A	Dead	Dead	Calf assumed to have died before May 29, 2006 or female not pregnant.

and a third mortality of unknown cause by September 22, 2006 near Meridian Lake (~ 13 km to the NW of the pen). Based on a sample size of 10 calves for the LSCCP and 7 calves for the wild population, the calf survival rate was 50% and 71% respectively. The uncollared captive calf was no longer "at heel" by September 22, 2006, but all other collared calves that had survived and the wild calves were still at heel at that time. The cause of death of the uncollared captive calf is unknown (Table 2).

The total count and classification of the Little Smoky caribou herd on September 22, 2006 was 73 caribou including 14 calves. This was the highest % calves (19%) observed up to that time based on 10 surveys that had been conducted between 1982 and this study. A final monitoring flight was completed on March 13, 2007. At that time, at least 3/5 remaining "penned" calves and 3/5 wild calves were observed alive (calves still made up 14.5% of the total of 55 classified caribou).

Discussion

The success of the LSCCP is difficult to measure given that the Alberta Government implemented a wolf control program in west-central Alberta during the same period with the primary goal of increasing caribou calf survival. Wolf removal occurred through helicopter gunning between December 2005 and March 2006 over the entire LSM range including the immediate vicinity of the pen. Wolf densities were believed to have been reduced from ~ 30 wolves/1000 km² down to 5 to 8 wolves/1000 km². The penned caribou were not exposed to predation during captivity and would have benefited once released.

The low sample size of calves available in the study provides a "marginal" opportunity to com-

pare survival rates between the penned calves and "wild" born calves. Based on the age of the LSCCP calves at release, it was anticipated the calves would have a greater chance of survival. Survival of penned calves may have been compromised by their mothers returning to the penning area during the summer and predisposing them to bear predation. This behavioral response of returning to the pen in the summer was also documented in the Yukon, but not with any apparent affect on survival of calves. There is no previous data related to location of calf mortalities in the Little Smoky herd (i.e., calves have never been collared before) and similarly, data on movements of bears has not been studied in detail. The two bear mortality sites were located approximately 2 to 3 km from the caribou enclosure in close proximity to the Little Smoky River. A river the size of the Little Smoky River would tend to be used in the spring and mid summer by grizzly bears (Nielsen et al., 2002). Black bears also select for riparian areas at this time of year (Czetwertynski, 2007). Although the supporting data to suggest a relationship between the calf mortalities and distance to the enclosure is limited, locating the enclosure a greater distance from a major river (where bear densities tend to be greater due to the presence of preferred bear forage) should be considered.

Woodland caribou appeared to adapt well to confinement and habituated to field staff readily. Dominance was apparent around the feed troughs, but not to any obvious detriment of any particular animal. The only apparent injuries accrued during the animals' confinement were the previously mentioned death of a newborn calf and one cow which suffered an abrasion to her side and back in late May that resulted in hair loss to the skin. The cow had fallen into a tree well/hole in the muskeg and suffered the injury while struggling to release herself. She didn't appear to be debilitated by the injury and she survived until the following spring (May 2007). (Her calf died by September 22, 2006, but it is not known if her injury in the pen contributed to this death).

If obvious benefits of penning were realized, they were masked by the simultaneous treatment of wolf control. Additionally, bear (or other) predation within the range of the LSM herd may be more significant than originally thought. The cost of penning (approximately \$40 000.00 CAN/calf) was much higher than wolf control (Alberta Fish and Wildlife Files). Penning is only effective if other land management and conservation strategies are implemented concurrently. In combination with the penning project, positive changes to the landscape (e.g., habitat condition) will serve to benefit calf recruitment and survival.

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The West Central Alberta Woodland Caribou Landscape Plan: Using a Modeling Approach to Develop Alternative Scenarios

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Abstract: Woodland caribou (Rangifer tarandus) are classified as threatened in Alberta. In support of Canada's Species at Risk Act, a Recovery Plan for Woodland Caribou in Alberta was completed in 2004 which required local implementation plans to be completed within 5 areas of the province. The West Central Alberta Caribou Landscape Plan (WCCLP) is the first of these to be initiated and it addresses the recovery strategies for 4 herds. Two aspatial computer models built on the STELLA[®] modelling platform (ISee Systems, 2007) were used to assist the planning team in evaluating cumulative effects and alternative scenarios for caribou conservation. The ALCES® (Forem Technologies 2008) modelling tool was used to forecast potential changes in the west central Alberta landscape over time. Yearly landscape condition outputs from ALCES® were then exported into a caribou-specific population model, REMUS® (Weclaw, 2004), that was used to project potential population responses by woodland caribou, other primary prey species [moose (Alces alces), elk (Cervus elaphus) and deer (Odocoileus sp.)] and wolves (Canis lupus) (Weclaw & Hudson, 2004). Simulated habitat management strategies that resulted in the highest likelihood of caribou recovery included the maintenance of a high proportion of old forest, the aggregation of industrial footprints and the reclamation of historic seismic lines (although the latter took decades to provide real dividends). Sharing of industrial roads, protection of fragments of old-growth, and expanding an already aggressive fire control strategy in Alberta had little additional effect on caribou recovery. Simulated population management strategies that were successful all involved decades of intensive wolf control, either directly or indirectly through intensive primary prey control (with the exception of woodland caribou) until old-growth forests recovered to densities that provided caribou habitat and decreased alternate prey of wolves. Although this modelling approach makes broad assumptions, it provides simple fundamental relationships that were useful in a multi-stakeholder team setting when evaluating the efficacy of different management strategies for the conservation of woodland caribou.

Key words: Alberta; anthropogenic features; computer modeling; caribou habitat; modeling; predator-prey; landscape planning; woodland caribou.

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Introduction

Woodland caribou (Rangifer tarandus) are classified as threatened in Alberta. In support of Canada's Species at Risk Act, a Recovery Plan for Woodland Caribou in Alberta was completed in 2004. It established the need for 5 individual range teams to assess and determine recovery actions at local scales within Alberta. In the province of Alberta, woodland caribou ranges are experiencing expanding oil and gas and timber harvesting activity that is dramatically altering habitat. The purpose of each range team was to develop and recommend strategies that would guide the recovery and management of woodland caribou populations and habitats within each caribou landscape. It was intended for these plans to fulfill the requirement of the federal Species at Risk Act (SARA) to develop an action plan for woodland caribou conservation. The West Central Caribou Landscape Planning Team (WCCLPT) was the first of these teams to be initiated.

The WCCLPT represented a cross-section of stakeholders with an interest in caribou recovery and management in the west central area of Alberta: Alberta Sustainable Resource Development (Chairperson, plus two members); and one member each from Alberta Tourism, Parks, Recreation and Culture; Alberta Energy; Aseniwuche Winewak Nation of Canada (Grande Cache); Treaty 8, First Nations of Alberta; Alberta Forest Products Association; Canadian Association of Petroleum Producers; Canadian Parks and Wilderness Society (CPAWS) - Edmonton Chapter; and Parks Canada (Jasper National Park). The WCCLPT reported directly to the Alberta Caribou Committee (ACC) Governance Board. The ACC is also a multi-stakeholder advisory committee whose mandate is to provide advice to the Government of Alberta (through the Deputy Minister of Alberta Sustainable Resource Development) and to implement or support "approved caribou population and habitat conservation and recovery programs" (Alberta Woodland Caribou Recovery Team, 2004).

Two aspatial computer models built on the STEL-LA® platform were used to assist the planning team in evaluating alternative scenarios for caribou conservation. The primary objectives of the exercise were to examine strategies that would conserve woodland caribou herds in west central Alberta.

Methods

The study area is located in west central Alberta, Canada (54°N, 119°W) and it encompasses 4 herds (Fig. 1). The area includes the upper foothills, subalpine and alpine ecoregions (Beckingham *et al.*,

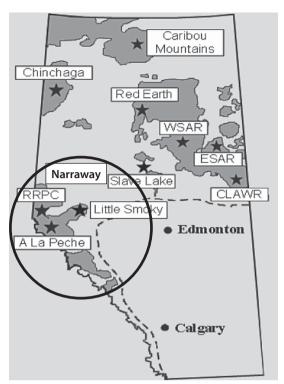


Fig. 1. Locations of woodland caribou herds in west central Alberta, Canada. Herds in west central Alberta that were examined in this study are indicated within the bold circle.

1996). The upper foothills ecoregion is characterized by an overstory of lodgepole pine (Pinus contorta) and white spruce (Picea glauca) with small patches of trembling aspen (Populus tremuloidies). The subalpine ecoregion is characterized by an overstory of Englemann Spruce (P. Englemannia) and subalpine fir (Abies lasiocarpa), while the alpine ecoregion has little overstory and is characterized by graminoids, sedges (Carex spp.) and bare ground. The A La Peche (ALP), Narraway (NAR) and Redrock-Prairie Creek (RPC) herds are categorized as mountain ecotypes (summer in the mountains, winter in the subalpine forest) while the Little Smoky (LSM) herd is categorized as a boreal ecotype (spends the entire year in the subalpine and upper foothills natural region). All of the mountain types (the NAR is the exception) spend at least part of the year in a National Park and/or a wilderness area where industrial activities are not permitted. The majority of the ALP herd resides for part of the year in Jasper National Park/Willmore Wilderness Park (WWP) while a small portion of the herd ~30) lives outside of these protected areas on forested lands available for oil/gas and timber development. The RPC herd spends the summer in the

WWP and winters in forested foothills which experience all industrial activities while the NAR herd winters on the border of Alberta and British Columbia and summers in the mountains of British Columbia (only the Alberta winter range portion was modeled). In general, there is a higher density of ungulates and more wolves in the eastern part of the study area compared to the west. The LSM herd experiences the highest density of industrial activity, primary prey and wolves.

ALCES (A Landscape Cumulative Effects Simulator: Forem Technologies) is a modeling tool that forecasts changes in a landscape over time and allows the user to assess the effects of different management scenarios on a series of indicators (e.g. Schneider *et al.*, 2003).

Detailed, spatially explicit information about the initial WCCLPT planning area was obtained from GIS data layers and included in the ALCES model. Nonspatial forecasts of human and natural disturbance were performed over a 100-year period (March 2006 was the initial month/year). These forecasts were evaluated by the equation developed for boreal herds in Alberta (including the LSM herd) (Sorenson *et al.*, 2008), which links the finite rate of caribou population growth rate (λ) to habitat condition:

 $\lambda = 1.191$ - (0.314 * amount of area within 250 m of an anthropogenic footprint) - (0.291 *proportion of stands < 50 years old of fire origin)

This provided an assessment of "habitat lambda" or the projected change in a woodland caribou population growth rate based on habitat alone (without any special predator and/or primary prey management intervention). The ALCES model used information provided from the Alberta Vegetation Inventory, forest inventory, hydrology and the anthropogenic footprint interpreted from landsat imagery. Future projections were made based on: 1)timber harvesting activities that would reduce the amount of older forests, 2) accelerated harvest of lodgepole pine designed to reduce the probability of mountain pine beetle (Dendroctonus ponderosae) spread, 3) estimates of energy development, 4) the natural range of variability, 5) wildfire and 6) mountain pine beetle spread projections.

Mitigation options that were explored in ALCES included: 1) reforestation and the reduction of access on existing anthropogenic footprint (5-8m wide seismic lines), 2) the aggregation of anthropogenic footprint to reduce fragmentation, 3) shared access

Table 1. Moose densities' used in the REMUS Model based on forest type and age in west central Alberta.

Forest Type	Forest Age (years)	Moose Density (per km²)	
Upland Lodgepole	0 – 30	Medium density (0.5)	
Pine – Like	31 – 80	Low strata (0.05)	
	> 80	Low strata (0.05)	
Lowland Black	0 – 30	Med. Strata (0.5)	
Spruce – Like	31 – 80	Low to Med. strata (0.3)	
	> 80	= Low strata (0.1)	
Riparian – Like	0 – 30	= High strata (1.35)	
	31 – 80	= High strata (1.35)	
	> 80	= High strata (1.35)	

¹ Moose densities are based on aerial survey results.

to reduce potential fragmentation, 4) reducing the width of anthropogenic footprints to reduce the total area affected, 5) establishing protected areas where industrial activity would be eliminated, 6) the retention of older forest (caribou habitat) and, 7) enhancing fire suppression (to maintain older forests).

Sensitivity analysis was conducted on a number of parameters that were anticipated to influence any/all of the objectives for woodland caribou maintenance and/or recovery. These included: 1) mitigation options reported above, 2) seismic lifespan, 3) fire rates, 4) energy & Annual Allowable Cut projections, 5) Mountain Pine Beetle outbreak rates and 5) forest conversions post-Mountain Pine Beetle outbreak.

Following the examination of future habitat scenarios, landscape projection data from ALCES (doesn't include the "habitat lambda" calculations) were exported to the program REMUS. REMUS is a population model also built on the STELLA platform that was used to project potential population responses by woodland caribou, other primary prey species (moose, elk and deer) and wolves (Weclaw & Hudson, 2004). REMUS was used to test different options with regard to predator and primary prey management against the habitat and anthropogenic footprint projections provided through ALCES and to identify knowledge gaps.

REMUS bases projections on predator/prey relationships with the basic premise of habitat affecting primary prey (either positively or negatively) and wolves responding to prey availability. Primary prey population response can either be generated through estimates of forage or through changes in primary prey density based on forest age. Neither forage

estimates nor population responses of primary prey to changes in forage were available for west central Alberta or anywhere in the province. Consequently, primary prey projections were based on changes in density of these species relative to forest age (e.g. moose; Table 1). These density estimates reflected aerial survey results from the study area and the upper limits were obtained from the published literature where available (Table 2 in Appendix).

At the strategic level of assessment, a decision was made to lump the number of forest types (within the "managed" portions of each of the 4 herd ranges using provincial lands) into 3 primary categories:

- a. Upland Pine Like Habitat includes all coniferous upland sites. This category provides the majority of terrestrial lichen production, which is the main winter forage for woodland caribou in west central Alberta.
- b. Lowland Black Spruce Like Habitat includes all coniferous lowland sites. This category provides the majority of arboreal lichens, which are an important component of woodland caribou forage in late winter when the daily freeze/thaw temperature change compromises "cratering" by woodland caribou for terrestrial lichens.
- c. Riparian Like Habitat includes any ecosite where the forest overstory is influenced by water. This category includes grasslands and white spruce stands that may contain some arboreal lichens.

Based on these forest categories, the following assumptions were included in REMUS to project primary prey response to forest age:

a. All forests between 0 and 30 years old would have the highest density of primary prey other than caribou (i.e. moose, elk and deer) because of the presence of suitable forage (Usher, 1978; Peek et al., 1976; Potvin et al., 2005; Rempel et al., 1997). The density of moose would be highest in riparian, moderate in lowland spruce and lowest in upland pine. Riparian was also the most important to deer and elk, with upland pine and lowland spruce at this age being of secondary and tertiary importance for these 2 species, respectively. This forest category would have the lowest density of caribou and the highest occurrence of wolves. In the presence of wolf predation this forest category would be the area where woodland caribou would have the highest probability of encountering wolves and presumably suffering mortality as a result of these encounters. Consequently, new footprint was included in early seral for assessing habitat effectiveness for primary

- prey other than caribou and significantly reduced as caribou habitat
- b. All forests between 31 and 80 years old would be of lower importance to moose, elk and deer as the forest overstory grew resulting in a corresponding reduction in palatable forage. Woodland caribou density would be higher than in the previous category as a result of lower primary prey densities resulting in fewer wolves (and encounters).
- c. All forests older than 80 years would have the lowest density of primary prey, the lowest encounter rate of woodland caribou and wolves, the best availability of terrestrial and arboreal lichens (Szkorupa, 2002) and the highest density of woodland caribou.

In order to project the potential outcomes of temporary predator management, the upper limits of primary prey densities were obtained from the literature and adjusted accordingly to reflect the habitat limitations of west central Alberta woodland caribou ranges. Estimates of mortality caused by other predators [i.e. grizzly bears (*Ursus arctos*), black bears (*U. americanus*), cougars (*Felis concolor*), etc] were obtained from the literature, but ultimately these were not included in final model runs in order to simplify the interpretation and explanation of model results.

The REMUS model is parameterized based on the assumption that the influence of primary prey density on wolf density will have a much greater influence on woodland caribou population response than availability of food (lichen). Consequently, forest age is the most important "driver" for the primary prey component and REMUS outputs track this indicator most efficiently. Because all linear features do not contribute significantly to changes in forest age, REMUS does not "properly" account for aggregation vs. dispersion of linear disturbance. Therefore, these metrics are more appropriately tracked in ALCES through the outputs of "Habitat Lambda" and density of linear features (km/km²). The cumulative changes resulting from both forest harvest and oil and gas development were tracked in ALCES for the RPC and NAR herds. However, there were critical forest harvest variables not made available in the ALP and LSM (i.e. annual allowable cut), so the ALCES outputs for those 2 herds only assess the oil and gas footprint through time.

We elected to use habitat specific moose and woodland caribou densities based on aerial surveys rather than the alternative option of changes in forage abundance available in REMUS to "drive" the model outcomes. This decision was based on: 1) aerial survey inventories being relatively up to date and

Table 3. A comparison of the anthropogenic footprint within the managed1 forest portion of 4 woodland caribou ranges in west central Alberta, March 2006.

		HE	RD	
Metric	Little Smoky	A La Peche (managed winter range) ¹	Redrock – Prairie Creek (managed winter range) ¹	Narraway (managed winter range) ¹
Area of Range (km²)	2927²	1716²	3026	1020
Km of Seismic Lines (km/km²)	8640 (3)	1890 (1.1)	1704 (0.6)	950 (0.9)
Area (ha) of Wellsites (ha/km²)	692 (0.2)	105 (0.06)	396 (0.1)	217 (0.2)
Km of Pipelines (km/km²)	1065 (0.4)	312 (0.2)	359 (0.1)	350 (0.3)
Km of Major Roads (>15m) (km/km²)	62 (0.02)	205 (0.1)	17 (0.01)	0.25 (0.00002)
Km of Minor Roads (>8m) (km/km^2)	1491 (0.5)	734 (0.4)	1389 (0.5)	634 (0.6)
Ha of cutblocks in the last 30 years (ha/km²)	25844 (8.8)	15134 (8.8)	23584 (7.8)	8011 (7.8)
% Range of Fire Origin < 50 Years	0.1	0	0.5	0
% of forest > 80 years	78%	84%	77%	79%
% of range within 250 m of anthropogenic feature	87%	59%	46%	56%
% of range > 80 years old and > 1000 ha	65%	65%	??	??

¹Managed winter range refers to that portion of the winter range that occurs outside of protected areas and is managed for multiple use.

available; 2) forage information not being available; 3) the relationship between forage availability and population response not being well documented and 4) aerial survey data tending to be more readily available for wildlife managers than forage inventory and it's relationship to population response. Additionally, after altering the REMUS model to predict multipleprey population responses (elk and deer) to multiplepredators (grizzly bears, black bears, cougars), we eventually decided to focus simply on moose, deer, caribou and wolves in order to make it easier to track changes between model runs and to simplify the explanation of cause and effect relationships to our multi-stakeholder audience and different departments within the Government of Alberta. Although this approach oversimplified the multitude of variables influencing woodland caribou conservation efforts, the main "drivers" of the issue were captured sufficiently to facilitate informed decision making.

Avoidance of anthropogenic features by woodland caribou has been documented in west central Alberta

Table 4. Modified GIS avoidance buffer parameters¹ used in REMUS © simulation modeling for four west central Alberta caribou herds, March 2008.

Feature	Distance Avoided (m)	% Avoidance
Cutblock	1000	100
Seismic Line	100	25
Road	250	50

GIS avoidance buffers were modified by the planning team from those cited in the literature.

(Smith et al., 2000; Oberg, 2001; Neufeld, 2006) and northeastern Alberta (Dyer et al., 2001). These authors argue that avoidance can result in functional habitat loss. Correlations between woodland caribou population response (λ) and the amount of anthropogenic footprint and forest burned have been published for 6 woodland caribou herds in Alberta including the LSM herd (Sorensen et al., 2008) and has recently

²Includes the West Fraser Portion of the range; however, the area modeled in the LSM and ALP Range was reduced as a result of West Fraser not providing data.

been expanded to 10 herds (Boutin & Arienti, 2008). These authors document different "amounts" of avoidance based on the type of feature and the time of year and this was factored into REMUS (Note: only the raw landscape data had been imported from the ALCES model and this didn't include negative coefficients of anthropogenic linear features included in the habitat lambda calculation). In GIS terms, these "buffers" on linear features are not avoided 100% of the time (usually the perceived effect decreases as the distance from the feature increases or as the feature becomes reclaimed) (Oberg, 2001; Neufeld, 2006; James & Stuart-Smith, 2000) and the seasonal effect is often more pronounced during the winter than during the summer (Dyer et al., 2001). Given the densities of features in the respective herd's ranges (Table 3), results often showed that functional habitat limits have been exceeded if woodland caribou continue to avoid anthropogenic features even in the absence of wolves. In order to simplify the number of different "buffers" in

REMUS and to understand the implications of these assumptions (sensitivity analysis) "compromise" values were used in the model (Table 4).

