PROCEEDINGS FROM THE CARIBOU GENETICS AND RELATIONSHIPS WORKSHOP

EDMONTON, ALBERTA, MARCH 8-9, 2003

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Department of Natural Resources and Environment
Government of the Northwest Territories

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9:15 – 10:15 Caribou Morphology
Anne Gunn, *Department of Resources, Wildlife and Economic Development, GNWT*

COFFEE BREAK

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Ian Hatter, *BC Ministry of Water, Land, and Air Protection*

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Serge Couturier, *Quebec Wildlife and Parks*

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John Nagy, *Department of Resources, Wildlife and Economic Development, GNWT*

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Keri Zittlau, *University of Alberta*

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Chair: David Shackelton, *University of British Columbia*

LIST OF PARTICIPANTS

POSITION PAPER PRESENTERS

Serge Couturier	Quebec Wildlife and Parks
Judith Eger	Royal Ontario Museum
Anne Gunn	Department of Resources, Wildlife and Economic Development, Government of the Northwest Territories
Lee Harding	SciWrite Environmental Sciences Ltd.
Ian Hatter	British Columbia Ministry of Water, Land, and Air Protection
John Nagy	Department of Resources, Wildlife and Economic Development, Government of the Northwest Territories
*Curtis Strobeck	University of Alberta
Keri Zittlau	University of Alberta

PANEL DISCUSSION PARTICIPANTS

†David Shackleton	University of British Columbia
Greg Wilson	University of Alberta

OTHER PARTICIPANTS

Theresa Aniskowicz	Canadian Wildlife Service, COSEWIC
Mathieu Dumond	Department of Sustainable Development, Government of Nunavut
Paul Frame	University of Alberta
Alistair Franke	University of Alberta
Frank Miller	Canadian Wildlife Service
Hal Reynolds	Canadian Wildlife Service

* Position paper not included in proceedings

† Moderator

INTRODUCTION TO THE WORKSHOP

The Caribou Genetics and Relationships Workshop was funded and organized by the Department of Resources, Wildlife and Economic Development of the Government of the Northwest Territories and the Department of Biological Sciences at the University of Alberta. The workshop was held at the University of Alberta in Edmonton, AB on March 8-9, 2003.

The purpose of the workshop was to gather caribou biologists to discuss caribou taxonomic classification. Historically, morphological and behavioural distinctions have been recognized among groups of caribou and used to support the existing formal taxonomy (summarized in Banfield, 1961[1]). However, over the last decade, the number of genetic analyses has increased. Genetic analyses using mitochondrial and nuclear DNA are changing our understanding of caribou evolutionary relationships. Consequently, the formal classification is in need of revision and our workshop was an exploratory step toward this by reviewing current knowledge on caribou genetics and evolutionary relationships.

Presently, nine subspecies of *Rangifer* are recognized, but as many as 55 species and subspecies have been previously described. The currently recognized subspecies are primarily differentiated according to morphological characteristics (e.g., skull and bone length, antler shape and dentition) and habitat specifications (boreal regions vs. arctic tundra and taiga). However, despite the general observed differences between subspecies, local

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[1] Banfield, A.W.F. 1961. A revision of the reindeer and caribou, genus *Rangifer*. National Museum of Canada, Bulletin No.177, Biological Series no. 66:1-137.

morphological variations occur within subspecies. This has led to confusion regarding caribou taxonomy in some instances. Furthermore, recent molecular evidence has suggested that genetic differences may not correspond to morphologically- and behaviourally-defined groups. To complicate this matter, some of the genetic information is poorly understood. Without an understanding of the evolutionary relationships among caribou, long-term management and conservation strategies may become difficult to apply.

The goal of the workshop was to define conservation units for caribou and to propose a hierarchical classification below the species level. We did this by addressing three objectives. First, we aimed to discern the information that genetic studies of caribou can reveal. Second, we discussed how current research could be used to define conservation units for long-term caribou preservation. Third, we attempted to identify gaps in existing knowledge.

The first half of the workshop focused discussions around caribou distribution and morphology, including overviews of caribou ecology and biology within various North American regions. The second half of the workshop focused discussions around the use of genetic data for describing differences among groups and culminated with explanations of recent genetic findings. The workshop concluded with a panel discussion, which addressed options for defining conservation units and for determining a classification for the genus *Rangifer*.

These proceedings include manuscripts describing the knowledge presented and discussed during the workshop. The organizers thank the authors and participants for their efforts in producing these papers and for making the workshop a success.

DISTRIBUTION OF CARIBOU IN NORTH AMERICA

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INTRODUCTION

The genetic relationships among caribou populations have become critical to their conservation status. A conservation status listing – such as threatened or endangered – moves governments to allocate resources, communities to adopt conservation plans, and individuals to consider the consequences of their resource use decisions (Harding, 1997; Possingham and others, 2002). With the impending passage of the proposed *Species at Risk Act*, listing may impose federal legal requirements. Under rules for the assignment of conservation status, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) not only recognizes species and subspecies that may be designated, but also varieties and morphologically and geographically separate populations. Sub-subspecific populations can be assigned conservation status as “nationally significant populations”. However, COSEWIC has experienced some uncertainty in deciding whether or not to consider for designation the populations of some species, particularly when their national significance or taxonomic distinctiveness is not obvious (COSEWIC 1998). In species where some subspecies, varieties, or populations may be stable while others are declining, the issue of classification becomes critical. This paper reviews the distribution of caribou in Canada as an introduction to the Caribou Relationships Workshop.

METHODS

Caribou numbers and distribution maps were obtained from published literature and from colleagues.

RESULTS

Five native subspecies are currently recognized in North America: Dawson's caribou, *R. t. dawsoni* (extinct); Barren-ground caribou, *R. t. groenlandicus*; Woodland caribou, *R. t. caribou*; Grant's caribou, *R. t. granti*; and Peary caribou, *R. t. pearyi*. Some authors split the last into *R. t. pearyi* of the northern and eastern islands in the Arctic archipelago and *R. t. pearyi/groenlandicus* of the southern and western islands.

A sixth subspecies, *R. t. tarandus*, was introduced from Kotzebue Sound, Alaska (where they had previously been introduced from Asia). They were brought across Alaska and the Yukon from 1929 to 1935 to the Tuktoyaktuk Peninsula, N.W.T., where a domestic herd remains.

The range in Canada and eastern Alaska is shown in Figures 1 and 2 (Banfield, 1974; Gray, 1999). The historical distribution of caribou is shown in Figure 2 (Gray, 1999).

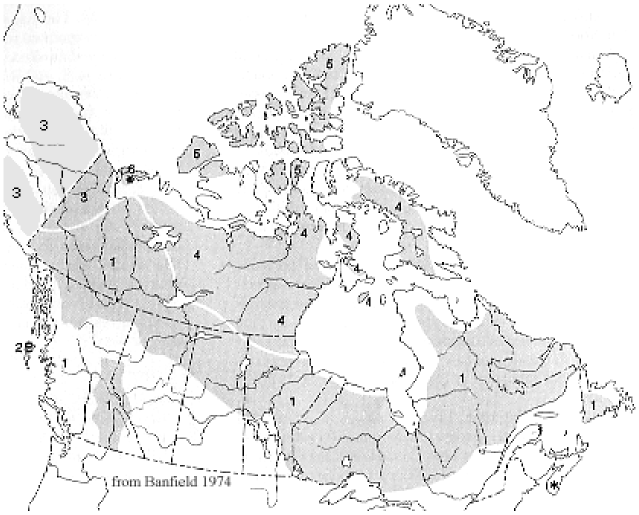

Figure 1. Caribou distribution in Canada and Alaska (modified from Banfield, 1974). Populations are: (1) *R. t. caribou*; (2) *R. t. dawsoni* (extinct); (3) *R. t. granti*; (4) *R. t. groenlandicus*; (5) *R. t. pearyi*; and (6) *R. t. tarandus* (introduced).