A series of multi-variable runs were also made to examine cumulative solutions to conserving caribou in each herd range. The variables that were manipulated included:

- 1. Primary prey management,
- 2. Predator control,
- 3. Both primary prey and predator control,
- 4. 0 and 10% active reclamation of seismic lines,
- 5. The age of the forest in 3 categories (0 to 30, 30 to 80, 80+ years)
- 6. Aggregation of oil and gas footprint (Aggregation of 0.1 = ~ 35% reduction in wellsites, pipelines and roads; Aggregation of 0.3 = ~ 75% reduction in wellsites, pipelines and roads).

The approach was to manipulate primary prey and predator densities against a landscape described by the following habitat and footprint trajectories:

The Healthy Pine Strategy (HPS) (a timber management strategy designed to restrict the spread

Table 5. Initial population numbers and management thresholds of species described in REMUS © simulation modeling for 4 west central Alberta woodland caribou herds, March 2008.

Herd	Species	Initial Number ^a	Management Threshold
Little Smoky	Caribou	72	100 - 150
$(2616 \text{ km}^2)^b$	Moose	905	<250
	Elk	136	No target
	Deer	1812	No target
A La Peche	Caribou	51	30 - 60
$(1396 \text{ km}^2)^b$	Moose	252	< 150
	Elk	113	No target
	Deer	511	No target
Narraway	Caribou	90	100 - 150
(1024 km²)	Moose	453	<100
	Elk	296	No target
	Deer	613	No target
Redrock/	Caribou	329	200 - 400
Prairie Creek (3026 km²)	Moose	1006	<300
(5020 Km)	Elk	254	No target
	Deer	2241	No target

^a Initial numbers of each species derived from known areas (km²) of habitat types and estimated densities within each habitat type.

of mountain pine beetle by harvesting 75% of lodgepole pine in the next 20 years) with deferral of harvest in portions of the ALP and LSM ranges. The Healthy Pine Strategy and a "20/30" rule (timber harvest is restricted when more than 20% of the caribou range is < 30 years old) was modeled in the RPC and NAR ranges.

- 2. Deferral of portions of each caribou range for the entire modeling run (i.e. 100 years).
- 3. Mountain Pine Beetle "Disaster" Scenario = 80% of pine stands (defined as pine making up > 80% of the overstory) suffering 100% mortality over 20 years.

REMUS runs were made both with avoidance buffers on (Table 4) and off. In order to compare outputs based on standard criteria for population management of both primary prey and wolves, consistent parameters and thresholds (upper and lower limits to initiate wolf control) were used in REMUS (Table 5). In general, wolf numbers had to be kept below 6.5 wolves/1000 km² to provide for woodland caribou stability or increase (Bergerud & Elliot, 1986) and

^bDoes not include the West Fraser portion of the LSM or ALP ranges.

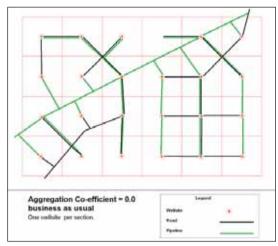


Fig. 2. An illustration of an aggregation co-efficient of 0.0 (Business as Usual) under the current Alberta Energy and Utilities Board guidelines of 1 well per mi² (2.59 km²).

moose had to be managed below 100/1000 km² before wolf numbers weren't expected to increase to a level detrimental to woodland caribou (Messier, 1995). Woodland caribou herd-specific goals were set to compare management strategies proposed by the team. For example, wolf management was initiated whenever the LSM herd fell below 100 individuals and it was terminated once the herd had grown to 150 individuals (Table 5). The number of years that wolf control was required to keep wolf densities below 6.5 wolves/ 1000 km² during a 100 year modelling projection was used as the common indicator when evaluating different scenarios evaluated through REMUS.

Results

Habitat Lambda

The 2 main habitat strategies that provided the most benefit for habitat lambda were the maintenance of older forest age and minimizing habitat fragmentation. Univariate simulations indicated that reclamation of the existing anthropogenic footprint (5-8m wide seismic lines) held promise over the long term. While reclamation strategies such as planting coniferous seedlings will not benefit caribou habitat in the short term, the anticipated long-term benefits are the reduction of palatable browse species (that support primary prey species) as the coniferous canopy "closes in", the reduction in Off Highway Vehicle access (and human disturbance) as lines are reforested and become impassable and a reduction in wolf traveling efficiency as a result of the elimination of packed

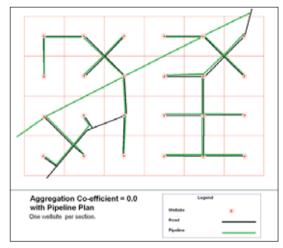


Fig. 3. An illustration of an aggregation co-efficient of 0.0 (Business as Usual) under the current Alberta Energy and Utilities Board guidelines of 1 well per mi² (2.59 km²) combined with a pipeline plan.

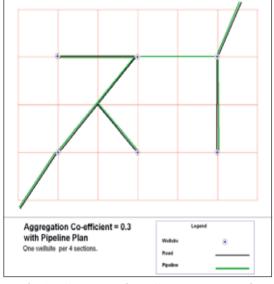


Fig. 4. An illustration of a wellsite aggregation of 0.3 complete with a pipeline plan. The average "industrial footprint" reduction compared to Fig. 3 is 75%.

snowmobile trails along these lines during winter and/or as tree density increases to impede travel. Ultimately, the lines will "blend" into the surrounding cover types over time, but even initial benefits may take in excess of 30 years to achieve.

The aggregation of industrial "footprint" was directed principally at oil and gas activity. [To a certain degree, timber harvest is much more aggregated given the exclusive tenure of forest management

agreements and the ability to plan over decades, although the need to average haul distances (harvest wood both proximally and distally to the mill) does compromise the ability to aggregate timber harvest]. The metric of aggregation is described as a "Dispersion Coefficient" with 0 being complete dispersion and 1 being complete aggregation (ALCES). On average, the density of wellsites for natural gas in the province of Alberta is 1 per mi² (2.59 km²) (Alberta Department of Energy, pers. comm.). Imposing a strategy of restricting pipelines to existing right-ofways (rather than allowing them to join wells via the shortest distance) has the potential to reduce the industrial footprint by up to 25% (Fig. 2 vs. Fig. 3). Applying a dispersion coefficient of 0.1 [1 per 2 mi²] (5.18 km²)} has the potential to reduce the overall footprint of the oil and gas sector by up to 35%, when combined with a pipeline plan. Moreover, a dispersion coefficient of 0.3 [1 per 4 mi² (10.36 km²)] may reduce the footprint by up to 75% when combined with a pipeline strategy, resulting in a significant reduction in fragmentation (Fig. 4).

Sharing of access is a sound strategy; however, > 50% of the existing access is already shared in most ranges and consequently, there was little room for improvement unless oil and gas activities were restricted to timber harvesting areas. This mitigation option did not provide any further benefits than those that have already been achieved and it becomes less significant as the overall footprint increases. Reducing the lifespan or width of the anthropogenic footprint was only modeled for a few "footprint" types because no options were provided by industrial participants and reducing the width of footprint had little to no effect. Establishing protected areas does provide caribou habitat benefits through a reduction in industrial activity and anthropogenic footprint. However, these benefits are only significant in the currently fragmented landscapes modeled if fire control (to maintain forest age), primary prey control (though hunting) and predator control are all available management options within the protected area. Old growth forest retention contributes to the maintenance of forest age by establishing targets for the amount of forest in the older age category. It can address both the principle of maintaining a proportion of forest > 80 years old and doing so in large patches. This strategy is one of the primary means of providing habitat for caribou at a landscape scale. Enhanced fire suppression is obviously very important to maintaining forest age. Alberta is one of the most aggressive fire-fighting jurisdictions in North America. Consequently, there is little room for improvement; however, maintaining this effort is very important.

A mountain pine beetle (MPB) outbreak would further compromise the ability of any of the other strategies to provide for woodland caribou habitat over time. The obvious implication to woodland caribou habitat is that the primary forest types that provide terrestrial lichens (pine forests) would suffer high mortality over a relatively short time period. To examine the potential significance of a MPB outbreak, we modeled 80% of pine stands (defined as pine making up > 80% of the overstory) suffering 100% mortality in 20 years. In order to populate the model, experts were asked for their opinion on ecological projections for each of the pine ecosites found in woodland caribou range. It is important to note that many of the pine ecosites have an understory and/ or a subordinate species in the overstory that would remain following a MPB outbreak. Consequently, the ecological projections suggest that these stands would revert to a very open forest type of the understory/ subordinate species (i.e black spruce, sub-alpine fir, etc) in contrast to a complete loss of the canopy. Terrestrial lichens often favour more open stands, therefore in the stands not dominated exclusively by pine; terrestrial lichens may not disappear immediately and in a few instances, may even be enhanced. There are at least 3 reasons to be concerned about a MPB outbreak: 1) Do the affected stands cease to provide either food or cover for woodland caribou, 2) Do the affected stands enhance habitat for primary prey (i.e. moose, elk and deer) thereby prompting a response by wolves? (Given the high % of stands that have other overstory species present, the projection is for these stands to be set back to a very open stand of the something other than pine which shouldn't result in a significant benefit to primary prey in most cases) and 3) Do the affected stands essentially stagnate as caribou habitat if they fail to regenerate for longer periods than clearcuts or fire regenerated stands? If a MPB outbreak occurs with the magnitude and speed that has been projected in these runs, the estimate is that only 30% of the stands can be salvaged (based on mill capacity and market) before the wood is no longer suitable for processing with current lumber milling. (It is possible that these stands may be suitable for pulp or other biomass harvesting in the future). Therefore a major consideration in terms of providing for long-term woodland caribou habitat is what to do with the remaining stands of dead pine. Options include some management action designed to regenerate a new pine stand (i.e. prescribed burn and/or scarification restoration treatment) or leave as is. The option of intervening with a management action benefits woodland caribou in the long term by re-establishing a new coniferous forest as soon

as possible. However, this doesn't pay dividends for caribou until ~ 80 years. Conversely, leaving MPB killed stands to regenerate to another overstory type can pay immediate dividends if a) the stand doesn't generate forage for primary prey, b) it continues to produce at least some of the benefits of the previous stand and c) by leaving the stand, the level of "intactness" is maintained. A strategy of managing a third of the stands affected with each treatment (salvage, actively regenerate, leave) appears to be a good compromise.

Relative habito tat lambda, industrial business-as-usual (BAU) scenarios were very detrimental to caribou habitat. Reclaiming 10% of the seismic lines annually provided benefits as did aggregating wellsites. In terms of forest age, the "Healthy Pine Strategy" was most detrimental followed by BAU and the Pine Beetle "Disaster" scenario. Maintaining a constant forest age (~80% ≥ 80 years old) was the most optimum. However, given the existing fragmentation of some of the ranges (particularly LSM), none of the "habitat scenarios" were sufficient to conserve caribou over time without some population management intervention.

Population Management
To provide a consistent comparison between herds and between sce-

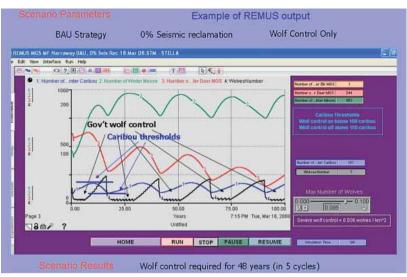


Fig. 5. Example of a REMUS computer model output for the Narraway woodland caribou herd in west central Alberta based on a 100 year scenario of business as usual for the oil and gas industry, no reclamation of seismic lines, wolf control initiated when the Narraway herd declines below 100 animals and wolves are controlled at 6/1000 km² until the caribou herd increases to 150 animals. Moose and deer are available for sport hunting, but aren't controlled.

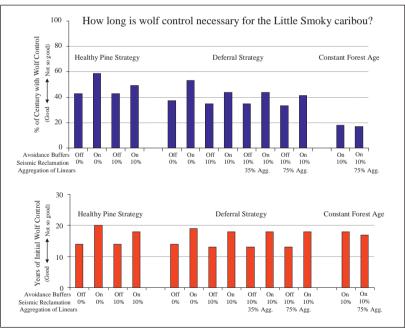


Fig. 6. A comparison of REMUS modeling results between the Health Pine Strategy, the 100 year Deferral Strategy and an Old Growth Strategy in the Little Smoky Range. The blue bars illustrate the number of years out of 100 when wolf control would be necessary and the red bars illustrate how many years would be *initially* required to achieve 150 caribou.

narios, "the number of years where wolf control was required to maintain woodland caribou numbers above management thresholds" (Table 5) was used as the common denominator. The outputs from the REMUS runs illustrated the timing and duration of wolf control, and the anticipated response by caribou, moose and deer (e.g. Fig. 5). The results of different scenarios were combined by herd to access the benefits (e.g. Fig. 6). The number of bouts of wolf control is not included in Fig. 6; however, the constant forest age scenario only requires 1 bout compared to other scenarios, but due to the current forest condition, the first bout is the same length as those strategies that have multiple bouts. For the runs in Fig. 6, the benefits of aggregating industrial footprint were not captured in the REMUS outputs because of lack of data for this herd. Running the analysis with GIS buffers on (simulating avoidance of anthropogenic features) suggests that a more prolonged period of wolf control is required. The buffer doesn't affect the age of the stand (i.e. the age remains the same regardless of the GIS buffer), but it does reduce the amount of older forest available to caribou to avoid predation, thereby making them more vulnerable in the model and reducing their rate of increase. The question remains whether avoidance of anthropogenic features by caribou would continue or be reduced during a period of wolf control. For example, woodland caribou might be avoiding anthropogenic features because the lines were frequented by more primary prey and thus wolves associated with them and/or because wolves use them as travel routes (James, 1999; James & Stuart-Smith, 2000). Conversely, human activity may be driving avoidance (Dyer et al., 2001) and therefore wolf control may not have any effect on caribou response to anthropogenic features.

Given the densities of wolves and primary prey in all woodland caribou ranges outside of the protected areas and the amount of anthropogenic footprint that already exists, there were no scenarios where the reduction of primary prey was sufficient to recover caribou in the short term, even with total exclusion of forest harvest and limited oil and gas development (i.e. The amount of existing early seral stage forest would continue to attract primary prey and therefore wolves at densities that wouldn't support woodland caribou until forest age recovered). However, as expected, concurrent primary prey/predator management did provide marked benefits in terms of reducing the number of years where predator control was required. To examine the difference between initiating only wolf control vs. wolf and primary prey control, wolf densities in the NAR range were reduced to 6/1000 km² and/or in combination with moose densities reductions to < 100/1000 km² whenever caribou numbers dropped below 100. Wolf control was removed whenever caribou exceeded 150. Invoking different levels of an old growth strategy reduced the need to control wolves when the only aggressive population management strategy was wolf control. Significant moose management (i.e. moose reduction over and above sport hunting – a.k.a. aerial gunning) dramatically reduced the duration of wolf control and increasing the old growth strategy reduced the number of years that "government" moose management was required in response to a reduction in young moose-producing forests (Fig. 7). (Note: The modeling results for the NAR herd do not have the benefit of 1) current landscape condition, 2) projected future landscapes or 3) predator/primary prey densities for the portion of the range that is located in British Columbia. Consequently, these results should be viewed with additional caution).

To compare similar strategies across herds, REMUS modeling results were categorized into those where recovery of woodland caribou required the least amount of wolf control, the best and worst scenarios for each herd with continued forest harvest and the Mountain Pine Beetle (MPB) Disaster Scenario. Each end of the spectrum was examined relative to seismic reclamation and aggregation of footprint (Fig. 3 & 4) although, as pointed out earlier, those 2 parameters do not contribute significantly to changes in forest age. Primary prey management wasn't included in this comparison, but as pointed out previously, it should reduce the number of years that wolf control was required if done aggressively. (MPB outputs were not available for the NAR or RPC herds during the preparation of this document).

Across herds, REMUS results indicate that maintaining forest age at the current level without any further forest harvest (Recovery), with 10% seismic reclamation and with a 75% reduction in linear footprint would require the fewest years of wolf control (Fig. 8). From the standpoint of wolf control, the next best scenario modeled in the LSM and ALP ranges would be if the more intact areas were deferred from forest harvest for 100 years, 10% seismic was reclaimed annually, anthropogenic footprint was minimized (75%) and there was no avoidance exhibited by caribou of any anthropogenic features (Best). The Healthy Pine Strategy without seismic reclamation and without aggregation of footprint required the largest amount of wolf control if there was avoidance by woodland caribou (Worst). Finally, the MPB Disaster Scenario (MPB) without seismic reclamation and aggregation of footprint required the most years of wolf control. Similar modeling results were

observed for the NAR and RPC with the fewest years of wolf control being predicted for a scenario of maintaining forest age at the current level (Recovery) and the most years of wolf control being associated with the Healthy Pine Strategy (Fig. 8).

Discussion

Simulated habitat management strategies that resulted in the highest likelihood of caribou recovery included the maintenance of a high proportion of old forest and the aggregation of industrial footprints. Sharing of industrial roads, protection of fragments of old-growth, and expanding fire control had little additional effect on caribou recovery. Simulated population management strategies that were successful all involved decades of intensive wolf control, either directly or indirectly through intensive alternate prev control. Recurrent cycles of wolf control appeared necessary until old-growth forests recovered to densities that provided caribou habitat and decreased alternate prev of wolves. Intensive strategies of direct or indirect wolf control are controversial, logistically difficult, and likely unsustainable over the meaningful time frames necessary for caribou recovery.

In REMUS we assumed no "prey switching" (i.e. wolves focusing on woodland caribou when faced

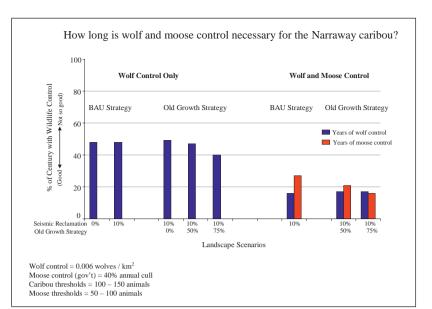


Fig. 7. A comparison of REMUS modeling results between the Business As Usual (BAU)¹ Strategy, Old Growth Strategies that maintain 0%, 50% and 75% of the forest > 80 years old and wolf control only vs. moose and wolf control in the Narraway Range. The blue bars illustrate the number of years out of 100 when wolf control would be necessary and the red bars illustrate how many years out of 100 that government moose control (i.e. probably couldn't be accomplished by sport hunting) would be required to maintain 100 - 150 caribou.

¹For the NAR herd, BAU is ensuring that no more than 20% of the range is < 30 years of age at any segment of time.

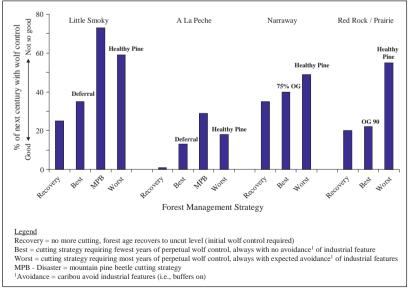


Fig. 8. Summary of both recovery (no further forest harvest) and forestry cutting strategies as functions of years of wolf control required to recover or maintain caribou populations in four west-central Alberta caribou herds.

with reduced moose densities) because it was difficult to find published information to include in the model. The potential for caribou to receive additional predation pressure when other primary prey is in decline is discussed by Hebblewhite *et al.* (2007) and Messier (1995). There is a high likelihood that this will occur since wolves would be expected to continue to hunt primary prey of any type based on the density of the prey's occurrence.

Based on modeling results, wolf control is expected to be effective in maintaining woodland caribou populations until habitat becomes limiting. However, the Recovery Plan for Woodland Caribou in Alberta provides direction that wolf control will be used as a temporary measure to provide for the maintenance of woodland caribou populations until habitat is restored to the extent that caribou can once again avoid predation at a sustainable level (see Lessard et al., 2005). Additionally, the Management Plan for Wolves in Alberta (Alberta Forestry, Lands and Wildlife, 1991) only permits wolf control for durations up to 5 years. Moreover, the logistical challenges of delivering an effective wolf control program over large areas and over long time periods have yet to be addressed. Finally, it is expected that the Alberta public will not support wolf control programs as a viable long-term solution to woodland caribou conservation since it is not a sustainable resource development approach compared to improving habitat condition.

Sensitivity analysis suggested that any additional reduction of primary prey populations over and above current hunter harvest rates would benefit woodland caribou conservation efforts. However, in isolation, upwards of 30% of these primary prey must be harvested annually to maintain wolves at low enough levels to conserve caribou and this requires an initial wolf reduction program to have any effect if prey switching is taken into account. The reduction of primary prey (moose, elk and deer) through hunter harvest is a strategy designed to (1) lengthen the recovery time for wolf populations following initial wolf control and (2) maintain lower densities of wolves post-control. However, controlling whitetailed deer through licensed harvest in the interest of maintaining low densities of alternate prey will be very challenging in woodland caribou ranges of west central Alberta if climate change results in the reduction of average annual snow accumulations.

In summary, although over-simplified, this modeling approach provided a good opportunity to examine "what-ifs" in a multi-stakeholder planning team setting and to present the findings to a variety of audiences. Timber harvest was shown by far to

have the most significant influence on forest age, while oil and gas development was the most significant influence on "habitat intactness". Although the potential for mountain pine beetle to have a serious impact on woodland caribou habitat is serious, it was not predicted to be as devastating as originally projected. Without significant reductions in forest harvest and development of the oil and gas footprint in west central Alberta, wolf control would be necessary for multiple decades over a 100 year planning horizon. Primary prey reduction should be carried out simultaneously with wolf management to reduce the frequency and duration of wolf control. Given the size of wolf pack territories and immigration from surrounding landscapes, land management decisions that affect caribou habitat must be considered from a much larger area than that based on the current caribou distribution in west central Alberta.

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Appendix

Table 2. Summary example of default settings and sources of parameter estimates used in REMUS for the LSM woodland caribou herd in west central Alberta.

PARAMETER	DEFAULT SETTINGS	SOURCE
Forest Trajectories in Pine, Spruce and Riparian REMUS categories	REMUS Pine- Pine and Mixed-wood; REMUS Spruce- Black Spruce, Tamarack + Bog-fen; REMUS Riparian- Hardwood, White Spruce, Up-shrub, Up-grass, Up-moss	West Central Modelling Working Group
	Note- Alberta Vegetation Inventory (AVI) definitions were: • Pine - (Pl+Pj+Pa+Pf+P) >= 80%) • Mixed-wood- (< 80% for deciduous or coniferous forest types) • Spruce- (Sb+Lt+Bog-fen) >= 80% • Hardwood- (Aw+Pb+Bw+A) >= 80% • White Spruce- (Sw+Se+Fb+Fa+Fd+La) >= 80%	

PARAMETER	DEFAULT SETTINGS	SOURCE
Footprint Types in Seismic, Well and Road REMUS categories	REMUS Seismic- (Minor Roads, Pipelines, Transmission Lines, Seismic Lines) REMUS Well- (Wells, Gravel Pits, Industrial Plants, Mines) REMUS Road- (Major Roads, Rail-lines) Note: Minor roads, clearing width a See and	West Central Modelling Working Group
	Note- Minor roads = clearing width \geq 8m and \leq 15m; Major roads = clearing width $>$ 15m	
Initial Caribou Densities (/ km²) in pine, spruce and riparian habitats	0.032, 0.032, 0.001	Resource selection functions Neufeld (2006); Saher & Schmiegelow (2005); Edmonds (1988); Fuller & Keith (1981); James (1999); Stuart-Smith <i>et al.</i> (1997); Shepherd (2006); Szkorupa (2002)
Caribou Carrying Capacity (/km²) in pine, spruce and riparian habitats	2.0, 2.0, 0.03	Modified from Lessard (2005); Skogland (1985); Klein (1968); Leader-Williams (1980)
Initial Number of Caribou and Management Thresholds	72, 100-150	Initial numbers derived from: a/known areas (km²) of habitat types and estimated densities within each habitat type, b/ non-systematic aerial surveys, c/ mark-re-sight surveys for collared caribou, d/ total counts and expert opinion
Initial Moose Densities (/km²) in pine, spruce and riparian habitats	0.2, 0.4, 0.8	Aerial surveys and expert opinion; Fuller & Keith (1981)
Moose Carrying Capacity (/ km²) in pine, spruce and riparian habitats	0.32, 1.05, 6.0	Osko <i>et al.</i> (2004); Lessard (2005); Crete (1989); Skogland (1985)
Initial Number of Moose and Management Thresholds	905, <250	Initial numbers derived from known areas (km²) of habitat types and estimated densities within each habitat type
Initial Elk Densities (/km²) in pine, spruce and riparian habitats	0.6, 0.4, 0.07	Aerial surveys and expert opinion
Elk Carrying Capacity (/km²) in pine, spruce and riparian habitats	0.01, 0.01, 0.3	Stelfox (1993)
Initial Deer Densities (/km²) in pine, spruce and riparian habitats	0.3, 0.8. 2.0	Aerial surveys and expert opinion
Deer Carrying Capacity (/km²) in pine, spruce and riparian habitats	0.5, 0.5, 4.0	Estimates from limited aerial survey results.
Initial Wolf Density (/km²)	0.025	Aerial counts;
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PARAMETER	DEFAULT SETTINGS	SOURCE
Wolf Territoriality (Maximum wolf density regulated by territorial behavior; /km²)	0.059	Messier (1994)
Target Maximum Wolf Density (/km²) with Wolf Control	0.006	Bergerud & Elliott (1986)
Maximum Growth Rate of Wolves (no wolf control)	r = 0.875; Max. = 2.40	See Weclaw & Hudson (2004)
Wolf Immigration Rate (/km²)	0.002	Estimated
Wolf Kill Rates	Function of pack size (x- pack size, y- kill rate)	See Weclaw & Hudson (2004)
Territory Size of Wolf Pack (km²)	950	See Weclaw & Hudson (2004); Kuzyk 2002
Wolf Predator Efficiency (P50; density of prey species at half the maximum killing rate)	0.46 (same for all prey species in all 3 habitats)	Messier (1994)
Proportion of Caribou Killed Annually by Other Predators	0.04^{1}	Dzus (2001); Weclaw & Hudson (2004)
Prey Switching	Off	
Caribou Avoidance of Cut- blocks (distance avoided-m; % avoidance in buffers)	0 or 1000, 100	Smith et al. (2000); Oberg (2001); Neufeld (2006); James & Stuart-Smith (2000); Dyer <i>et al</i> . (2001)
Caribou Avoidance of Seismic Lines (distance avoided-m; % avoidance in buffers)	100, 25	Smith <i>et al.</i> (2000); Oberg (2001); Neufeld (2006); James & Stuart-Smith (2000); Dyer <i>et al.</i> (2001)
Caribou Avoidance of Roads (distance avoided-m; % avoidance in buffers)	250, 50	Smith et al. (2000); Oberg (2001); Neufeld (2006); James & Stuart-Smith (2000); Dyer et al. (2001)
Caribou Avoidance of Wells (distance avoided-m; % avoidance in buffers)	No avoidance	Smith et al. (2000); Oberg (2001); Neufeld (2006); James & Stuart-Smith (2000); Dyer et al. (2001)
Target Moose Hunting (proportion of antlered and antlerless harvested annually)	0.40 antlered; 0.40 or 0.35 antlerless	Expert opinion on achievable levels when considering access and past hunting statistics
Target Elk Hunting (proportion of antlered and antlerless harvested annually)	0.20, 0.30	Expert opinion on achievable levels when considering access and past hunting statistics
Target Deer Hunting (proportion of bucks, does and young harvested annually)	0.06, 0.06, 0.02	Expert opinion on achievable levels when considering access and past hunting statistics
Caribou Harvest (proportion of calves, yearlings and adults poached, harvested by 1st Nations or vehicle collisions annually)	0, 0, 0.03	Dzus (2001); McLoughlin et al. (2003)

 $[\]ensuremath{^{1}}\xspace$ later reduced to 0 to simplify model interpretation.

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Terrestrial lichen response to partial cutting in lodgepole pine forests on caribou winter range in west-central British Columbia

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Abstract: In west-central British Columbia, terrestrial lichens located in older, lodgepole pine (Pinus contorta) forests are important winter forage for woodland caribou (Rangifer tarandus caribou). Clearcut harvesting effectively removes winter forage habitat for decades, so management approaches based on partial cutting were designed to maintain continuous lichen-bearing habitat for caribou. This study tested a group selection system, based on removal of 33% of the forest every 80 years in small openings (15 m diameter), and two irregular shelterwood treatments (whole-tree and stem-only harvesting methods) where 50% of the stand area is cut every 70 years in 20 to 30 m diameter openings. The abundance of common terrestrial lichens among the partial cutting and no-harvest treatments was compared across five replicate blocks, pre-harvest (1995) and post-harvest (1998, 2000 and 2004). The initial loss of preferred forage lichens (Cladonia, Cladina, Cetraria and Stereocaulon) was similar among harvesting treatments, but there was greater reduction in these lichens in the openings than in the residual forest. After eight years, forage lichens in the group selection treatment recovered to preharvest amounts, while lichen in the shelterwood treatments steadily increased from 49 to 57% in 1998 to about 70% of pre-harvest amounts in 2004. Although not part of the randomized block design, there was substantially less lichen in three adjacent clearcut blocks than in the partial cuts. Regression analysis pre- and post-harvest indicated that increased cover of trees, shrubs, herbs, woody debris and logging slash corresponded with decreased forage lichen abundance. In the short-term, forestry activities that minimize inputs of woody debris, control herb and shrub development, and moderate the changes in light and temperatures associated with canopy removal will lessen the impact on lichen. Implementation of stand level prescriptions is only one aspect of caribou habitat management. A comprehensive approach should consider all factors and their interactions to maintain a viable population of woodland caribou in west-central British Columbia.

Key words: British Columbia; caribou; forest management; lichen; *Rangifer tarandus caribou*; silvicultural systems; winter range.

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Introduction

The northern woodland caribou ecotype (*Rangifer tarandus caribou*) (Heard & Vagt, 1998) in the Chilcotin region of west-central British Columbia (B.C.) is estimated at 2175 animals (Youds *et al.*, 2002). This population is designated as 'Threatened' by the

Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and qualifies for protection and recovery under the Canadian *Species at Risk Act* (SARA).

The historic range of northern caribou in the Central Interior has become increasingly restricted

due to past forest development, access issues, private land ownership and other development (Youds et al., 2002). In other jurisdictions, development has been linked to declines in caribou populations (Edmonds, 1988; Cumming & Beange, 1993; Smith et al., 2000). In order to manage development, the Northern Caribou Strategy component of the Cariboo-Chilcotin Land Use Plan (CCLUP) (Youds et al., 2002) delineated the current caribou range (about 1.5 million hectares) into no-forest-harvesting areas and parks (31%), conventional clearcut forest harvesting areas (52%), conventional clearcuts within a natural seral distribution zone (4%), and "modified" (partial cut) harvest areas (13%). The research trial described in this paper was initiated in 1994 to test silvicultural systems that could be used in the "modified" harvest area zone (> 180 000 ha) to maintain caribou habitat while allowing for timber extraction.

A key habitat component affected by forest harvesting is lichen, which is the major winter forage of woodland caribou throughout their range (Edwards et al., 1960; Scotter, 1967; Ahti & Hepburn, 1967). The northern caribou ecotype in British Columbia craters for terrestrial lichens and sometimes grazes arboreal lichens in the winter (Wood, 1996; Johnson et al., 2004). In west-central B.C., fecal fragment analysis indicated that both terrestrial and arboreal lichens are important forage during winter, comprising 68% of the caribou's diet and occurring in about equal proportions (Cichowski, 1989), although field observations indicated that terrestrial lichens are preferred.

In west-central British Columbia, during winter the two largest herds of caribou are found primarily in low-elevation lodgepole pine forests that are older than 80 years (Cichowski, 1989). Caribou preferentially select older stands on poorer growing sites because they have greater lichen abundance (Cichowski, 1989) than immature stands. Two habitat selection studies in Alberta showed that caribou preferred pine stands older than 75 years because they had sufficient quantities of forage lichens (Edmonds & Bloomfield, 1984; Shepard *et al.*, 2007).

The common practice of clearcut harvesting of lodgepole pine on an 80 year rotation (Daintith et al., 2005), reduces the amount of terrestrial lichens substantially in west-central B.C. (Enns, 1992; Goward et al., 1998; Miège et al., 2001a) and elsewhere (Eriksson, 1975; Woodard, 1995; Harris, 1996; Webb, 1998; Coxson & Marsh, 2001), at least in the short term. Retrospective studies on fire origin stands (Braulisauer et al., 1996; Hooper & Pitt, 1996; Goward et al., 1998; Coxson & Marsh, 2001) and on older clearcuts (Woodard, 1995; Harris, 1996, Racey et al., 1996; Webb, 1998) indicate that recovery could take several

decades. The degree of damage due to harvesting is influenced by season of harvest (summer or winter), harvesting method (stem-only or whole-tree), and whether or not harvesting is followed by site preparation (Kranrod, 1996). The decline of lichen can be attributed to sudden exposure to new environmental conditions (Kershaw, 1985), as well as physical damage, ground disturbance and debris loading (Eriksson, 1975; Kranrod, 1996; Webb, 1998; Miège *et al.*, 2001a). Other than the preliminary work done by Miège *et al.* (2001a), there is no published literature on the immediate impact of partial cutting on terrestrial lichens or their rate of recovery.

Large areas with sufficient, accessible forage are necessary so caribou can live at relatively low densities in order to successfully evade predators (Bergerud et al., 1984; Seip, 1991). Widespread application of clearcutting reduces the amount of usable caribou habitat, effectively shrinking their range. The goal of this project is to examine silvicultural systems and forest harvesting techniques that could retain terrestrial and arboreal lichen continuously in space and time.

Lodgepole pine forests in west-central British Columbia are provincially unique (Meidinger & Pojar, 1991). The cold, dry climate and undeveloped soils have resulted in the open canopy stands with pine regeneration often in the understory, and these stands persist, barring fire or insect attack, more than 300 years without climaxing to more shade-tolerant species. The structure of the stands led to the possibility of using silvicultural systems that employ partial cutting. Two silvicultural systems (irregular group shelterwood and group selection) and two harvesting techniques (whole-tree and stem-only) were selected for this study, which tests the hypothesis that the abundance of terrestrial lichens is not adversely affected by the degree of partial cutting or harvesting system associated with the first entry of each silvicultural system. Data were collected preharvest (1995) and several times post-harvest (1998, 2000 and 2004) in partial cut and no-harvest treatments in five replicate blocks.

Study area

The study area was located about 110 km northwest of Alexis Creek, B.C. on a gently rolling, high-elevation plateau (52°28′N, 124°43′E) and is located in the winter range of the Itcha-Ilgachuz caribou herd. The five study blocks in the trial were established in the very dry, cold Sub-Boreal Pine–Spruce (SBPSxc) and very dry, very cold Montane Spruce (MSxv) biogeoclimatic subzones (Steen & Coupé, 1997). In both

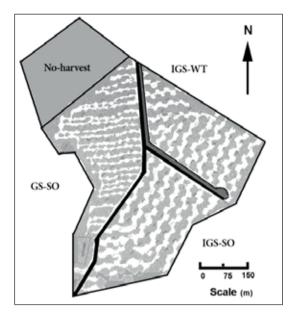


Fig. 1. Layout of block 5 showing the treatments: irregular group shelterwood – stem-only harvesting (IGS-SO), irregular group shelterwood – whole-tree harvesting (IGS-WT), group selection – stem-only harvesting (GS), and no-harvest.

subzones, lodgepole pine is the dominant tree species and undergrowth is low growing. Kinnikinnick (Arctostaphylos uva-ursi) and pinegrass (Calamagrostis rubescens) in the SBPSxc are replaced by crowberry (Empetrum nigrum), twinflower (Linnaea borealis), grouseberry (Vaccinium scoparium), and feathermosses (mostly Pleurozium schreberi and Dicranum spp). A rich variety of lichens, especially Cladonia spp., occur in both subzones. In all blocks, herbs such as northwestern sedge (Carex concinnoides) and bunchberry (Cornus canadensis) occurred in low abundance (1 to 2%). Soopalallie (Sheperdia canadensis) grows in small patches throughout the study area, while common juniper (Juniperus communis) was the most abundant shrub in the SBPSxc.

The five study sites are spread along a 30-km gradient that rises in elevation from 1280 m in the east (SBPSxc) to 1670 m in the west (MSxv) and are described in more detail in Waterhouse *et al.* (2010). Sagar *et al.* (2005) describes the changes in air temperature, soil temperature and rainfall across the elevation gradient in clearcuts and partial cuts.

The forests at the blocks were initiated after stand-destroying wildfires 220–300 years ago. Stands in the SBPSxc are much more open than those in the MSxv due to drier site conditions and past mortality from mountain pine beetle (*Dendroctonus ponderosae*).

Based on 1995 cruise data, the maximum tree height was 17 m and gross volume was 110 m³/ha in the SBPSxc, whereas maximum tree height was 20 m with gross volume of 270 m³/ha in the MSxv sites. Tree densities (trees greater than 12.5 cm diameter at 1.3 m) ranged from about 800 stems per hectare in the SBPSxc to 1400 stems per hectare in the MSxv. A mountain pine beetle infestation in the early 1980s killed 7 to 21% of the canopy trees, and the latest mountain pine beetle infestation killed about 4% of canopy trees by 2003, and 16% by 2004.

Methods

Experimental design

A complete randomized block design was chosen for the study. Five blocks were selected from current blocks laid out for operational harvesting. Each block was between 60 and 113 ha, and was divided into four equal-sized treatment units of approximately 15 to 28 ha. The three partial-cutting treatments and no-harvest treatment were randomly assigned to the treatment units in each block (Fig. 1). Data were collected pre-harvest in 1995, then post-harvest in 1998, 2000 and 2004. In 2001, three clearcuts (>34 ha) adjacent to the trial blocks (1, 3 and 5) were added for descriptive purposes. Data were collected in these blocks in 2001 and 2005.

Silvicultural systems and harvesting description

Two silvicultural systems in combination with two harvesting methods were tested: irregular group shelterwood (IGS) with stem-only (SO) harvesting, IGS with whole-tree (WT) harvesting, and group selection (GS) with SO harvesting. The two irregular group shelterwood systems were designed to harvest 50% of the stand area every 70 years in openings ranging from 20 to 30 m in diameter. These systems were developed to provide partial shade for terrestrial lichen sites in the harvested openings. With stemonly harvesting, debris from topping and de-limbing was left in the harvested openings to maintain longterm site productivity (Wei et al., 2000), but was aggregated to minimize the impact on terrestrial lichens and to create open space for planting trees. With whole-tree harvesting debris from topping and de-limbing is piled and burned at the roadside. The third silvicultural system, a GS system in combination with stem-only harvesting, was designed to harvest approximately one-third of the stand in 15-m wide openings every 80 years. This system was developed for sites with abundant arboreal lichen. All treatments were cut with a feller-buncher in the winter of 1996 (January to April) on a 30-cm snowpack.

In the stem-only system, a processor worked in the stand and a forwarder was used to move tree boles to the road; in the whole-tree system, a grapple-skidder pulled trees to a roadside area for processing. A post-harvest Global Positioning Survey of the blocks found that the average area cut was 39% in the IGS and 28% in the GS and that the opening sizes were within the targeted range (Waterhouse *et al.*, 2010). An additional 3-7% of the IGS-WT treatment was clearcut to make a processing and burning area. The clearcuts were harvested using the whole-tree method at the following times: block 1 (winter 1996), block 3 (summer 1994) and block 5 (summer 1996).

Data collection

Pre-harvest (summer 1995), across the 20 treatment units (5 blocks x 4 treatments) a total of 900 plots were installed and measured. A grid, based on 50-m interval spacing, was used to permanently locate 36–50 plots within 50 m of the boundaries of each treatment unit. Forty plots were installed in each clearcut. At each plot, a rebar pin was set flush to the ground. Next, a 0.8-m radius aluminum hoop (2.0 m²) with an inlaid equilateral triangle was placed on the ground in order to locate a second pin. The pins were used to position the sample hoop at each assessment.