Figure 2. Current and historic distribution of woodland caribou (from Gray 1999).

Barren-ground caribou

Twelve herds are recognized totaling 1,646,800 caribou (Russell and Daniel, 2001). The largest are the Qamanirjuaq (496,000), Bathurst (349,000), Beverly (286,000), Ahiak (200,000), and Bluenose (100,000) herds.

Woodland caribou

Woodland caribou were once distributed throughout the boreal forest and Rocky and Columbia Mountains of Canada and the United States and well into the Carolinian forest of eastern Canada and the United States as shown in Figure 1 (Gray, 1999). Currently, 24 herds or populations are known, totalling more than 1,023,156 caribou (Russell and Daniel, 2001).[*] About half the populations are decreasing or are in one of the “at risk” categories (e.g., threatened) or of unknown status, while the others are stable or increasing.

The woodland caribou populations for Alberta and British Columbia are summarized in the next section.

Alberta

Dzus (2001) gives the distribution of woodland caribou in Alberta as shown in Figure 3 from records during 1967 to 2000. In the figure, the triangles are observations of caribou from several sources, the dots are telemetry points, and the question marks are areas with several sightings or potentially suitable habitat.

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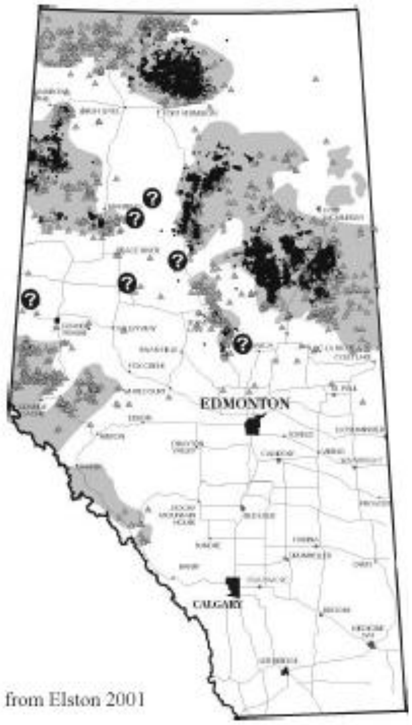
[*] Does not include Manitoba populations



from Elston 2001

Figure 3. Distribution of woodland caribou in Alberta (from Dzus 2001; see text for explanation).

Dzus (2001) states that all woodland caribou in Alberta are currently on that province's "Blue List" (threatened) because of reduced distribution, declines in regional populations and threats of further declines associated with human activities. He gave the trend in relative population size, expressed as a percentage increase or decrease based on productivity data, for caribou populations in the Rocky Mountains foothills on the west and east sides of the Athabasca River as shown in Figure 4 and for four boreal populations as shown in Figure 5. Although the populations have been decreasing overall and the distribution is shrinking, the number of caribou in the province remains largely unknown.

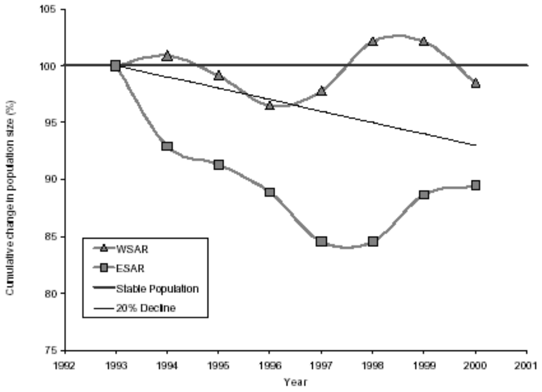


Figure 4. Trends in relative abundance of caribou populations on the west and east sides of the Athabasca River (from Dzus 2001).