A line intercept method was used to quantify substrates, lichens and mosses. The intercept (130 cm) was measured along the edge of the triangle opposite the first pin to avoid any trampling that may have occurred during plot establishment. The observer used an adjustable T-square to level the hoop and look directly over the area to be measured. The intercept was read twice. On the first pass, the observer recorded the amount and type of substrate. A continuous record was made along the transect, noting each substrate and its' length if it equaled or exceeded 0.5 cm. Substrate was divided into five categories: mineral soil, humus and fine litter (less than 1 cm in diameter), mixed humus and mineral soil, rock, and woody debris (medium class was woody debris greater than 1 cm but less than 7.5 cm in diameter, including branches, twigs and cones; coarse class was greater than 7.5 cm in diameter).

On the second pass, the following lichen and moss species were recorded: boreal feathermoss (*Pleurozium schreberi*, *Ptilium crista-castrensis*, and *Hylocomium splendens*), *Dicranum spp.*, other moss species, *Cladonia gracilis*, *Cladonia cornuta*, *Cladonia ecmocyna*, other *Cladonia* species, *Cladina* species, *Peltigera aphthosa*, other *Peltigera* species, *Stereocaulon* species, and *Cetraria* species. A complete list of the arboreal and terrestrial lichen species found in the study area is

reported elsewhere (Miège et al., 2001b). Post-harvest, three categories were used to describe lichen health: dead, sickly and healthy. Sickly lichens were severely discolored, partially broken and very dry, while dead lichens were structurally disintegrating, not adhered to the ground surface, and discoloured or bleached. Pre-harvest (1995), all lichens and mosses were assumed to be healthy.

Site conditions assessed for each plot were slope, aspect, position and shape for both meso- and microslope (Luttmerding et al., 1990). Soils were described in terms of moisture regime, drainage, texture, and form and depth of humus layer (Steen & Coupé, 1997). In each 2-m² plot, the type and amount of plot disturbance (compression, and displacement from humans, wildlife and harvesting), percent cover of slash from logging and wind fall, and percent cover and modal height of vegetation by layer (shrubs, dwarf shrubs, herbaceous vegetation, and coniferous tree regeneration (<1.3 m tall)) were estimated (Luttmerding et al., 1990). Starting in 2004, percent cover of individual plant species was also measured in the 2-m² plots. An estimate of percent cover of trees taller than 1.3 m was obtained using a periscope that vertically projected a grid of points at 12 degrees into the canopy.

Data analyses

All data analyses were performed with SAS, Version 9.1.3 (SAS Institute Inc., 2004). Lichen and moss data were organized into 13 response variables: boreal feathermoss, *Dicranum* spp., moss (all species), *Cladonia gracilis, Cladonia cornuta, Cladonia ecmocyna, Cladonia* (all species), *Cladina, Peltigera aphthosa, Peltigera* (all species), *Stereocaulon, Cetraria*, and *Stereocaulon*). The grouping of preferred species is based on information from several sources (Edmonds & Bloomfield, 1984; Thomas & Hervieux, 1986; Cichowski, 1989; Thomas *et al.*, 1996). Prior to analysis, intercept lengths for each response variable (previously converted to %) were averaged (over plots) for each block and treatment unit.

The preferred group of lichens was analyzed with a two-way (block \times treatment) ANOVA of the treatment-unit means, which were approximately normally distributed. Scheffé's multiple range tests were used to compare all pairs of treatments.

For species that were relatively common but had non-normally distributed mean abundances (moss, *Dicranum*, *Peltigera*, *Cladonia*, and *Cladonia ecmocyna*), a non-parametric analysis of variance—Friedman's two-way (block × treatment) test with adjustment for ties (Hollander & Wolfe, 1973)—was used to test for

treatment effects. The overall significance of treatment differences and the significance of differences between all pairs of treatments (adjusted to account for multiple comparisons) were determined by referring to Tables 39 and 41 in Odeh *et al.* (1977). Both total abundance (i.e., the combined abundance of healthy, sickly, and dead specimens) and the abundance of healthy specimens alone were analyzed. Variables with many zero values (i.e., species that occurred infrequently or in low abundance) were not analyzed.

The ANOVA and Friedman analysis were repeated for plots located in open areas and for those located in forested areas. In both cases, the corresponding measurements for the no-harvest treatment were included for comparison. Parametric and non-parametric results were considered significant at $\alpha = 0.05$.

Regression analysis of correlations between preferred lichen and predictor variables of interest (i.e., woody debris [medium plus coarse litter] % intercept, logging slash % cover, shrub % cover, dwarf shrub % cover, herb % cover, regeneration % cover, and tree % cover) were conducted for the pre-harvest and each year of post-harvest data. The regression model (based on the theory of normally-distributed data) was fitted to the line-intercept (abundance) data for

the group of preferred lichen species because it had relatively few zeroes (i.e., occurred in most plots). The following model was fitted:

$$\sqrt{l} = \mu + \sum_{v=1}^{m} \varphi_v x_v + t_i + b_j + t b_{ij} + \varepsilon_{ij}$$

where l is the length of the line-intercept (a square-root transformation was applied to enhance the normality of the data); μ is a constant (intercept); φ_1 , φ_2 , ..., φ_m are unknown regression coefficients; the selected variables $(x_1, x_2, ..., x_m)$ describe the environmental conditions at the transect location; the subscripts i (= 1, 2, 3, 4) and j (= 1, 2, 3, 4, 5) denote treatment and block; { t_i } are dummy variables representing treatment effects not captured by the variables x_i , x_2 , ..., x_m ; { b_j } and { tb_{ij} } are random block and treatment \times block (treatment unit) effects; and ε_{ij} is the residual (random) error. The random effects b_p , tb_{ij} , and ε_{ij} were assumed to be independent, normally distributed random variables with zero means and constant variances.

Backward elimination was used to select predictor variables $\{x_1, x_2, ..., x_m\}$ from the following candidates: shrub cover, dwarf shrub cover, herb cover, regeneration cover, tree cover, woody debris cover

Table 1. Average percent cover on the line intercept followed by frequency of occurrence. Data were collected in 1995 from five blocks along an elevation gradient.

Biogeoclimatic subzone			SBF	Sxc				MS	Sxv	
Block	:	L	2	2	3	3		ĺ		5
Elevation (m)	12	90	13	20	14	20	14	95	16	20
% Intercept and plots (n)	Avg.%	(195)	Avg.%	(199)	Avg.%	(201)	Avg.%	(154)	Avg.%	(151)
Boreal feathermosses	0.2	(9)	0.2	(4)	6.1	(92)	29.2	(127)	18.0	(99)
Dicranum spp.	0.3	(33)	0.2	(23)	2.1	(85)	9.4	(140)	9.4	(115)
All moss species	1.6	(104)	0.5	(42)	9.9	(150)	43.8	(153)	30.7	(140)
Peltigera apthosa	2.9	(89)	0.5	(22)	3.4	(91)	1.0	(40)	2.0	(49)
All Peltigera spp.	11.6	(176)	5.8	(155)	6.5	(149)	1.5	(60)	2.4	(62)
All Cetraria spp.	1.5	(151)	0.8	(100)	0.6	(91)	0.1	(13)	0.2	(26)
Cladonia gracilis	3.1	(153)	2.7	(133)	0.6	(65)	0.2	(22)	0.3	(20)
Cladonia cornuta	0.6	(79)	0.2	(33)	0.3	(36)	0.2	(27)	0.1	(13)
Cladonia ecmocyna	2.0	(129)	0.6	(42)	4.3	(131)	3.3	(94)	6.3	(106)
All Cladonia spp.	9.8	(192)	7.5	(180)	9.1	(186)	5.6	(126)	7.7	(117)
All Cladina spp.	2.1	(88)	0.6	(34)	0.6	(38)	0.8	(24)	0.5	(10)
All Stereocaulon spp.	1.4	(58)	2.7	(64)	0.5	(31)	0.1	(8)	0.3	(9)
All preferred lichens	14.9	(192)	11.6	(190)	10.8	(187)	6.6	(134)	8.8	(126)

and slash cover. The treatment dummy variables $\{t_i\}$ were added to the list of potential predictors; these variables were included or excluded as a group.

Parameters were estimated by the residual (restricted) maximum likelihood (REML) method (PROC MIXED in SAS). A pseudo R^2 for the regressors and random effects (Downer & Benfield, 1999) was calculated for each model, and a likelihood ratio test was used to assess the overall significance of the regressors. Regression results were considered significant at $\alpha = 0.05$.

Results

Pre-harvest (1995)

Lichens were fairly abundant across the trial blocks; however, some species and species groupings changed with biogeoclimatic subzone (Table 1). The group of species that is considered preferred by caribou (Cladonia, Cladina, Cetraria and Stereocaulon) ranged from 11 to 15% in the SBPSxc blocks and from 7

to 9 % in the MSxv blocks. Within the preferred lichen group, *Cetraria*, *Cladonia gracilis*, *Cladina* and *Stereocaulon* occurred more frequently and had greater abundance in the three lower elevation SBPSxc blocks than in the MSxv blocks. *Cladonia ecmocyna* and other *Cladonia* species made up 86 to 91% of the preferred lichen community in the two highest elevation blocks in the MS. Mosses (mostly boreal feathermoss and *Dicranum* spp.) achieved maximum abundance (31 to 44%) in the MS blocks, moderate abundance in the mid-elevation SBPS block (10%) and low abundance (<2%) in the two lowest elevation SBPS blocks. There were no significant ($P \le 0.05$) differences pre-harvest (1995) among the treatments for preferred lichen or other subsets of lichens and moss species.

Post-harvest treatment effects

The strongest treatment differences in the preferred lichen group occurred in 1998 (2.5 years post-treatment) and 2000 (4.5 years post-treatment). The no-harvest treatment had significantly more healthy

Table 2. Comparison of abundance (% of transect line covered) of preferred lichens among treatments using parametric analysis of variance (df = 3, 12). Least-square means and standard errors shown with different letters are significantly different at α = 0.05 based on Scheffé adjusted *P*-value. All health classes include healthy, sickly and dead lichens.

Year		·	No-harvest	IGS-SO ¹	IGS-WT ²	GS-SO ³	F	P
1995	All health classes	Whole	11.3 ± 1.8°	10.0 ± 1.8°	11.0 ± 1.8 a	9.9 ± 1.8 ª	0.28	0.84
1998	All health classes	Whole	11.6 ± 1.4°	6.6 ± 1.4 ^b	8.2 ± 1.4 ab	6.9 ± 1.4 b	6.86	0.0061
2000	All health classes	Whole	12.1 ± 1.5°	7.1 ± 1.5 b	8.9 ± 1.5 ab	7.9 ± 1.5 b	7.95	0.004
2004	All health classes	Whole	12.1 ± 1.5 °	8.2 ± 1.5 b	9.3 ± 1.5 ab	11.2 ± 1.5^{ab}	5.04	0.02
1998	Healthy	Whole	11.1 ± 1.3°	4.9 ± 1.3 b	6.3 ± 1.3 ^b	5.2 ± 1.3 ^b	8.98	0.0022
2000	Healthy	Whole	11.4 ± 1.5 ª	5.3 ± 1.5 b	7.4 ± 1.5 b	6.7 ± 1.5 b	11.76	0.0007
2004	Healthy	Whole	11.3 ± 1.4°	6.8 ± 1.4 ^b	7.8 ± 1.4^{ab}	$10.3\pm1.4^{\mathrm{ab}}$	4.97	0.02
1998	Healthy	Forest	11.1 ± 1.3°	6.0 ± 1.3 ^b	7.1 ± 1.3^{ab}	5.8 ± 1.3 b	6.13	0.009
2000	Healthy	Forest	11.4 ± 1.5 ª	6.4 ± 1.5 b	8.3 ± 1.5^{ab}	7.2 ± 1.5 b	7.54	0.004
2004	Healthy	Forest	11.3 ± 1.4°	7.1 ± 1.4°	7.8 ± 1.4 ª	11.0 ± 1.4^{a}	4.34	0.03
1998	Healthy	Openings ⁴	11.1 ± 1.3°	3.5 ± 1.4 ^b	4.0 ± 1.4 ^b	4.0 ± 1.4 ^b	9.77	0.002
2000	Healthy	Openings ⁴	11.4 ± 1.5 °	3.6 ± 1.4^{b}	$4.9 \pm 1.4^{\mathrm{b}}$	$5.2 \pm 1.4^{\mathrm{b}}$	16.16	0.0002
2004	Healthy	Openings ⁴	11.3 ± 1.4°	6.5 ± 1.5 ^b	$7.7~\pm~1.5^{\rm ab}$	8.5 ± 1.5 ab	4.20	0.03

¹ irregular group shelterwood with stem-only harvesting.

² irregular group shelterwood with whole-tree harvesting.

³ group selection with stem-only harvesting.

⁴ In the no-harvest treatment, there are no openings created by logging but the treatment unit mean is used for comparison.

preferred lichen than the three other treatments (Table 2). The three treatments had a similar drop (43 to 51%) in lichen abundance. When the forest and opening plots were separated within each treatment, lichen cover was significantly lower in the openings than the no-harvest treatments in both 1998 and 2000. The effect was not as strong when lichen cover was compared between the residual forest and no-harvest treatment. In 1998, the two stem-only treatments were significantly different from the no-harvest treatment, while in 2000, only the IGS-SO treatment remained significantly lower. There was comparatively less lichen in the openings than in the residual forest within each treatment, in both years.

By 2004, the overall treatment effect for healthy, preferred lichens remained significant (p = 0.02), but the differences among the treatments changed from the previous assessments. The IGS-SO treatment still

had significantly less preferred lichen (6.8%) than the no-harvest treatment (11.3%), but the GS-SO and IGS-WT were no longer significantly different from the no-harvest treatment. The amount of preferred lichen in the GS-SO treatment (10.3%) was similar to the no-harvest treatment (11.3%) and the preharvest amount (9.9%). In the IGS-WT treatment, the amount of lichen increased from 6.3% in 1998 to 7.8% in 2004, while in the IGS-SO treatment, the amount of lichen increased from 4.9% in 1998 to 6.8% in 2004 (Table 2). Figure 2 shows the trend in treatment means over time. The overall tests of treatment effect were significant for the subsets of data from the residual forest and openings, but the treatment differences were no longer significant when pairs of treatment means were compared among the forested treatments (Table 2). There were larger gains in lichen abundance in the openings than in the

Table 3. Comparison of openings in the partial cuts and no-harvest treatments using non-parametric analysis of variance (based on Friedman's Chi) for healthy species and groupings of species post-harvest. Rank sum differences marked with an * are statistically different at $\alpha = 0.037$ (experiment wide error rate).

				Difference	e between tre	atment ran	k sums		
Species	Year	Chi	Р	IGS-SO ^a vs No- harvest	IGS-WT ^b vs No- harvest	GS-SO° vs No- harvest	IGS-SO vs IGS-WT	GS-SO vs IGS-SO	GS-SO vs IGS-WT
Dicranum spp.	1998	13.65	< 0.001	-15*	-6	-10	9	5	-4
	2000	10.35	< 0.009	-13*	-5	-9	8	4	-4
	2004	10.47	< 0.009	-13*	-8	-10	5	3	-2
All moss species	1998	9.00	< 0.023	-12*	-8	-6	4	6	2
	2000	8.76	0.023	-12*	-5	-5	7	7	0
	2004	9.00	< 0.023	-10	0	0	10	10	0
All Peltigera spp.	1998	4.20	>0.21	-8	-6	-4	2	4	2
	2000	7.32	0.06	-11*	-6	-5	5	6	1
	2004	4.92	0.210	-7	-8	-3	-1	4	5
Cladonia ecmocyna	1998	10.68	0.005	-12*	-11*	-7	1	5	4
	2000	10.68	0.005	12*	-11*	-7	1	5	4
	2004	7.32	0.055	-10	-9	-7	1	3	2
All Cladonia spp.	1998	9.24	< 0.023	-11*	-10	-9	1	2	1
	2000	13.56	< 0.001	-15*	-8	-7	7	8	1
	2004	4.92	0.210	-8	-7	-3	1	5	4

^a irregular group shelterwood with stem-only harvesting.

b irregular group shelterwood with whole-tree harvesting.

^c group selection with stem-only harvesting.

Table 4. Percent cover (mean and standard deviation) for species and species groupings per treatment for all blocks in 1995 (pre-harvest) and 2004 (all health classes). Three clearcuts adjacent to the trial blocks were added for comparison using 2005 data.

				Cover (%)		
Species	Year	No-harvest	IGS-SO ^a	IGS-WT ^b	GS-SO°	Clearcut
		n = 229	n = 225	n = 223	n = 223	n = 120
Feathermosses	1995	6.7 ± 16.9	8.7 ± 18.6	12.9 ± 22.8	9.7 ± 21.0	
	2004-05	9.3 ± 19.0	5.2 ± 12.6	8.7 ± 15.3	6.5 ± 15.5	1.6 ± 1.9
Dicranum spp.	1995	3.7 ± 8.5	4.0 ± 8.8	4.0 ± 7.8	3.3 ± 7.0	
	2004-05	4.7 ± 8.7	2.5 ± 5.7	3.3 ± 5.7	2.9 ± 6.5	0.6 ± 0.4
All moss spp.	1995	12.2 ± 20.5	15.0 ± 22.5	19.2 ± 26.8	15.0 ± 23.8	
	2004-05	15.9 ± 22.6	8.7 ± 15.7	13.6 ± 18.3	10.5 ± 18.0	2.3 ± 2.7
Peltigera aphthosa	1995	1.3 ± 3.5	$1.7~\pm~4.1$	3.2 ± 6.1	1.9 ± 4.1	
	2004-05	2.2 ± 5.4	1.3 ± 3.1	2.1 ± 4.6	1.4 ± 3.3	0.1 ± 0.1
All <i>Peltigera</i> spp.	1995	5.3 ± 6.8	6.1 ± 7.9	6.5 ± 8.5	5.8 ± 8.5	
	2004-05	7.7 ± 9.6	5.6 ± 7.5	5.0 ± 6.0	5.3 ± 7.0	1.6 ± 2.0
Cetraria spp.	1995	0.7 ± 1.1	0.7 ± 1.3	$0.7~\pm~1.4$	0.6 ± 1.1	
	2004-05	1.1 ± 1.6	$0.7~\pm~1.2$	0.9 ± 1.4	0.9 ± 1.5	0.8 ± 0.7
Cladonia gracilis	1995	1.3 ± 2.4	1.8 ± 3.2	1.1 ± 2.0	1.8 ± 3.5	
	2004-05	0.4 ± 1.2	$0.7~\pm~1.5$	0.3 ± 0.8	$0.7~\pm~1.6$	0.2 ± 0.3
Cladonia cornuta	1995	0.4 ± 0.9	0.3 ± 0.7	0.3 ± 0.7	0.2 ± 0.6	
	2004-05	0.3 ± 0.7	0.2 ± 0.6	0.3 ± 1.5	0.2 ± 0.7	0.1 ± 0.1
Cladonia ecmocyna	1995	2.7 ± 6.0	3.1 ± 5.9	3.6 ± 7.3	3.1 ± 4.5	
	2004-05	3.8 ± 5.5	2.2 ± 3.9	2.9 ± 5.3	3.2 ± 4.6	1.4 ± 1.1
All <i>Cladonia</i> spp.	1995	8.6 ± 8.1	8.2 ± 8.2	8.3 ± 8.5	7.5 ± 6.7	
	2004-05	$8.7~\pm~8.2$	6.8 ± 6.9	6.3 ± 6.7	8.6 ± 8.1	3.6 ± 1.9
Cladina spp.	1995	0.8 ± 3.1	0.9 ± 2.6	1.0 ± 2.7	1.2 ± 3.4	
	2004-05	1.2 ± 3.1	$0.7~\pm~1.7$	1.0 ± 2.6	1.2 ± 3.2	0.7 ± 0.6
Stereocaulon spp.	1995	1.6 ± 5.7	0.7 ± 3.8	1.1 ± 3.6	0.9 ± 3.9	
	2004-05	1.5 ± 5.2	0.3 ± 1.7	1.2 ± 3.7	0.9 ± 3.8	0.2 ± 0.2
Preferred lichens	1995	11.6 ± 10.3	10.4 ± 10.8	11.1 ± 10.6	10.1 ± 9.1	
	2004-05	12.4 ± 10.4	8.5 ± 8.0	9.3 ± 8.9	11.6 ± 10.5	5.3 ± 3.0

^a irregular group shelterwood with stem-only harvesting.

^b irregular group shelterwood with whole-tree harvesting.

^c group selection with stem-only harvesting.

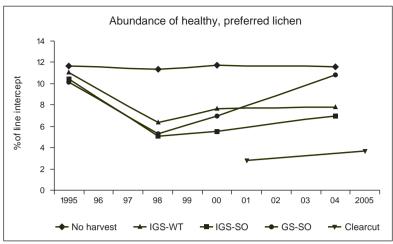


Fig. 2. Mean abundance of healthy, preferred lichen by year and treatment in the main trial (n = 5) and adjacent clearcuts (n = 3). IGS-SO: irregular group shelterwood with stem-only harvesting; IGS-WT: irregular group shelterwood with whole-tree harvesting; GS-SO: group selection with stem-only harvesting

residual forest but there remained significantly more lichen in the no-harvest treatment than in the openings within IGS-SO (Table 2).

There were sufficient data to compare some individual species and groups of species between the no-harvest treatments and the openings in the partial cut treatments (Table 3). Mosses and *Dicranum* spp. were significantly lower in cover in the openings compared to the no-harvest treatment in 1998, 2000 and 2004. *Cladonia* spp. and *Cladonia ecmocyna* were all less abundant in the openings, especially in the IGS treatments, when compared to the no-harvest treatment in 1998 and 2000. All *Peltigera* spp. were only significantly lower in the IGS-SO openings in 2000. The mean and standard deviation by treatment for species and species groupings for 1995 and 2004 are shown in Table 4.

Abundance of lichen and moss in the three adjacent clearcuts

In 2001, the average amount of healthy, preferred lichen in clearcuts was about one quarter of that found in the no-harvest treatments in the adjacent trial blocks and about half of that found in the partial cuts in 2000 (Fig. 2). By 2005, the average amount of healthy, preferred lichen in clearcuts increased from 2.8 to 3.7%. Cladonia made up 65% of the preferred lichen group in 2000 and 60% in 2005. All species measured in the clearcuts were present in the no-harvest treatments. In 2005, Cladonia ecmocyna was 25% of the preferred lichen sample, followed by Cetraria (21%), Cladina (18%) and Stereocaulon (6%).

Mosses in the mid-elevation block averaged less than 1% compared to 7.4% in the no-harvest treatment (2004), and in the highest elevation block, they averaged 2 to 5% (2001 and 2005, respectively) compared to 39% in the no-harvest treatment (2004).

Variables that could affect abundance

Variables (substrate [humus, mineral soil, rock, and woody debris from natural litter and logging slash], disturbance [human, harvesting, wildlife], and vegetation [shrubs, dwarf shrubs, herbs, tree regeneration and overstorey trees]) that could influence the abundance of lichen and

moss species were very similar among treatments preharvest (Table 5). Pre-harvest and in the no-harvest treatments over time, humus was the most common substrate (92-95%) with woody debris (coarse and medium litter) and rock up to 3.5% each. Postharvest in the partial cuts, humus decreased slightly, while woody debris increased 2-6%, depending on the treatment. In addition, woody debris identified as logging slash was input into all the treatments. Maximum values were recorded in 1998 and 2000 (IGS-SO: 12%, GS-SO: - 10% and IGS-WT: 5%) when it was easiest to identify debris from logging origin. Cover of rock, mineral soil and mixed soil remained unchanged. In the three adjacent clearcuts, cover of woody debris in 2001 was 12% and logging slash was 20%. The most disturbance (up to 3%) in the plots occurred in 1995 due to compression by humans installing the plots.

Although partial cutting removed 28 to 39% of the forest, there was not an equivalent decrease in overhead canopy cover. In 1998 to 2004, it averaged 31–39% in the partial cuts compared to 46% in the no-harvest treatment (Table 5). There was 0.3% overhead canopy cover recorded in the clearcuts in 2005. Shrubs ranged from 4 to 8% cover in the partial and clearcut treatments, which was similar to the no-harvest treatments. By 2000 and 2004, dwarf shrubs in the partial cuts had increased by about 2–6% from the pre-harvest amount and in comparison to the no-harvest treatments over time. There was a similar amount of dwarf shrub in the clearcuts and partial cuts (14 to 19%). Herbs in the

Table 5. Mean percent cover of soil and litter substrates, logging slash, disturbance, and vegetation layers by year and treatment

1995 94.0 ii 0.1					(n = 22) DIOLS	DIOLS			(n = 223 plots)	blots)			(n = 225 blots)	5 plots)		(n=120 plots)	plots)
94.0 ii 0.1	178 21		2004	1995	1998	2000	2004	1995	1998	2000	2004	1995	1998	2000	2004	2001	2005
ii 0.1		92.8	92.3	92.0	89.0	86.7	9.98	95.0	0.96	93.8	92.4	94.0	93.0	90.4	90.4	80.2	78.0
ć	.2	5.3	8.0	1.0	0.1	0.2	0.2	0.0	0.0	0.0	0.5	9.0	0.2	0.2	0.2	2.1	2.2
Mixed Soil 0.5 U.	0.3).1	0.1	6.0	9.0	0.1	0.2	0.1	0.4	0.1	0.2	0.1	0.2	0.1	0.2	2.9	1.4
Rock 2.9 4.0	0.	3.0	2.9	2.6	2.3	2.3	2.6	1.0	1.2	1.2	1.5	0.7	8.0	0.7	0.7	2.2	3.2
Litter - coarse 1.7 2.0	0.	2.3	1.7	1.9	2.8	8.9	1.8	1.9	2.0	2.0	1.3	3.5	2.8	5.0	3.3	3.1	4.3
Litter - medium 1.4 1.3	.3	1.6	2.3	1.9	3.6	3.9	8.5	1.7	2.5	2.9	4.1	1.8	3.0	3.8	5.2	0.6	10.9
Logging slash 0.0 0.0	0.	0.0	0.0	0.0	12.3	12.4	9.1	0.0	5.0	5.4	2.2	0.0	6.6	6.7	6.1	20.1	14.8
Disturbance 2.4 1.1	.1 (6.0	1.3	3.1	1.1	8.0	1.0	1.7	1.0	0.5	1.3	2.8	1.4	0.7	1.2	5.6	8.0
Shrubs 6.4 6.3		6.7	8.5	7.8	5.1	6.5	6.9	5.1	4.0	5.8	6.1	0.9	4.7	7.2	8.0	3.6	4.5
Dwarf shrubs 9.1 7.3		12.5	10.1	12.3	8.4	15.9	14.3	13.0	8.7	16.4	15.1	13.3	10.3	19.0	17.4	15.0	16.9
Herbs 2.1 1.6	9.	3.1	2.0	2.8	2.2	4.8	4.0	2.5	2.6	5.0	4.0	2.3	1.9	4.8	3.1	12.8	17.4
Regeneration 0.3 0.2	.2 (5.4	0.5	0.5	6.0	0.7	8.0	6.0	6.0	0.7	0.7	0.7	0.4	0.7	0.7	2.0	3.4
Trees 38.8 44.8		47.2	45.4	39.1	31.2	32.2	30.4	48.8	39.8	43.2	36.5	42.2	37.9	38.2	37.5	0.0	0.3

no-harvest treatment and pre-harvest in the partial cuts averaged 2 to 3%, and increased in the partial cuts by 1 to 2% by 2004. Herbs in the clearcuts averaged 17% by 2005, and the most abundant species were northwestern sedge (Carex concinnoides) (6%), fireweed (Epilobium angustifolium) (2%), spike trisetum (Trisetum spicatum) (3%), shortawned ricegrass (Oryzopsis pungens) (1%), bunchberry (Cornus canadensis) (1%), and foxtail barley (Hordeum jubatum) (1%). All these species were 1% or less in the no-harvest treatments and partial cuts.

Regression analysis using plots from the partial cut and no-harvest treatments Pre-harvest, the abundance of preferred forage lichen was significantly negatively related to cover of woody debris, herbs, dwarf shrubs, shrubs, and trees, while regeneration cover and treatment effects were the only non-significant variables (Table 6). This indicates that the best growing locations in the forest for lichen have minimal woody debris, and few herbs, dwarf shrubs, and shrubs, and spots with less overhead cover from trees. In the post-harvest analyses in 1998, 2000 and 2004, logging slash, woody debris, dwarf shrubs, and herbs continued to be negatively related to the abundance of preferred lichen (Table 6). Trees were not significant factors in 1998, but in the next two assessments cover from overstorey trees was again negatively associated with preferred lichen abundance. Regeneration (small pine trees) remained non-significant. Treatment effects (lower abundance in the partial cuts compared to the noharvest) were significant in all years for the IGS treatments, but only in 1998 and 2000 in the GS treatment. Overall R² values ranged from 0.23 pre-harvest to 0.29 to 0.34 post-harvest.

Discussion

Immediate response to harvesting

There is little available literature on the impact of partial cutting on terrestrial lichens in caribou winter range. However, it has been hypothesized that

Significant intercepts and coefficients for linear multiple regression models using healthy, preferred lichen as the dependent variable in 1995, 1998, 2000, and 2004 (n = 899)Table 6.

	1995		1998		2000		2004	
	Mean ± Std	Ь	Mean ± Std	Ь	Mean ± Std	Ь	Mean ± Std	Ь
Logging slash	n/a		-0.0250 ± 0.0027	<0.0001	-0.0200 ± 0.0038	<0.0001	-0.0180 ± 0.0048	<0.0002
Woody debris	-0.0350 ± 0.0059	<0.0001	-0.0270 ± 0.0054	<0.0001	-0.0150 ± 0.0041	0.0003	-0.0280 ± 0.0047	<0.0001
Shrubs	-0.0130 ± 0.00510	<0.0117	-0.0130 ± 0.0054	0.0138	ı		ı	
Dwarf shrubs	-0.0160 ± 0.0038	<0.0001	-0.0160 ± 0.0042	0.0002	-0.0150 ± 0.0032	<0.0001	-0.0160 ± 0.0036	<0.0001
Herbs	-0.0540 ± 0.0122	<0.0001	-0.0420 ± 0.0094	<0.0001	-0.0340 ± 0.0062	<0.0001	-0.0400 ± 0.0083	<0.0001
Regeneration	1		ı		ı		ı	
Trees	-0.0030 ± 0.0014	0.0491	ı		-0.0020 ± 0.0011	0.0415	-0.0060 ± 0.0014	<0.0001
IGS-SO*-no-harvest	ı		-0.7460 ± 0.1822	0.0009	-0.7600 ± 0.1463	<0.0001	-0.4280 ± 0.1676	0.0218
IGS-WT ^b -no-harvest	1		-0.6900 ± 0.1800	0.0016	-0.5150 ± 0.1436	0.0028	-0.4460 ± 0.1652	0.0168
GS-SO'-no-harvest	1		-0.7480 ± 0.1818	0.0008	-0.5140 ± 0.1464	0.0030	1	
Intercept	3.49 ± 0.24	<0.0001	3.36 ± 0.22	<0.0001	3.48 ± 0.22	<0.0001	3.71 ± 0.24	<0.0001
R^2	0.23	<.0001	0.32	<0.0001	0.34	< 0.0001	0.29	<0.0001

partial cutting could promote continued terrestrial lichen growth by interrupting the normal succession pattern to feathermoss dominance in the northern part of British Columbia (Sulyma & Coxson, 2001). Snyder (1987) recommended trying selective logging in older pine stands, in west-central Alberta, to increase light to promote lichen abundance. Preliminary work in west-central B.C. suggested small openings would have less impact on lichens than clearcuts (Enns, 1998; Miège et al., 2001a).

group selection with stem-only harvesting.

b irregular group shelterwood with whole-tree harvesting.

irregular group shelterwood with stem-only harvesting.

Our results showed that both the group selection and irregular group shelterwood systems using stem-only harvesting were associated with a 43 to 51% decline in the amount of preferred terrestrial lichens (particularly Cladonia) within 2.5 years of winter harvesting. In the first two post-harvest assessments, the group selection and irregular group shelterwoods were not significantly different from each other. Also, the greatest reductions were in the openings but lichens in the residual forest were also impacted. Morphotypes of lichen growing in subdued light are not well adapted to sudden exposure to stronger light conditions when the forest canopy is removed. Lichens that can grow in full sunlight have darker pigmentation and a much thicker upper cortex to protect their chlorophyll from oxidation (Kershaw, 1985).

The amount of physical damage can influence the mortality of the lichens. Kranrod (1996) in west-central Alberta, in a pre- and post-harvest study, documented an immediate post-harvest reduction in lichen of at least 50% in summer-logged treatments, whereas in winter-logged treatments, there was minimal impact after six months.

A number of studies from across Canada report lower lichen abundance in young clearcuts (Woodard, 1995; Harris, 1996; Webb, 1998; Goward *et al.*, 1998), but they are not supported by pre-treatment data. Similarly, we found that adjacent clearcuts had much less lichen cover (2.8%) than the no-harvest treatments (11.7%), even 5 to 7 years post-harvest.

Recovery over time

Generally, the rate of recovery can be influenced by the amount of lichen fragments available post-harvest (Harris, 1996; Webb, 1998) and the number of colonies that survive harvesting. Comparative studies show that young stands of logging origin have more lichen than those of fire origin because of the availability of fragments and colonies (Webb, 1998; Coxson & Marsh, 2001). Furthermore, winter harvesting leaves more undisturbed colonies from which to reinitiate (Coxson & Marsh, 2001).

We found that the quantity of lichen in the forested and cut portions of the treatments has been recovering since 1998. It has been especially rapid in the small gaps (15 m diameter) associated with the group selection system, where in 2004, the quantity of lichen approximated the pre-treatment level. The shelterwood treatments were at 68% and 71% of their pre-treatment level in 2004 so a longer period of time is required. However, by 2004, the whole-tree harvesting treatment was not statistically different from the no-harvest treatment, possibly indicating a shorter-term impact.

The speedy recovery of lichens in the group selection treatment compared to the shelterwood treatments may be due to the small diameter of the openings and less area cut. The greater coverage by the residual trees in the group selection treatment would more effectively block light and maintain cooler, shadier conditions. This may have particularly facilitated recovery of the lichens classified as sickly in the initial 1998 measurement. Also, woody debris left over from the stem-only harvest may have further ameliorated microclimate conditions to facilitate recolonization. Goward *et al.* (1998) and Enns (1998) both comment on thalli growing in the shelter of logs or tip-up mounds often appear robust, while those in more exposed sites are dead or moribund.

The amount of time required to fully recoup the pre-treatment lichen amounts in the shelterwood treatments is unknown. A simple linear extrapolation of the shelterwood results for the first eight years of our study suggests about 20 years to recover lichen to pre-harvest levels, while clearcuts would require about 30 years. These estimates are consistent with information from retrospective studies on stands originating from clearcutting or fire. Generally, the amount of time to recover lichen appears to depend on the geographic area, intensity of the disturbance, and the lichen species present.

In west-central Alberta, Woodard (1995) and Snyder & Woodard (1992) found total lichen cover (predominantly *Cladonia* and *Peltigera*) equaled that occurring in unlogged stands 20 to 30 years after clearcutting.

In Ontario, the dominant species, *Cladina stellaris, Cladina rangiferina* and *Cladina mitis*, were exceedingly abundant in older clearcuts (43 to 46 years, horselogged and not site prepared) compared to mature stands (Harris, 1996). Racey *et al.* (1996) estimated that logged areas could function as caribou winter habitat after 40 years and that removal of the organic matter was necessary to ensure succession to a jack pine–lichen community rather than to black spruce–feathermoss community. In Sweden, Eriksson (1975) suggested that some areas reforested after clearcutting were "fair" reindeer range in 20 to 30 years.

Studies on pine stands originating from fire in western Canada give some indication that development of lichen mats takes at least 40 years. In the vicinity of the study area, Goward et al. (1998) found stands aged 42 to 70 years had abundant preferred lichen (14 to 25% cover). Similarly, Braulisauer (1996) and Hooper & Pitt (1996) described stands aged 67 to 85 years as having a mean cover of 16% of preferred species, which was consistent through stands up to 385 years old, though the proportion of Cladonia decreased and Cladina increased over time. Further north in British Columbia, Cladina dominated the forest floor surface in 50-100 years stands (Coxson & Marsh, 2001). Snyder (1987) reported that in westcentral Alberta, similar to west-central B.C., equal quantities of preferred lichen were found in 50- and 200-year-old lodgepole pine stands, but species shifted from Cladonia to a mix of Cladonia, Cladina and Peltigera. In north-east Alberta and northwest Saskatchewan (Carroll & Bliss, 1982), the recovery of the lichen mat (dominantly Cladina) in jack pine stands (Pinus banksiana) is 45 years.

Based on the estimated rate of recovery of lichens and other published results, the final cut planned for the shelterwood silvicultural systems in 70 years should be more than sufficient to recover terrestrial lichen in the context of a mature forest. The group selection system, planned on an 80-year cutting cycle, was designed for sites with substantial arboreal lichen as well as terrestrial lichen. Although the terrestrial lichen has rapidly recovered, it could take a long time to recover arboreal lichen in the gaps. This is due to the time it takes to develop stand attributes, such as defoliated branches, stable environmental conditions and adequate ventilation that are conducive to heavy lichen loading (Goward & Campbell, 2005). With the system fully implemented, at any point in time, more than one third of the forest is over 80 years and one third is over 160 years, so sufficient arboreal lichen should be available to caribou. This is preferable to the clearcut method which directly removes all the arboreal lichen-bearing trees. Indications from local studies (Braulisauer, 1996; Hooper & Pitt, 1996; Goward et al., 1998) are that the forests in the Montane Spruce and especially in the Sub-boreal Pine Spruce zones will maintain a reasonable component of terrestrial lichen throughout the life cycle of the managed forest, unlike some other jurisdictions where pine–lichen stands over time transition to predominantly feathermoss (Racey et al., 1996; Brakenhielm & Liu, 1998; Sulyma & Coxson, 2001; Coxson & Marsh, 2001).

The silvicultural systems also affect other plant species that may compete with preferred lichen species for space and resources, but also may have some forage value for caribou. Peltigera, mosses, grasses, sedges, conifer needles, dwarf shrubs and shrubs are found at low levels in caribou diets (Scotter, 1967; Edmonds & Bloomfield, 1984; Thomas & Hervieux, 1986; Cichowski, 1989; Thomas et al., 1996). Peltigera, Stereocaulon, "winter-green" vascular plants, and green parts of sedges and grasses have higher protein content and are thought to increase the digestibility of Cladonia, Cladina and Cetraria species, which have high carbohydrate value but low protein value (Person et al., 1980; Klein, 1982; Edmonds & Bloomfield, 1984). We found that Peltigera species remained common within the partially cut treatments, though mean abundance dropped in the openings. Also, abundance of herbs (mostly grasses and sedges), shrubs, and "winter-green" dwarf shrubs (predominantly Linnaea borealis, Arctostaphylos uva-ursi and Empetrum nigrum) only increased by a few percent in the partial cuts so did not pose an increased competitive threat. Overall, the partial cutting silvicultural systems have provided a range of food sources in close proximity for caribou.

In contrast, clearcuts lost a large amount of preferred lichen and *Peltigera* species, while sedge and grass cover increased by 11%, and cover of shrubs and dwarf shrubs remained similar to the partial cuts. With the absence of lichens from young clearcuts, the other species may be of little use to caribou in the winter. The significantly greater herb response in the clearcuts is noteworthy as it has the potential of making those areas more attractive during summer to deer and moose—the primary prey of wolves. Although fewer caribou use these areas in the snow free seasons, any habitat alteration that could lead to greater wolf numbers is of concern to caribou which are sensitive to increased predation (Seip, 1991; 1992).

Method of harvesting

Whole-tree and stem-only harvesting were selected for this study because both types are used in westcentral B.C. There were concerns associated with each method. In the pilot study for our trial, Miège *et al.* (2001a) found that the slash generated through onsite processing covered the lichens, causing mortality. Conversely, whole-tree skidding, even on snow, could cause more physical damage to the lichen mat, and the associated roadside processing area would severely reduce lichen cover.

A direct comparison between the two shelterwood treatments showed no significant differences in preferred lichens between the treatments over the eight-year study period. The amount of physical disturbance (compression and displacement) was minimal in both systems, and opening size and area cut were similar, suggesting similar changes in environmental conditions such as light, occurred in the two treatments. However, by 2004, the whole-tree system, unlike the stem-only system, was no longer significantly different from the no-harvest treatment. Possibly the lower slash input (5%) in the whole-tree treatment (compared to the stem-only system [12%]) was enough to cause the non-significant difference from the no-harvest treatment. However, the impact of the roadside processing area (3 to 7% per treatment unit) associated with whole-tree harvesting was not included in the treatment effect. Kranrod (1996) concluded that stem-only harvesting, when in combination with winter logging and no scarification, retained the most lichen immediately post-harvest because the debris piles moderated the micro-environment within the clearcut.