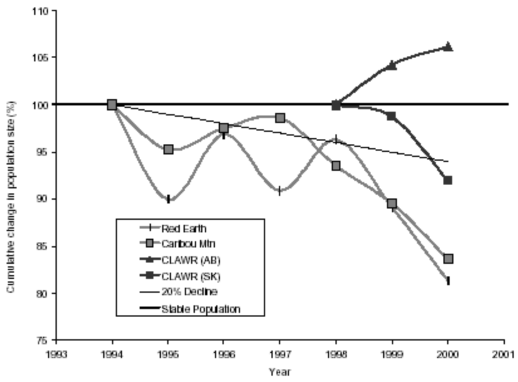


Figure 5. Trends in relative abundance of four boreal populations of caribou (from Dzus, 2001).

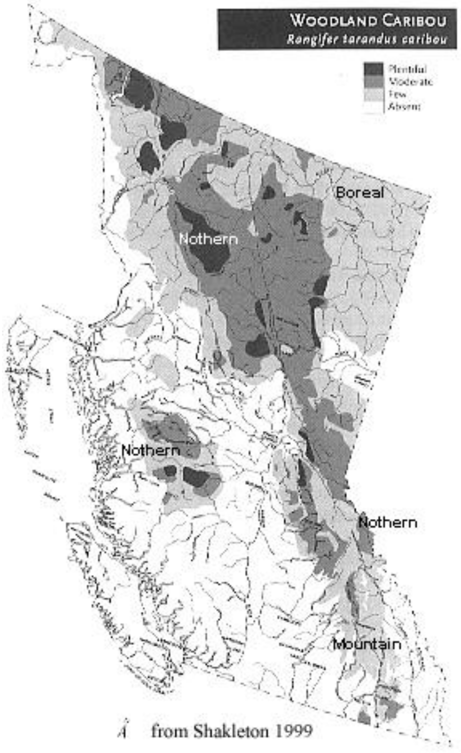
British Columbia

Three ecotypes of woodland caribou are recognized in British Columbia: boreal populations in the northeast, about which little is known; “northern” caribou in the coastal and northern mountains, which have relatively long seasonal migrations and forage in winter on terrestrial lichens; and mountain caribou of the Columbia Mountains, which generally tend to undertake twice-annual (fall and spring) migrations to low elevations, and feed in midwinter on arboreal lichens at high elevations (Figure 6). A few caribou also occur in the southern Rocky Mountains, nominally of the northern ecotype. Managers recognize 42 subpopulations that vary in size from the Spatsizi herd, with 2,200 caribou, to the George Mountain herd, which has declined to approximately 5 caribou.

The archaeological record shows that caribou followed the retreating ice sheets approximately 10,000 years ago into southeastern B.C. from glacial refugia in the United States, along the Pacific Coast and possibly other locations

(MacDonald, 1996). The range may have contracted somewhat during the hypsothermal, or warmer period about 5,000 years ago, but likely expanded during a slightly cooler and wetter climatic period know as the Little Ice Age beginning about 1500 AD.

Spalding (2000) reviewed the history. Caribou populations in the province once numbered about 20,000 to 24,000 in 1970, fell abruptly to about 10,500 and then rose to about 13,000 by 1992. It has since risen to about 16,500 (Spalding, 2000) or 18,400.[2]



from Shakleton 1999

Figure 6. Woodland caribou distribution in British Columbia (Shackleton 1999) showing boreal, northern and mountain ecotypes.

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[2] BC Government Web site: http://wlapwww.gov.bc.ca/soerpt/5wildlife/caribou.html

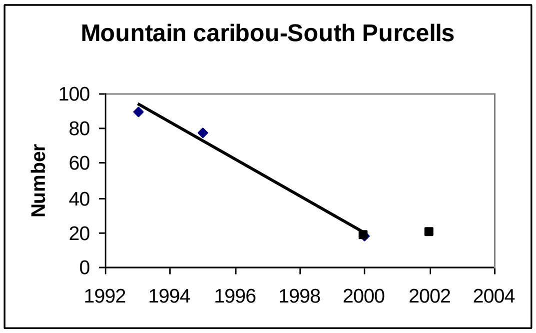

Figure 7. South Purcell southern mountain caribou population (Kinley 2002).

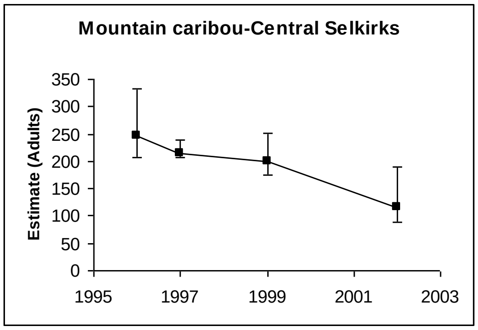

Figure 8. Central Selkirk southern mountain caribou population (Hamilton and Wilson 2002).

Most of the change in the 1970s was in the population of “northern caribou” ecotype of the Coast Mountains and northern Rocky Mountains, since they were far more numerous than the “mountain caribou” ecotype of the Columbia Mountains. However, mountain caribou populations in the southeast have begun to decline at an accelerated rate (Hamilton and Wilson, 2002; Kinley, 2002) as shown in Figures 7 and 8. Four southern herds previously considered stable are now in decline.

In 2000 the provincial status of mountain caribou was revised from “Special Concern” to “Threatened.” In the same year, boreal caribou in the northeast and all of the caribou in the southern two thirds of British Columbia were designated as “Threatened” by the COSEWIC. Caribou populations are stable in 16%, declining in 11% and extirpated in 31% of their historic range. Demographic trends are unknown over 17% of historical range. The management objective in 1985 was 20,000 caribou (Ritcey, 1985) and has not been officially updated. The major threat to mountain caribou is habitat fragmentation, which combines habitat loss with increasing predator populations and increasing susceptibility of caribou to predation (Mountain Caribou Technical Advisory Committee, 2002).

Tests of genetic distance and similarity (Mountain Caribou Technical Advisory Committee, 2000, citing K. Zittlau, Univ. of Alberta, unpubl. data) suggest very strong differentiation between all woodland caribou local populations that were sampled. The local population in the South Purcells is particularly distinct, with 100% of individuals correctly assigned to it. This suggests that these ecotypes may not be monophyletic, but rather developed their unique behaviours multiple times as they adapted to local conditions. From a genetic perspective, “this suggests that there is currently no reason why animals from a healthy population of Northern Caribou could not be transplanted into a Mountain Caribou population” (Mountain Caribou Technical Advisory Committee, 2002, p. 8).

Grant’s caribou

Grant’s caribou are distributed throughout the Yukon and Alaska; most are migratory. Thirty-two populations are recognized, totaling 835,365 caribou (Russell and Daniel, 2001). The largest are the Western Arctic herd of Alaska (430,000), Porcupine herd of Yukon and Alaska (123,000), and the Mulchatna herd of Alaska (120,000).

Peary caribou

Peary caribou are confined to Arctic Islands and to the mainland of the Boothia Peninsula, although some individuals occur on the mainland in winter as far south as the Hayes River and (rarely) west to the Yukon. Four metapopulations have been recognized (Figure 9) (Gunn and others, 2000), but the status of those in the "southern tier" of islands is in doubt. Miller (1991) and others have referred to them as "Arctic Islands caribou," "*R. t. peary/groenlandicus*," or "*R. t. groenlandicus/pearyi*," based on morphological differences from northern and northeastern ecotypes. However, recent genetic evidence (Eger and others, 1999; Zittlau and others) suggests two things:

1. The migratory herd that summers on Victoria Island and winters on the mainland – the Dolphin and Union herd – are more closely related to barren-ground caribou.
2. The remaining Peary caribou metapopulations are quite distinct below the subspecies level.

Until these relationships are resolved, Harding (in prep., 2003) recommended retaining the name "Peary caribou" (*R. t. pearyi*), for all caribou of the archipelago except the Dolphin and Union herd and the barren-ground caribou of the Baffin Island region.