Key factors that affect lichen abundance

In our regression analysis, factors such as woody debris and vegetation cover that were negatively related to lichen abundance pre-harvest, continued to be significant post-harvest. The direct comparison between harvesting systems (WT and SO) showed no statistical differences. However, harvesting did increase the amount of woody debris, particularly in the SO system. This debris occupies forest floor space, making it unavailable for lichen. Furthermore, in the MSxv and SBPSxc biogeoclimatic subzones, the process of decay is slow, so the debris remains solid and dry for a long time. In moister environments, as described by Racey et al. (1996) and Harris (1996), colonization of stumps is rapid, and coverage of slash piles occurred in 40 years (Harris, 1996). When slash is deposited on the ground, it crushes lichen. Low suspended slash can prevent light and precipitation from reaching the lichen, and it creates a poorly ventilated environment that encourages the growth of fungal mats. Conversely, high suspended slash and areas adjacent to slash piles may provide refugia for lichen in the short and long term.

The increased light and moisture in the partial cuts stimulated a small amount of growth of herbs and dwarf shrubs. Whether lichen can colonize the area occupied by these plants as stands redevelop is unknown. Lichen occupancy increased as tree cover decreased, implying that natural gaps with more light are the best locations for lichens. Perhaps after the initial shock of exposure, lichens may grow exceptionally well in gaps until the young stand redevelops.

Management implications and conclusions

The group selection and irregular group shelterwood treatments maintain forage lichen in the residual stand. Recovery of terrestrial lichens in the group selection system occurred within eight years of harvest, and possibly will happen within 20 years in the shelterwood systems. The group selection system is recommended for 20% of the modified harvesting area, which supports the most arboreal lichen in addition to terrestrial lichen. Survival and growth of planted trees in the openings is sufficient for the planned rotation periods (140 or 240 years) (Waterhouse et al., 2010). Natural regeneration is also a viable silvicultural option for openings in the SBPS blocks as they were sufficiently regenerated in seven years (Steen et al., 2007). Also, treefall studies indicate that the stands have remained very stable (Waterhouse & Armleder, 2004).

An estimated 20-year recovery of forage in the shelterwood treatments does not necessarily mean that the residual forested component can be harvested earlier than the planned removal in 70 years. Foremost, lichens growing in the first entry openings will be negatively affected to some degree by the removal of the adjacent forest. Secondarily, prime winter habitat is not only determined by the quantity of forage lichens but the context in which they are available. There may be enough terrestrial lichen in immature stands, but these stands are less desirable (Schaefer and Pruitt, 1991). Also, removal of the forest canopy results in increased winter snow depths relative to the forest, making it more energetically demanding for caribou to access lichens (Schaefer, 1996). Johnson et al. (2001) found that when snow conditions (depth and density) limited access to terrestrial lichens, caribou switched to foraging on less abundant arboreal lichens. It may take several decades to recover the snow interception capacity of older stands.

In the cold, dry ecosystems of west-central B.C., aggressive forest harvesting and site preparation methods are not necessary to destroy feathermoss mats and re-initiate succession to lichen communities. Winter logging and no site preparation causes

the least immediate damage to pre-harvest lichen mats (Harris, 1996; Kranrod, 1996; Enns, 1998; Webb, 1998; Coxson & Marsh, 2001). A direct comparison found that stem-only or whole-tree harvesting similarly reduced lichen; however, there was more slash deposited in the stem-only system, and regression analysis pre—and post-harvest showed that increases in woody debris and slash were associated with a significant reduction in lichen abundance. Others (Kranrod, 1996; Enns, 1998; Goward et al., 1998) suggest that once woody debris is in place, it helps maintain lichen. There is the added advantage of leaving woody debris for long-term site productivity (Wei et al., 2000).

High tree mortality caused by mountain pine beetle has complicated this trial. Beetle attack was first recorded in 2003, and by 2008, the pine beetles had killed about 60% of the mature trees on the trial blocks. Some implications to the lichen community, and subsequently to northern caribou, are discussed by Armleder & Waterhouse (2008).

Partial cutting remains an effective management tool to manage caribou habitat in west-central B.C. where timber harvesting is a management reality. However, large areas with no development are also part of the overall strategy for maintaining caribou.

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Harvest impacts on caribou population dynamics in South West Greenland

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Abstract: We examined the effects of hunting on caribou populations in South West Greenland from year 1999 to 2007. In the Ameralik area a reported average annual harvest of 2950 caribou coincided with a population decline from 31 000 (90% CI: 22 000 - 44 000) animals in 1999 to 8900 (90% CI: 5800 - 13 000) in 2007. A survey estimate from 2006 indicates that a suggested target caribou density of 1.2 / km² was met. A Bayesian population model estimates the annual replacement for Ameralik at minus 170 individuals (90% CI: -550 - 460), which indicates that the target density may or may not be maintained even in the total absence of a hunt. For the Qeqertarsuatsiaat area an average annual harvest of 230 caribou appears to have left the density unaffected, remaining steady on target with an abundance of approximately 5000 individuals. The harvest in this area increased from 100 animals in 2000 to 440 in 2006. With an estimated 2007 replacement of 190 (90% CI: -190- 960) caribou per year the target density may not be maintained in the future unless hunting restrictions are implemented. The density of caribou in Qeqertarsuatsiaat may, however, be maintained over the short term if the emigration of animals from Ameralik into Qeqertarsuatsiaat continues.

Key words: Greenland caribou; harvest; population dynamics; Rangifer tarandus groenlandicus, South West Greenland.

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Introduction

Caribou (Rangifer tarandus groenlandicus) in West and Northwest Greenland are segregated into approximately ten populations that are separated by the Greenland Ice Cap, glaciers and wide fjords. The fjords often penetrate from the sea to the Ice Cap and generally run parallel to the seasonal migration of caribou. Most caribou populations in West Greenland are small and relatively isolated with only a small degree of gene flow between them (Jepsen,

1999). Caribou have been abundant, however, in mid-West Greenland for at least the last decade, and the three largest populations are found in what has become known as the North, Central and South regions (Fig. 1).

There are no large predators in the terrestrial ecosystem in West Greenland, and herbivore diversity is low. In the South region the only permanent resident herbivores that share range with caribou are arctic hares (*Lepus arcticus*) and ptarmigan (*Lagopus*

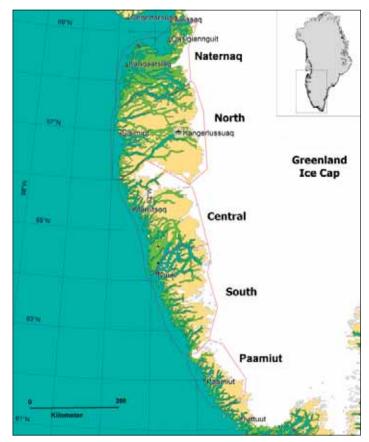


Fig. 1. Caribou regions in West Greenland. This paper describes the impact of hunt on the caribou population in the South region.

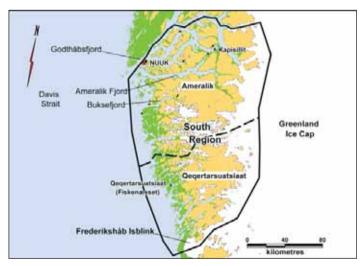


Fig. 2. Details of the South region; area within solid black outline is approx. 13 500 km². The hatched line separates the northern Ameralik (8400 km²) and the southern Qeqertarsuatsiaat (5100 km²) areas.

mutus). The South region is located immediately south of Greenland's capital Nuuk, and it contains the third largest caribou population in West Greenland.

In the absence of predators, the limiting factors on the populations include intra-specific competition, range capacity, pathogens and human harvest, as well as stochastic weather events and climatic changes. Since 2001 quotas were increased resulting in greater harvests and may now have become one of the strongest limiting factors on some of the populations. In this paper we examine the impact of recent harvests on the caribou population in the South region, specifically in the northern Ameralik and the southern Qeqertarsuatsiaat areas.

Background

The South region, known as caribou hunting regions 4 and 5, has a seasonally ice-free area of approximately 13 500 km². Steep sided fjords and a rugged alpine terrain characterize this region (Fig. 2). Coastal lowlands are minimal and much of the region has an elevation greater than 200 metres. The northern border is the large Godthåbsfjord that cuts from the sea to the Greenland Ice Cap. The Frederikshåb Isblink, which is a large glacial tongue of the Greenland Ice Cap, forms the southern boundary. To the west is the Davis Strait, and to the east is the Greenland Ice Cap. The region is divided into two areas that provide two sub-populations of caribou; the northern Ameralik (8400 km², hunting region 4) and the southern Qeqertarsuatsiaat (ca. 5100 km², hunting region 5). The region's largest human settlement is Nuuk, the capital of Greenland, with about 15 000 inhabitants. It is situated on the region's northern border at the mouth of Godthåbsfjord. There are two small hamlets; Kapisillit, located in the inner reaches of Godthåbsfjord, and Qegertarsuatsiaat, situated on the seacoast about 100 km south

of Nuuk. Development of the region is limited to a hydro power plant at the head of Buksefjord, with a transmission line to Nuuk. Roads are limited to the settlements, and do not link settlements nor penetrate the terrain.

Recent history

Following aerial surveys in the 1990s, the Greenland government's caribou managers thought that caribou populations throughout West Greenland were low in number, while the consensus from local hunters indicated substantially larger populations (Cuyler et al., 2002, 2003, 2005, 2007; Cuyler, 2007). New improved abundance surveys beginning in 2000 supported the hunters' knowledge. The 2001 aerial survey resulted in a caribou estimate of 32 000 (CV: 18%, Table 1) for the Ameralik portion of the South region (Fig. 2). This was seven times greater than the estimate of 4500 from 1996 (Ydemann & Pedersen, 1999), and caribou density was almost four times greater than a proposed target caribou density of 1.2 / km2 (Kingsley & Cuyler, 2002; Cuyler et al., 2003, 2005; Cuyler, 2007).

Following the large numbers of caribou, hunters observed habitat degradation; caribou-lichen heaths had become overgrazed where they had been deep and plentiful, and the once lush expanses of crowberries (*Empetrum nigrum*) were trampled (Cuyler *et al.*, 2007). In the years following 2001, the government's caribou managers decided to attempt to reduce West Greenland caribou populations towards the target density. Harvest levels were raised by greatly increased

caribou quotas in 2000, 2001 and 2002, and by extending the hunting season. Free/unlimited harvest over the extended season was permitted in 2003, and this raised harvest levels further by permitting several thousand sport hunters to partake in the caribou hunt, which until then had been monopolized by commercial hunters.

The target caribou density of 1.2 / km² was based on studies of carrying capacity in North America and Finland (Haber & Walters, 1980, Helle *et al.*, 1990) and correlations between observed densities and changes in caribou productivity, dispersal or the condition of the range (Kingsley & Cuyler, 2002). Although not based on studies of the carrying capacity of West Greenland ranges, the target density

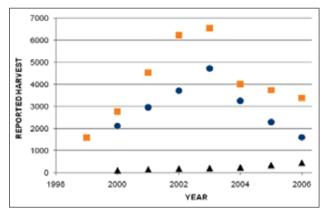


Fig. 3. Total reported caribou harvest (sport & commercial combined) for the South region (orange squares), divided into the northern Ameralik (blue circles) and southern Qeqertarsuatsiaat (black triangles) areas. Unlimited harvests were permitted after 2002.

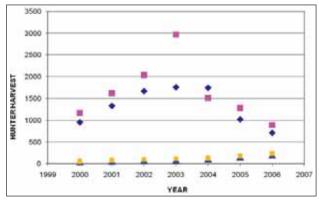


Fig. 4. Reported caribou harvest by sex (sport & commercial combined) for the South region, the Ameralik area (pink squares, female; blue diamonds, male) and Qeqertarsuatsiaat (yellow squares, female; light blue diamonds, male) area. Unlimited harvests were permitted after 2002.

may favour the preservation of vegetation quantity, quality and availability. If true, the latter would ultimately benefit the body condition, health and productivity of West Greenland caribou, and may provide the foundation for sustainable harvests.

With hunting seasons lengthened and quotas increased or unlimited, the reported total harvest increased (Fig. 3, Table 2) to a maximum of about 7000 caribou in 2003, and then fell to between 3000 and 4000 annually (Greenland Self Rule, unpubl.). Since harvest reporting was voluntary, the actual harvests may have been far larger than the estimated values. For example, commercial harvest was severely under reported. In 2005, only eight out of approximately 100 commercial hunters reported

their caribou harvest. Meanwhile, the Greenland commercial hunter organization (KNAPK) stated that 80% of the commercial harvest, which was sold at public market in Nuuk, came from the Ameralik area (Cuyler *et al.*, 2007).

The trend of the total harvest over time in the Ameralik area shows an initial increase, coinciding with increasing quotas, followed by a peak harvest of 4700 caribou in 2003, which matched the first year of unlimited harvest. Although unlimited harvests continued in the years following, the caribou harvest from Ameralik declined. This may have reflected a decline either in total caribou abundance, or in the number of animals in the areas that were accessible to hunters. In contrast, the caribou harvest from Qeqertarsuatsiaat increased from 100 caribou in 2000 to 440 in 2006.

Prior to 2000, the reported harvest was comprised of 90% males (*Loison et al.*, 2000). Following recommendations from the Greenland Institute of Natural Resources to harvest more females, however, more females were reported harvested than males in Ameralik (Fig. 4, Table 3) in all but one year. Meanwhile sex ratios in the Qeqertarsuatsiaat harvest were almost even.

The 2006 aerial survey of the Ameralik area resulted in an estimated caribou population of approximately 9680 (90% CI: 6515 - 13 147), which constituted a 70% decrease in abundance from 2001. This indicated that the target density had been reached. Local commercial hunters agreed with the decrease in abundance, and reported that there had been no increase in natural mortality based on their own observations (Cuyler *et al.*, 2007). No significant change could be shown in Qeqertarsuatsiaat, which remained at just over 5000 caribou and a density of 1 / km² (Cuyler *et al.*, 2007).

Method

Bayesian population dynamics model

We used Bayesian statistical analysis to examine the recent population dynamics of caribou in the Ameralik and Qeqertarsuatsiaat areas. We fitted an age and sex structured population dynamic model to the abundance data, subtracting the annual estimates of the sex and age-specific harvest from the population. As the time period for which we have area specific harvest data is relatively short, from 2000 to 2006, we applied an exponential population dynamic model. Although we have only two abundance estimates, we allow ourselves to fit the model to the abundance data in order to maintain a best first estimate of the current production levels.

The exponential model implies that we have no control over regulating factors and therefore we cannot make long-term predictions. But under all circumstances, long-term predictions in caribou are often problematic because caribou may have fluctuating or cyclic dynamics. This implies that traditional density regulated models cannot likely describe caribou population dynamics: relevant models need also to consider delayed density dependent factors that may have a strong influence on the dynamics. A clearer understanding of such processes in West Greenland caribou requires harvest and abundance data for a much longer period of time.

During our analysis we focus on the effects of the recent increase in harvest on caribou population dynamics for the South region. During the 2000-2006 period, the reported caribou harvest from the South region increased from under 3000 to a maximum of about 6500 individuals in 2003, and then declined to about 3,400 individuals in 2006. We attempt to determine whether observed abundance changes are the direct result of harvest. Further, we examine whether the target density was reached, and attempt to estimate what harvest levels are needed in the future to maintain or approach the target.

Data

From 2001 to 2006 total abundance was estimated twice by aerial strip surveys (Table 1). Both surveys used the same design and included identical transects

For 2003, 2004 and 2005 the annual harvest of caribou (Table 2) from each herd in the South region was estimated using details from hunter harvest reports, which include information of among other things, the location, sex, age category and rump fat depth of each animal. Location was often missing from the hunter reports and the Greenland Self Rule government's total annual harvest data is only available per municipality and not per caribou population. We estimated the harvest from the Ameralik and Qegertarsuatsiaat herds by comparing each municipality's total annual harvest from all six caribou populations in West Greenland to the relative percentage of harvest from each population contained in the hunter reports with location data. The individual estimates of caribou killed per population by each municipality were then summed to obtain a total annual harvest from each population. Detailed harvest databases, however, were not available for 2000, 2001 and 2002. To obtain estimates of annual harvest for these years, a population's average percentage of the total annual harvest for the years 2003, 2004 and 2005 was applied against the total harvest for 2000,

Table 1. Estimates of total caribou abundance (N) for the Southern population divided into Ameralik and Qeqertarsuatsiaat. N includes all age classes, and cv is given in %. (Cuyler et al., 2003, 2007; Cuyler, 2007).

Year	SOUTH N	cv	Ameralik N	cv	Qeqertarsuatsiaat N	cv
2001	37 252	15	31 880	18	5372	39
2006	14 871	13	9680	21	5224	29

Table 2. The estimated total annual harvest of male and female caribou in Ameralik and Qegertarsuatsiaat.

Year	Ame	eralik	Qeqertarsuatsiaat		
	Male	female	male	female	
2000	953	1163	46	55	
2001	1331	1623	64	77	
2002	1669	2036	81	96	
2003	1760	2965	86	113	
2004	1746	1514	111	124	
2005	1017	1276	156	180	
2006	709	889	205	235	

Table 3. The average age and sex-structure of the caribou harvested from the Southern population.

A 00 (1100mg)	SOUTH		Ame	eralik	Qeqertarsuatsiaat		
Age (years) –	male	female	male	female	male	female	
Calf <1	.11	.08	.11	.08	.11	.096	
Juvenile 1-2	.52	.41	.52	.41	.55	.45	
Adult ≥3	.37	.50	.37	.51	.34	.46	
Total	1.00	1.00	1.00	1.00	1.00	1.00	

2001 and 2002 (Greenland Self Rule, unpubl. data). For 2006, in the absence of keyed-in hunter reports and a total harvest estimate, we used the average change in total harvest between years 2003, 2004, 2005 to project the 2006 harvest.

The age-structure for the male and female harvest for each area (Table 3) was estimated from hunter reports. These reports were used to separate the harvest into calves, juveniles and adults. For each area the age-structure in the harvest was estimated from the average age structure over the whole period. The adult harvest included all animals aged over 3-years, under the assumption of no age-class selectivity, a

stable age-structure, an annual adult survival rate of 0.91.

Population dynamic model

The applied population dynamics is exponential with constant survival and fecundity rates in an age-and sex-aggregated model.

Let the number of animals in age classes larger than zero be

$$\begin{split} N_{t+1,a+1}^{m/f} &= \left(N_{t,a}^{m/f} - C_{t,a}^{m/f} \right) \, s_a & 0 \leq a \leq x-2 \\ N_{t+1,x}^{m/f} &= \left(N_{t,x}^{m/f} - C_{t,x}^{m/f} \right) \, s_x + \left(N_{t,x-1}^{m/f} - C_{t,x-1}^{m/f} \right) \, s_{x-1} \end{split}$$

where s_a is age specific annual survival,

$$N_{t,a}^{m/f}$$

is the number of males/females of age a at the start of year t, x is the lumped age-class (x = 5),

$$C_{t,a}^{m/f}$$

is the harvest of males/females of age *a* during year *t*, with the relative age distribution of the harvests being sex specific, the same in all years, and given by Table 3, provided that the harvest will not exceed the abundance in any age class. If instead the harvest exceeds the abundance in an age class, harvest in that age class is set to the abundance of that class. This distribution of harvests is continued until it is possible to distribute the remaining harvests in accordance with the age-structure in Table 3.

Let the annual survival rate s_a of animals of age a be

$$s_a = \begin{cases} s_{juv} s_{ad} & \text{if } a = 0 \\ s_{juv} & \text{if } 1 \le a \le a_{ad} \\ s_{ad} & \text{if } a > a_{ad} \end{cases}$$

where s_{juv} is the survival rate of 'juveniles' given the survival of their mother, s_{ad} is the survival rate for adults, and $a_{ad} = 1$ is the greatest age at which the 'juvenile' survival rate applies.

The number of births at the start of year t, Bt, is

$$B_t = \sum_{a=a_{m}}^{x} B_{t,a}$$

where a_m is the age of reproductive maturity, and Bt, a, the number of births in age class a, is

$$B_{t,a} = bM_{t,a}^f$$

where b is the fecundity rate for mature females, and $M_{t,a}$ is the number of mature females in age class a at the start of year t, defined as

$$M_{t,a}^f = \begin{cases} 0 & \text{if } a_m > a \\ N_{t,a}^f & \text{if } a_m \le a \end{cases}$$

Assessment models

We applied three assessment models: S: The Southern population (Ameralik & Qeqertarsuatsiaat combined), A: Ameralik, and Q: Qeqertarsuatsiaat.