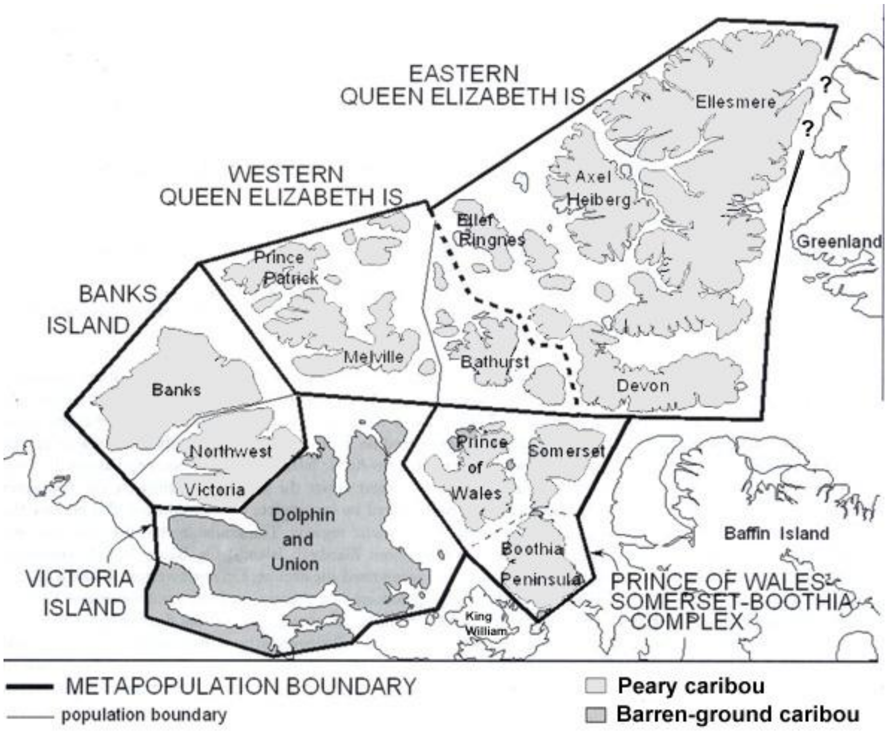

Figure 9. Distribution of Peary caribou and barren-ground caribou of the Dolphin and Union herd (Harding in prep. modified from Gunn and others, 2000).

Peary caribou and barren-ground caribou populations have all suffered major declines, but have not varied in synchrony. Harding (in prep., 2003) compiled data for the major populations or metapopulations as shown in Figures 10 to 17.

The best documented reason for the Peary caribou decline has been severe fall or spring conditions characterized by warm weather that occurs after snow is on the ground followed by freezing, which creates a glaze of ice or layering of ice crusts in the snow (Gunn and Dragon, 2000; Harding, 1974; Miller, 1991; Miller and others, 1977). This prevents grazing by caribou and muskoxen, even though adequate forage may be available underneath the ice, and has resulted in major population crashes of both ungulate species in synchrony. If it occurs in the fall, the glaze may persist through winter. These conditions may be related to global warming (Ferguson, 1996; Gunn, 1998b; Harding, in prep., 2003; Miller, 2001). In some cases, however, such icing conditions have not been documented (but may have occurred) or were not obviously associated with population crashes, and the muskox and caribou populations did not decline synchronously (Ferguson, 1991; Larter and Nagy, 1995; Nagy and others, 1996). Excessive hunting has been implicated as a contributing factor in some of these cases, but not others. Other causes or contributing factors, such as competition with muskoxen, excessive predation and forage depletion, have been suggested, but not documented (Ferguson, 1987; Ferguson and others, 2000; Gunn, 1993; Gunn, 1998a; Gunn and Dragon, 1998).

Resolving the genetic relationships among caribou populations in the Arctic Islands is critical to their survival. If different populations have different behavioural or physiological adaptations to adverse winter conditions, or that facilitate their adaptation to changing climates, then different conservation strategies may be needed.