Statistical methods

The population dynamic models were estimated from the abundance data by projecting the population given the historical harvests, with the initial abundance drawn from a prior distribution of the abundance in the first year of the iteration (assuming a stable age-structure given the fecundity and harvest of that year). A Bayesian statistical method (e.g., Berger, 1985; Press, 1989) was used, and posterior estimates of the model parameters and other management related outputs were calculated. This implied an integration of the product between a prior distribution for each parameter and a likelihood function that links the probability of the data to the different parameterisations of the model.

Prior distributions

The values and prior ranges of the different parameters for all the assessment models are listed in Table 4. Annual survival rates of 0.90 and 0.92 have previously been applied to adult caribou in West Greenland (Bergerud, 1980; Cuyler & Østergaard, 2005). We applied a Beta (a: 98.5; b: 9.74) prior with mean 0.91 and variance 0.00075 to adult survival, with the choice of variance being rather arbitrary to capture uncertainty in survival beyond the point estimate of 0.91.

Fifteen late winter herd-structure counts in West Greenland observed calf percentages per female between 0.16 and 0.77, with an average value of 0.47 calves per female and a variance of 0.036. We applied a Beta (a:2.72; b:3.12) prior with mean 0.47 and variance 0.036 to annual reproduction for adult females, which implies that the majority of first year mortality is incorporated into our estimate of reproduction.

As our estimate of annual reproduction is based on the late winter calf percentage, the majority of first year mortality is incorporated into our reproduction estimate. Our estimate of first year survival should thus be correspondingly small. However, having no estimate of calf survival for the remaining time of the first year we applied the adult survival prior also to caribou in age-class zero.

Several female caribou in West Greenland in 1996-97 had their first calf in their second summer, being less than two years old (Cuyler & Østergaard, 2005). Normally, however, female caribou have their first calf in their third summer (Dauphine, 1976, Adams & Dale, 1998, Russell & McNeil, 2005). We applied a uniform prior for age of first reproduction from one to three years capturing this range for reproductive maturity.

Table 4. Prior distributions for the different assessment models. The list of parameters: s_{ad} is adult survival, s_{jar} juvenile survival, b the birth rate, a_m the age of reproductive maturity, \mathfrak{V} the fraction of females at birth, and N_0 the abundance in the first year of the iteration (given in thousands). The type of probability distribution is given by superscripts; u = uniform, i = discrete uniform, b = beta, and b = aparameter with fixed value. The first number of an entry in the table is the minimum value if b = u or b = u, the mode if b = u and a fixed parameter value if b = u. The second number is the maximum value if b = u or b = u, and the mean if b = u.

Model	$\mathcal{S}_{_{ad}}$	$\mathcal{S}_{_{juv}}$	b	$a_{_m}$	θ	$N_{_{ m o}}$
S	.92, .91	.92, .91	.45, .47	$1, 3^{i}$.5 ^p	15, 70"
A	.92, .91	.92, .91	.45, .47	$1, 3^{i}$.5 ^p	15, 70"
Q	.92, .91 ^b	.92, .91	.45, .47	$1, 3^{i}$	$.5^p$.5, 18"

Apart from the distributions given in Table 4, for each randomly selected parameter set, the upper bound on the juvenile survival rate was always set to be less than or equal to the randomly selected value for the adult survival rate.

Bayesian integration

The Bayesian integration was obtained by the sampling-importance-resampling routine (Berger 1985; Rubin 1988), where n_1 random parameterisations θ_i ($1 \le i \le n_1$) are sampled from an importance function $b(\theta)$. This function is a probability distribution function from which a large number, n_1 , of independent draws of θ can be taken. $b(\theta)$ shall generally be as close as possible to the posterior, however, the tails of $b(\theta)$ must be no thinner (less dense) than the tails of the posterior (Oh & Berger, 1992). For each drawn parameter set θ_i the population was projected from the first year with a harvest estimate to the present. For each draw an importance weight, or ratio, was then calculated

$$w(\theta_i) = \frac{L(\theta_i)p(\theta_i)}{h(\theta_i)}$$

where $L(\theta)$ is the likelihood given the data, and $h(\theta)$ and $p(\theta)$ are the importance and prior functions evaluated at θ . In the present study the importance function is set to the joint prior, so that the importance weight is given simply by the likelihood. The n_1 parameter sets were then re-sampled n_2 times with replacement, with the sampling probability of the ith parameter set being

$$q_i = rac{w(heta_i)}{\sum_{j=1}^{n_i} w(heta_j)}$$

This generates a random sample of the posterior distribution of size n_2 . The resample of the posterior distribution was set to $n_2 = 5000$, and the n_1 sample from the joint prior being 1 000 000.

The method of de la Mare (1986) was used to calculate the likelihood L under the assumption that observation errors were log-normally distributed (Buckland 1992)

$$L = \prod_{t} \exp \left(-\frac{\left[\ln \left(N_{t}^{i}/N_{t}\right)\right]^{2}}{2cv_{t}^{2}}\right)/cv_{t}$$

where N_i is the projected and N_i the point estimate of the observed total abundance at time t, and cv_i is the coefficient of variation of the abundance estimate at time t.

If the importance function is adequately specified, the mean of the importance sample for each parameter should approach the mean from the true posterior distribution, given a sufficiently large sample. To illustrate whether the sampled posterior quantities can be assumed to be representative of the true posterior distribution, convergence diagnostics were calculated. One such diagnostic is the maximum importance weight of a parameter set relative to the total summed importance weight over all n_1 draws, another is the total number of unique parameter sets in the resample of n_2 parameter sets, and a third is the maximum number of occurrences of a unique parameter set in the resample.

Results

Posterior distributions

The maximum importance weight of a parameter set relative to the total sum of importance weights for all drawn parameter sets was essentially zero for all assessments. The number of unique parameter sets in a resample of 5000 parameter sets was greater than 4805 for all models, while the maximum occurrences of a unique parameter set in the resample across all models was 4. The model specific statistics are given in Table 5. The posterior estimates and their 90% credibility intervals are given in Table 6.

Table 5. Sampling statistics for the Bayesian runs of the different assessments models. Sample is the number of draws from the importance function; Weight is the maximum importance weight of a draw relative to the total importance weight of all draws (given in percent); Unique is the number of unique parameter sets in the resample of 5000 parameter sets; and Max is the maximum occurrence of a unique parameter set in the resample.

Model	Sample	Weight	Unique	Max
S	1 000 000	0.0	4805	4
A	1 000 000	0.0	4837	4
Q	1 000 000	0.0	4963	2

Table 6. Parameter estimates for the different assessment models. The estimates are given by the median and the 90% credibility intervals of the posterior distributions. r is the exponential growth rate, N_s the abundance in 1999, N_T the abundance in 2007, and ry the replacement yield in 2007.

Model		S_{ad}	$S_{_{juv}}$	b	$a_{_m}$	r	$N_{_{ m o}}$	$N_{_{ m T}}$	ry
South	Median	.90	.91	.26	2.0	00	37	13	-210
	5 th	.85	.85	.09	1.0	07	27	10	-760
	95 th	.94	.95	.53	3.0	.06	51	17	620
Ameralik	Median	.90	.91	.27	2.0	00	31	8.9	-170
	5 th	.85	.85	.09	1.0	08	22	5.8	-550
	95 th	.94	.95	.58	3.0	.08	44	13	460
Qeqertarsuatsiaat	Median	.91	.91	.39	2.0	.04	5.2	5.3	190
	5 th	.86	.86	.14	1.0	05	2.9	3.2	190
	95 th	.95	.95	.70	3.0	.14	9.3	8.7	960

The realised prior and posterior distributions of the population dynamic parameters for the Southern population, and Ameralik and Qeqertarsuatsiaat sub-stocks showed that in all cases, updating of the prior to the posterior indicated a smaller population dynamic growth rate than assumed by the joint prior. For all cases most of the updating was towards lower reproduction, while for the survival rates, the posterior distributions remain closer to their prior. These differences may reflect the constraints of the model, more than they reflect the true values for the parameters in West Greenland caribou.

While the abundance data and the estimated projections showed a marked decline in abundance from 2000 to 2006 for Ameralik, the abundance remained relatively stable for Qeqertarsuatsiaat (Figs. 5, 6).

Southern population

The Southern population is estimated to have declined from 37 000 (90% CI: 27 000 – 51 000) individuals in 1999 to 13 000 (90% CI: 10 000 – 17 000) individuals in 2007. The latter abundance corresponds to a density of 1.0 / km², which is below the target density. For the hypothetical case of no hunting, the abundance should have remained relatively stable at about 37 000 individuals, given an estimated growth rate of 0% (90% CI: -7% - 6%) per year.

Ameralik

For Ameralik the abundance is estimated to have declined from 31 000 (90% CI: 22 000 – 44 000) individuals in 1999 to 8900 (90% CI: 5800 – 13 000) individuals in 2007. The latter abundance corresponds to a density of 1.1 / km², which is close to the target caribou density of 1.2 / km².

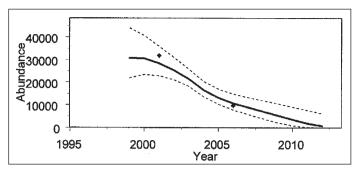


Fig. 5. The point estimates of abundance and the projected median and 95% CI for Ameralik.

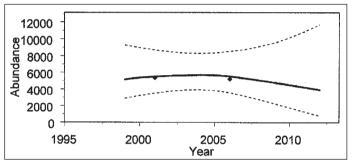


Fig. 6. The point estimates of abundance and the projected median and 95% CI for Qeqertarsuatsiaat.

Qeqertarsuatsiaat

For Qeqertarsuatsiaat the abundance is estimated to have increased slightly from 5200 (90% CI: 2900 - 9300) individuals in 1999 to 5300 (90% CI: 3200 - 8700) individuals in 2007, with an estimated growth rate of 4% (90% CI: -5% - 14%) per year in the absence of harvest. The 2007 abundance corresponds to a density of 1.0 / km², which is just below the target of 1.2 / km².

Discussion

We conclude that the strong decline in the Southern population is the result of a hunt with an average harvest of almost 3200 caribou per year since 2000. Should the annual harvest remain at the 2006 level of 1900 caribou, we expect from the model that this population will continue to decline to an abundance of 2790 (90% CI: 425 - 9164) individuals by 2012. This corresponds to a density of only 0.2 / km², which is considerably below the target of 1.2 / km². The current negative replacement yield of -210 (90% CI: -760 - 620) caribou per year, suggests that the target density may or may not be maintained in the complete absence of a hunt.

It is the steep decline of the caribou population in Ameralik that is causing the decline for the overall population. For the hypothetical case where no hunting is allowed, the abundance in Ameralik would have remained relatively stable with an estimated exponential growth rate just below zero [0% (90% CI: -8% - 8%) per year]. Therefore we conclude that the steep decline of caribou in the Ameralik area is the result of hunting with an average harvest rate of 2950 individuals per year in this area since 2000.

Should the annual harvest remain at the 2006 level of 1600 caribou we expect that Ameralik will continue to decline to an abundance of only 860 (90% CI: 0 - 6123) individuals by 2012. This gives a density of only 0.10 / km², which is far below the target. The negative 2007 replacement yield of -170 (90% CI: -550 - 460) caribou per year, suggests that this sub-stock may or may not be able to maintain the target density in the complete absence of a hunt.

In contrast, replacement was positive for the Qegertarsuatsiaat compo-

nent of the Southern population. We can conclude that the average harvest of 230 caribou per year in this area since 2000 has been close to the yearly recruitment level, thus maintaining the caribou density close to the target of $1.2\ /\ km^2$.

The 2007 replacement for Qeqertarsuatsiaat is estimated at 190 (90% CI: -190 - 960) caribou per year. However, the harvest of caribou from this area has increased over the 2000-2006 period. The 2006 harvest of 440 individuals exceeds the point estimate of current replacement yield and, thus, given the scenario of stable harvest at present levels, we would predict the abundance to decline to 3900 (90% CI: 800 - 12 000) individuals by 2012, which would correspond to a density of 0.8 caribou per square kilometre. Some harvest restrictions in this area may be required to align future harvests with the replacement yield of 190 caribou per year.

In brief, the results indicate that 1) the abundance of caribou in Ameralik declined from 2001 to 2006, 2) that the target density (1.2 / km²) was reached, and 3) that the population dynamic growth rate between 2001 and 2006 was estimated at approximately zero if no hunting had occurred. It appears that the increased harvest, with annual harvest rates between

3000 to 4500 individuals, caused the strong decline in abundance over this five-year period. Should harvest levels remain constant, then a further population decline may occur.

Following the late winter aerial population survey in 2006, harvest restrictions were implemented for the autumn 2006 hunting season. The season was reduced from 14 weeks to five, but unlimited harvests remained.

Although harvest is the likely cause of this great reduction in the caribou population of Ameralik from 2000 to 2006, questions still remain. Will the Ameralik caribou population continue to decline, and will the Qeqertarsuatsiaat caribou population remain stable? Although Qeqertarsuatsiaat caribou abundance appeared stable despite increasing harvest from 2000 to 2006, this may have been primarily due to an increased emigration from Ameralik during the same period (Cuyler *et al.*, 2007). The observed movement of Ameralik caribou southward, expanding into Qeqertarsuatsiaat, is supported by local hunters.

The 2007 and 2008 harvest data are not yet available. Despite the model projections presented here, during the autumn 2008 local hunters (pers. comm.) subjectively observed that Ameralik caribou were once again abundant but skinny, and that there were many cow-calf pairs, while Qeqertarsuatsiaat caribou were fat. The next aerial survey of the South region will be March 2011. Given our incomplete understanding, there is room for uncertainty and debate regarding recruitment and future abundance of these two caribou populations.

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Limiting factors for barren-ground caribou during winter – interactions of fire, lichen, and snow

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Numbers of barren-ground caribou across the Canadian central Arctic have declined since the late 20th century. For example, the Bathurst herd has decreased in abundance from 472 000 (±72 900) caribou in 1986, to 128 000 (±27 300) animals in 2006. Traditional ecological and scientific knowledge suggests that the Bathurst herd may be in the downward phase of a 30 to 60 year cyclic trend; however, the mechanisms that drive and limit this population are not well understood. While we cannot dismiss forage limitations to caribou during summer, studies suggest that the supply and accessibility of forage on the winter range can markedly affect population dynamics. Considering the high numbers of Bathurst caribou during the 1990s and the above average burn rates during the same period, a deficiency of winter forage may have contributed to the current decline. I will use Resource Selection Functions (RSF) to investigate the influence of fire on the distribution of Bathurst caribou during winter. A RSF is a statistical model that allows one to quantify the large-scale selection strategies of animals and calculate the relative probability that an individual or group will use a resource unit. I will use satellite collar data from Bathurst cows (1996 to 2008) and habitat attributes such as vegetation cover, age of burn, snow conditions, and sources of human disturbance to generate RSF models. These models will allow me to identify important winter range habitats and develop quantitative relationships between recent burns and the distribution of caribou. Habitat relationships derived for the Bathurst caribou may have application to other central arctic herds experiencing similar dynamics and possibly increases in fire frequency resulting from climate warming.

An integrated approach to communicating and implementing community-based caribou health monitoring

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Management of caribou involves diverse stakeholders with unique objectives. While these multiple stakeholders have a shared interest in caribou and a common desire for their long-term sustainability, there have been important and often severe conflicts between caribou using communities and scientists and government management agencies. These conflicts often reflect differing world views and insufficient meaningful communication between these groups. Scientists and government agencies are now realizing the important role that communities can play in identifying issues, contributing Traditional Ecological Knowledge and as collectors of scientific data, but continue to struggle to find effective ways of interacting with communities effectively. The five communities within the Sahtu region of the Northwest Territories (NWT) (Deline, Tulita, Norman Wells, Colville Lake, and Fort Good Hope) utilize barren-ground and woodland caribou and have a strong interest in maintaining sustainable caribou populations. During a NWT Biophysical Study workshop held in 2002, elders and community observers requested more training for youth in science and for more involvement of hunters and community members in research. In response to these apparent needs, in 2003 we initiated a long-term, integrated approach to foster community-based caribou monitoring and education. Annual trips via winter road have been made to all schools in the Sahtu from 2003 to 2008 to provide hands-on learning for 300 to 500 children each year about diverse wildlife health topics. At the same time, interviews were conducted with 31 hunters and elders to document their traditional knowledge of caribou health. Local caribou hunters were employed as monitors to collect tissue samples and measurements for body condition and disease monitoring from 69 caribou and we meet with them annually. Each year, a graduate student from a southern university in the veterinary or biological sciences has participated in the program, obtaining invaluable experiences working with northern communities and wildlife health issues. The program has evolved over the last six years in response to community input, results of empirical research, and traditional knowledge that are evaluated in an integrated manner.

Application of a molecular tool to describe the diversity and distribution of gastro-intestinal parasites in northern caribou

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Climate change is driving a northward shift in the distribution of North American wildlife, including ungulates. Temperate ungulates are host to a diversity of gastrointestinal nematode species, many of which are not found in woodland and barren-ground caribou (Rangifer tarandus). Some of the most pathogenic of these parasites are those of the family Trichostrongylidae which are known to induce considerable morbidity and mortality in livestock globally. Although invasion of new trichostrongylid species to high latitudes may have significant impact on the health of naïve (unexposed) caribou populations, the northern diversity and distribution of most species is unknown. In fact, our recent trichostrongylid survey of 20 wild ungulates in central Alberta and Saskatchewan revealed four new host and seven new geographic records. A challenge to determining parasite diversity is that many trichostrongyid eggs are morphologically indistinguishable and post-mortem recovery and examination of adult nematodes is necessary to establish species identification. To better describe the diversity of parasite fauna that may infect northern caribou, we have developed a rapid, non-invasive tool, Single Stranded Conformation Polymorphism (SSCP), for broad-scale screening of cervid fecal pellets for trichostrongylid parasites. SSCP is a simple PCR-based technique that allows for species-specific electrophoretic discrimination using ITS-2 rDNA from parasite eggs. Trichostrongylid eggs in fecal pellets from three ecotypes of caribou, white-tailed deer (Odocoileus virginianus), mule deer (O. hemionus) and elk (Cervus elaphus) are being screened using SSCP to determine parasite diversity and range along two north-south transects in western Canada. Results outlining trichostrongylid diversity and distribution and implications for threatened woodland and barren-ground caribou populations will be reported. Baseline data on parasite biodiversity and distribution will provide a platform from which managers and veterinarians can monitor parasite range expansion in a warming climate and identify key parasite related risks.

Besnoitiosis in caribou: What we know and what we don't know

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Besnoitia spp. are protozoan parasites known to occur in many species worldwide. Besnoitia tarandi has been described in caribou and reindeer in which it is often associated with hair loss, skin thickening and ulcerations. In Rangifer species, cysts of Besnoitia often induce inflammation and are observed mainly in the sclera and subcutaneous tissues, and to a lesser extent in other organs such as lungs and testes. Very little is known about the significance of this parasite on caribou health. However, it has been hypothesized that massive infections could impede the animal's tolerance to exercise and movement and therefore contribute to mortalities. In addition, extensive infections implicating the testicular appendages might impact the fertility of caribou as reported in other species. It is believed that B. tarandi has a two-host life cycle with caribou as intermediate hosts. Carnivores and biting arthropods have been respectively suggested as potential definitive hosts and vectors of B. tarandi. Presently, the gaps in understanding the life cycle of B. tarandi prevent any attempts to assess the potential effects of the changing arctic environment on the balance between this parasite and its hosts. In order to better characterize the ecology of this parasite in Canadian migratory caribou herds, our research team wishes to present data on the distribution of B. tarandi in association with body condition, gender and age and the potential association between intensity of infection with fertility and tolerance to exercise.

Characterization of woodland caribou (*Rangifer tarandus caribou*) calving habitat in the boreal plains and boreal shield ecozones of Manitoba and Saskatchewan

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As recovery plans are being developed or implemented for boreal caribou, it is becoming important to further examine the spatial and temporal characteristics of areas used at calving and to identify site and landscape attributes that may be selected by the animals. In order to do this, we analyzed the movement and habitat use pattern of 31 animals in the boreal plains and boreal shield ecozones. GPS telemetry data were obtained from 12 female boreal caribou from the Kississing-Naosap herd in Manitoba between 2002 and 2005, and 19 females from the Smoothstone-Wapawekka herd in Saskatchewan between 2005 and 2007. Based on movement rates, LOESS curves were used to identify eight distinct seasons for both herds. Reduced movement rates, involving a rate of 50 m/h or less for a minimum of a week, were used to identify 20 calving sites in the Smoothstone-Wapawekka herd, 13 calving sites in the Kississing-Naosap herd, and their associated pre- and post-calving areas. Vegetation characteristics at the site and landscape scales were examined using Forest Resource Inventory, roads, trails, fire and cutblocks data. Paired-logistic regression was used to assess calving habitat selection at the site scale and generalized estimating equations were used for the landscape scale analysis. Selection was seen to occur at the landscape scale for calving areas in both herds however, no identifiable trends were seen to occur at the site scale based on vegetation characteristics. The predictive maps of calving and potential calving habitat generated for both herds are providing key management information for the protection of boreal caribou during the calving season.

Spatial and temporal variations in lichen forage biomass as estimated from LANDSAT 5 satellite images

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We conducted our study at the Hardangervidda reindeer population in southern Norway. This population has fluctuated more than five fold during the last 40 years and has suffered previous periods of overgrazing. Managers have deliberately reduced population numbers by subscribing high hunting quotas aiming to recover pasture quality and reindeer body condition. We therefore wanted to estimate the spatiotemporal distribution of lichen winter forage and to test for possible trends and changes in lichen biomass. We used a LANDSAT 5 scene recorded in August 2003 as our master data set. This image was classified into a land cover map with 9 different habitat classes. In this process we used a supervised classification method (KNN) and approximately 5000 ground truths were taken as training points. In our land cover map lichen ridges could be classified with a user accuracy of approximately 80%. In order to estimate lichen biomass we later reduced our land cover map to a 1 bit information mask (lichen ridge, not lichen ridge) and tested for linear relationships between spectral properties in areas classified as lichen ridges and measures of lichen biomass taken in the field. We found that lichen biomass could be estimated on the basis of a simultaneous application of two different indices (NDLI), and a normalized index derived from band 4 and 5 ($R^2 = 0.70$, P < 0.001). Estimates of the lichen biomass reviled large spatial variation with less biomass in central and more heavily grazed parts of the area. Since the 1980s the reindeer population has been reduced from approximately 25 000 animals to approximately 6000 animals in 2003. By comparing our analysis of the 2003 scene to LANDSAT 5 images recorded in 1983 and 1994 we found an overall increment in lichen biomass of approximately 82%, but also that re-growth of lichens had a significant spatial component with less increment in central areas.

Use of fecal genotyping to estimate population demographics in the North Interlake woodland caribou herd

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The North Interlake woodland caribou herd in Manitoba is part of the boreal woodland caribou population listed as threatened under COSEWIC. In order to monitor the North Interlake herd, fecal samples were collected from 2004 to 2007 providing a source of DNA for use in mark-recapture modeling. For each collection, the range was systematically surveyed using fixed-wing aircraft and the cratering sites were accessed via helicopter. Collection of samples took place when snow was present (early and late winter) to allow for tracking and location of caribou cratering areas and to prevent degradation of DNA present in the mucosal coat surrounding fecal pellets. Following DNA amplification, genotypes were scored at six polymorphic loci using GeneMarker software and then compared using GenAlEx 6.1; where samples matching at five of six loci were considered as matches and samples with missing genotype information at two or more loci were excluded from analyses. In total, 610 samples were collected from the six surveys, whereby 190 unique genotypes were obtained with a sex ratio of 1.03:1.00. MARK software was used to derive population estimates. Closed population estimates using the 2007 samples (two collections of 303 samples total) demonstrated a population size of 145 animals (95% confidence interval: 115 to 175). As the precision of this estimate is 21%, it is proving useful in management. For open population modeling done using samples collected 2004-2007, we obtained a population growth rate, lambda, of 1.00 (95% confidence interval: 0.98 to1.02). We recommend the continued collection of fecal samples for DNA analysis as a valuable and noninvasive technique in acquiring demographic information on threatened woodland caribou.

Development and survival of *Ostertagia gruehneri* under natural and artificially warmed conditions on the Canadian tundra

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Abstract: Climate change in the Arctic is occurring at an unprecedented rate and is anticipated to alter the ecology of northern ecosystems, including the patterns, diversity, and transmission of infectious diseases. Ostertagia gruehneri is the most common gastrointestinal nematode in caribou and can cause decreased food intake, weight loss, and reduced pregnancy rates in Rangifer species. Because O. gruehneri has a direct life-cycle that includes a free-living stage, the development and survival rates of this parasite are influenced by climate and climate change. To investigate the response of the free-living stages of O. gruehneri to climate change field experiments were done from May to September 2007-08 at the Tundra Ecosystem Research Station (TERS), Daring Lake, Northwest Territories. Fecal plots containing O. gruehneri were established on the tundra under natural and artificially warmed conditions. Plots were sampled throughout the summer to determine development and survival rates of O. gruehneri and to compare between the two climate regimes (natural vs. warmed). Effects of both temperature and relative humidity on development and survival were investigated. Results from these field seasons will be used, together with laboratory experiments, to develop and validate a predictive model for the impacts of climate change on the epidemiology of O. gruehneri.

Caribou, primary prey and wolf spatial relationships in northeastern Alberta

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It is widely accepted that increases in industrial development have contributed to woodland caribou declines in Alberta. The current working hypothesis is that industry-induced changes in caribou range have reduced the ability of this species to spatially separate from primary prey, and that this has resulted in increased predation by shared predators such as wolves. Two factors appear important: (1) seismic exploration lines and other linear features may increase wolf hunting efficiency; and (2) industrial disturbances, such as forestry, may increase the quantity and quality of food needed to support higher primary prey densities, which may in turn cause wolf numbers to increase. Although evidence continues to build in support of this hypothesis, we still lack key information that is highly relevant to effective management. For example, does spatial overlap between caribou, and primary prey and predators increase because of changes on caribou range alone or is the adjacent upland habitat crucial, i.e. at what scale do we need to conduct our management activities? We used a simultaneous multi-species (caribou, moose, deer, beaver, and wolf) study approach to assess the following objectives in the West Side of the Athabasca River (WSAR) caribou range. First, has predation risk for caribou in WSAR increased in the last 10 years (i.e. since major increases in forestry and oil and gas activity)? Second, if caribou predation risk has increased, is this due to an increased number of predators, increased predator efficiency, or both? Third, are the changes driven by changes on caribou range, surrounding areas, or both?

Stability of reindeer harems according to male age and social rank

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Sexual selection is the evolutionary process that favours adaptations that increase mating success of individuals. It encompasses "intra-sexual competition" as well as "mate choice". During the rut, reindeer (Rangifer tarandus) form harems, i.e. a gathering of individuals where a dominant male ("the harem bolder") is chasing subordinate males and herding females to monopolise all matings. Despite being herded by males, females can move from a harem to another. Thus, harems are not stable and the factors affecting females' movements are not well known. We investigated whether age and social rank of males would influence the stability of harems. We predicted that the most dominant and aged males should control more stable harems because females should stay in these harems but should leave harems controlled by younger and more subordinate males. From 1996 to 2005, we manipulated the male age structure and the sex ratio of a reindeer herd at Kutuharju (Kaamanen, Finland). Male dominance and to a lesser extent their age affected harem stability. Dominant males controlled more stable harems. Nevertheless, the stability of harems tended to increase with the age of the harem holder too. The stability of the harems decreased with the percentage of males of all ages in the population as a consequence of increased intra-sexual competition, but was not affected by the percentage of adult males. Our study suggests that the stability of harems is determined primarily by the ability of the dominant male to control females' movements. Dominance status of a male, rather than its age, is most important in controlling more stable harems.

Relationship between landscape connectivity and gene flow for boreal caribou: clues for conservation

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In order to ensure the protection of long-ranging species, the composition and configuration of a landscape - which determine landscape connectivity or the degree to which the landscape facilitates or impedes the movement of organisms - must be assessed. Landscape connectivity influences the species' ability to access habitat, avoid predators, move between core parts of a range and between ranges and contribute to gene flow. Knowing that different species experience landscape in scale-dependent ways and that a given landscape might appear connected to some species while fragmented to others, we used telemetry, habitat and genetic data from different caribou ranges in Manitoba and Saskatchewan to assess the importance of landscape connectivity and identify movement thresholds at different spatial scales; telemetry data for the seasonal and home range scales and genetic data for the landscape or meta-population scale. Using these thresholds, it is then possible to identify biologically relevant clusters of habitat, as these areas most contribute to overall landscape connectivity. For management purposes, the identification of these clusters may point to targeted restoration efforts in proximity of small clusters to increase the size of these core areas or the protection of movement corridors to ensure linkages between these core areas. In cases where movement between clusters is limited, each area may correspond to different ecological units or ranges that can then be analyzed or managed separately. These spatial analyses and results offer additional tools to land use and recovery planners, to support the establishment and management of protected areas. They spatially represent the composition and distribution of core habitat areas and as importantly, corridors allowing for movement and gene flow on these vast landscapes.

Predator assessment in Alberta's woodland caribou ranges

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Woodland caribou (*Rangifer tarandus caribou*) are threatened in Alberta. This status designation is supported by empirical evidence of declining mountain and boreal populations, a northward recession in distribution, and herd-specific changes in range use. These trends are strongly linked to anthropogenic footprint, which in turn may be driving increases in the densities of primary prey and thereby wolves in and around individual caribou ranges. More wolves mean a greater probability of wolf-caribou interactions and as such, higher rates of caribou mortality. Wolf densities in most of Alberta's ranges are unknown but are expected to be greater than in an undisturbed wolf-primary prey-caribou system. This prediction has prompted provincial and national recovery teams to recommend wolf control as a short term recovery strategy for caribou, if the need for control is clearly demonstrated. The Alberta Caribou Committee's Research and Monitoring Subcommittee (RMS) intends to determine if and where this need exists by measuring wolf densities in and around multiple caribou ranges over the next three years. This project is part of a larger research and monitoring program that has been proposed by the RMS, which is designed to test the hypotheses that predation pressure is the proximate cause of the caribou declines and habitat change is the ultimate cause of the caribou declines. In doing so, the RMS will test the validity of wolf control, restoration of current footprint, and limiting future footprint as recovery options for caribou. As such, this program is critical for designing, implementing, and evaluating caribou recovery efforts in Alberta.

A comprehensive and corporate caribou observation database for Ontario

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Caribou recovery documents from across Canada concur on the importance of monitoring caribou range use and population health. In Ontario, large amounts of caribou observation data exist from surveys and studies. These data have substantial value when designing and implementing caribou habitat conservation measures, particularly on a highly dynamic landscape. These data existed in many different places and forms making effective, efficient and consistent use difficult. Ontario developed a comprehensive caribou observation database to act as a secure, corporate repository for all past and future caribou observation data. Data types include point and polygon data associated with caribou collaring data, historical observations, calving surveys, directed studies, traditional knowledge and casual observations from the public. The long term vision is to support applications that report on the provincial status of caribou as a mechanism for tracking success of recovery efforts. This database has been incorporated into Ontario's Natural Resource Values Information System (NRVIS) where most other data used to support resource management planning is housed. Features of this database include 1) province wide user-access for data entry and edit where authorized, 2) point and polygon data types, 3) ability to manage historic and contemporary data, 3) direct links to metadata such as survey and study details, or scientific reports associated with the data, 4) records of areas surveyed whether or not caribou evidence was observed, 5) links between observations and collected specimens. Significant issues included data sharing, data sensitivity, use of data from non-government sources, mandatory provision of data when collected using government funds, and maintenance of data standards and integrity. Of primary importance was the commitment of data providers and users to quality assurance throughout the data life cycle. It is anticipated this database will stimulate spin-off research and knowledge generation that that will advance caribou recovery efforts. Monitoring and reporting at the national level using shared jurisdictional data will require national resolution of many of these same issues.

Distance- versus patch-based movements of woodland caribou during spring dispersion in northern Quebec

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Habitat selection studies are widespread in the scientific literature on woodland caribou (Rangifer tarandus caribou). Knowledge of habitat selection informs our understanding of caribou biology and life history requirements. Recent innovations in GPS telemetry have allowed us to track animal locations over space and time with remarkable accuracy, greatly enhancing our understanding of space use patterns and allowing us to more closely examine the role of scale and landscape heterogeneity in movements of woodland caribou. In conjunction, new spatial statistics and mechanistic approaches to resource selection analysis serve to reduce error in model selection and explain how landscape covariates influence caribou behaviour. With a view to maximizing functional connectivity between winter and summer ranges in managed landscapes of Northern Quebec, we first distinguished between biologically relevant seasonal phases in caribou movement by modeling distance moved over time using polynomial regression (Ferguson & Elkie, 2004a), identifying seasonal cut-off periods where the second derivative equals zero. We were interested in understanding how caribou perceive and respond to the heterogeneous landscape so we first tested for the presence of scalar activity in caribou movements. For each study animal (n=25) we fit a broken stick model to the ln frequency of movement rates recorded during spring dispersion, where appropriate establishing a unique rate criterion (r) per animal (Johnson et al., 2002a) in order to differentiate between intrapatch and interpatch movements. Intrapatch movements are thought to represent foraging or resting phases whereas interpatch movements are associated with distance-based migratory activity; therefore we treated the two processes differently. We used kernel density estimates (plug-in method) for all points associated with patch-based movements during spring dispersion to define use-intensity levels for resource patches. Polytomous logistic regression was used to model patch resource selection by woodland caribou (Rittenhouse et al., 2008). In contrast, conditional logistic regression was used to model interpatch (i.e. distance-based) movements and a Step Selection Function (SSF) was built describing where a given animal was most likely to be found from one relocation to the next (Fortin et al., 2005b). Candidate models included covariates for road density, distance to forest cutovers, recent burns, terrestrial lichen abundance, coniferous forest, open wetlands, and distance to waterways. Results will be presented and application of models to connectivity analyses will be discussed.

Frame size and caribou population cycles: a modeling approach

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In North America, and likely in Eurasia, large migratory Rangifer populations experience distinct phases in abundance (increase, stable or decrease). As caribou populations in northern North America have experienced at least three complete variations in the last century they can be classed as cyclical. Currently, populations appear to be either at a low or are declining across Arctic North America. There is concern that under increased industrial development, climate change and greater hunter access, populations currently at a low in their cycle may take longer to recover and that the population trough may be lower. However, the exact timing of the cycles and their amplitudes can vary among populations. Various theories have been presented to explain why a Rangifer population cycles, and why some populations appear relatively synchronized in their phases of abundance. It is generally conceded that both phenomena relate to continental-scale climatic phenomenon which influences the caribou's environment. We are investigating whether the environmental driver(s) influence the population through nutritional stress in the individual. We assume that for migratory Rangifer the mechanism will result in distinct patterns in body size throughout the cycles, and that this outcome should be observable in extant data sets such as jaw and leg bone measurements, and body mass. In times of limited resource availability, smaller frame size individuals would be at an advantage because of lower energetic demands for non-productive energy requirements (maintenance, and possibly activity), leaving more net energy available for productive requirements (gestation and lactation in the female). Conversely, during periods of high resource availability, larger frame individuals would be at an advantage through greater calf survival. In this paper we use a modeling approach to explore the theoretical characteristics of frame size in Rangifer throughout a population cycle. Using a North American data base for body condition of caribou, we examine frame size across herds throughout various stages of a population cycle with the objective to speculate on management implications of our findings.

Does the basic ecology of woodland caribou (*R.t. caribou*) vary within different environmental settings? A comparison of movement patterns in female caribou inhabiting different ecosystems in north-eastern Canada

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While caribou in Newfoundland and Labrador share the same subspecific status (R.t. caribou), they occur in markedly different environments. In Newfoundland they inhabit the Boreal Shield ecozone, a region characterized on the Island by a continental climate, dense fir and spruce forests as well as extensive barrens, peatlands, high moose densities, and no wolves since 1920 (though in recent years a wolf-like predator, the coyote, has established itself). In Labrador, they occur predominantly within the Taiga Shield, a subarctic region characterized by open spruce forests and fens, low moose densities, and both resident and transient wolves associated with large herds of migratory caribou that winter within the sedentary herd ranges. Further, the phylogeography of Newfoundland caribou suggests they evolved from a southern clade while sedentary caribou in Labrador are of mixed northern and southern ancestry. Taken collectively, environmental and evolutionary factors suggest that the basic ecology of caribou living within these areas may differ in spite of their shared taxonomy. We tested the hypothesis that caribou residing within different ecosystems exhibit dissimilar movement patterns and timing of seasonal behaviours. Movement patterns were contrasted between Labrador and Newfoundland caribou and at the local population level. Mean daily displacement (and standard error) of radio-collared caribou from 7 herds in insular Newfoundland (104 animals 2005 to 2007), and 2 herds in Labrador (200 animals, 1985 to 2005) was calculated. Our objectives were to 1) determine the number of phases demarcating changes in rates and variability of movements; 2) characterize the associated degree of displacement and identify possible ecological correlates; and to 3) assess whether variation (if any) in the number, timing, duration of 'biological seasons' could be explained at the ecosystem level or local population level. Results will aid in the characterization of biodiversity within the caribou subspecies within north-eastern Canada, and suggest the degree to which environmental variation may lead to ecological divergence.

A simple time series approach can be used to estimate individual wild reindeer calving dates and calving sites from GPS tracking data

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In this paper we examined individual movement patterns in 58 GPS collared wild reindeer females. Data was collected over a seven year period between 2001 and 2008 in four different reindeer populations in southern Norway. In total we were able to collect and analyze data from 93 individual calving seasons (1° of May to 1° of June). We tested our data for any patterns or sudden changes in mean daily movement parameters (step-length between 3 hour fixes, turn angle and bearing) in a moving time window of 1 through 7 days. Typically individual movement rates changed from app 1000 to 3000 meters / 3 hour to less than 200 meters / 3 hour during the calving period. Turn angle and bearing also varied temporally although the possible trends in these data were far less evident. By comparing individual movement parameters to observations of females at the calving grounds, we conclude that the observed changes in movement patterns can be used to estimate individual calving dates and to locate individual calving sites.

Factors affecting the body condition of female-calf pairs in two herds of migratory caribou in Northern Québec/Labrador

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In Northern Québec and Labrador, more than one million migratory tundra caribou range over nearly a million square kilometres. Of the two recognized populations, Rivière-aux-Feuilles herd is very large and may be declining; Rivière-George herd is currently estimated at about half the size of Rivière-aux-Feuilles herd but may be increasing. The factors influencing body condition of tundra caribou are poorly understood, but are essential to our understanding of natural and human-induced variations in the survival and reproductive success of individuals and in population dynamics. We compared the body condition and parasite load of 20 female-calf pairs in each herd during June (calving) and October-November (weaning) 2007. Adult females from Rivière-George herd were heavier than those from Rivière-aux-Feuilles herd, but they did not differ in skeletal size. Calves from Rivière-George herd were much heavier and larger at birth and at weaning than those from Rivière-aux-Feuilles herd. Combining the June and autumn datasets, we compared adult female body condition following lactation and calf body condition and early growth in the two herds. Differences in body condition of female-calf pairs appear to be useful indicators of demographic changes and could reflect the quality of available summer habitats. Our results suggest that Rivière-aux-Feuilles herd may be declining.

Insect-weather indicies and the effects of insect harassment on caribou behaviour and activity budgets

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Many barren-ground caribou (*Rangifer tarandus groenlandicus*) populations in the Central Arctic are experiencing declining numbers. Possible causes include conditions on the post-calving/summer range, especially harassment by biting and parasitic insects. Insect harassment alters habitat use and activity budgets of caribou, potentially leading to reduced forage intake and elevated energy expenditures. This is of particular concern as climatic warming is predicted to increase the duration and intensity of insect activity. In this study, I collected weather, insect catch, and caribou behaviour data on the summer range of the Bathurst caribou herd in the Northwest Territories/Nunavut in 2007 and 2008. I used count models within a generalized linear model framework to explore the relationship between weather parameters and insect activity. The best models, selected using Akaike's information criteria (AIC), were used to develop a correlative insect-weather index applicable across the Bathurst range. Additionally, I developed models of fine-scale caribou behaviour as a function of vegetation type, phenological stage, topography, time, and insect activity. Model sets were developed for six behaviour categories, and the most parsimonious models selected using AIC. In this poster presentation, I will discuss results regarding insect indices and factors affecting fine-scale caribou behaviour (completion of analysis expected by September/October 2008). In continued work on this project, these results will be used in conjunction with GPS collar data and energetics modeling to explain patterns of movement and habitat use at coarser spatiotemporal scales, as well as to explore consequences for caribou population productivity.

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- Use body text in 12 point size and double spacing with 4 cm margins on both left and right sides. Do not hyphenate at the right margin.
- Italics shall be typed. Taxonomic names in Latin (genus and species; e.g. Rangifer tarandus tarandus), book titles and journal names shall be written in italics.
- Submit manuscript in email attachment (use ordinary programs and versions) and forward also one good quality hardcopy. When accepted, the author submits the final manuscript as email attachment.

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Rangifer

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