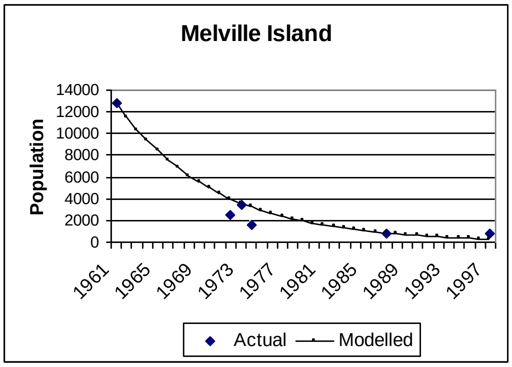

Figure 10. Melville Island Peary caribou populations (Harding, in prep.).

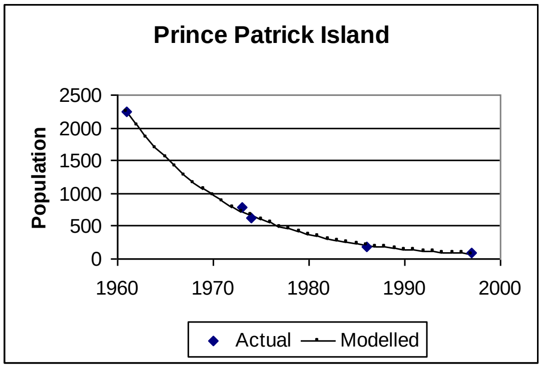

Figure 11. Prince Patrick population of Peary caribou (Harding, in prep.).

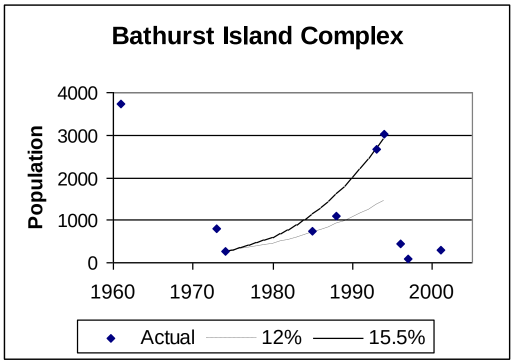

Figure 12. Bathurst Island population of Peary caribou showing calculated rates of increase for the period 1975-1995 (Harding, in prep.).

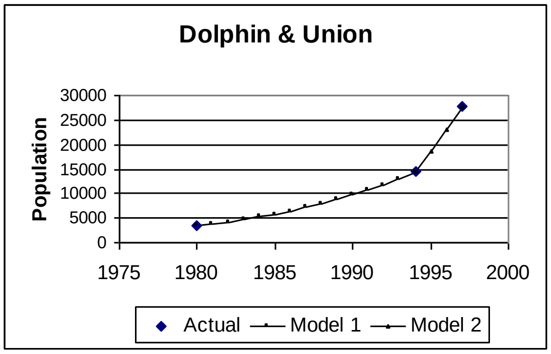

Figure 13. Dolphin and Union population of barren-ground caribou (Harding, in prep.).

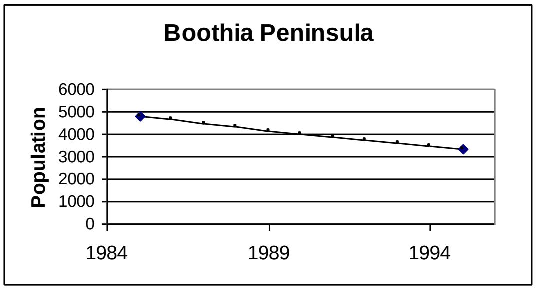

Figure 14. Boothia population of Peary caribou (Harding, in prep.).

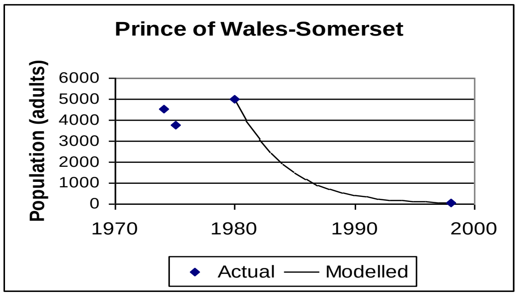

Figure 15. Prince of Wales population of Peary caribou (Harding, in prep.).

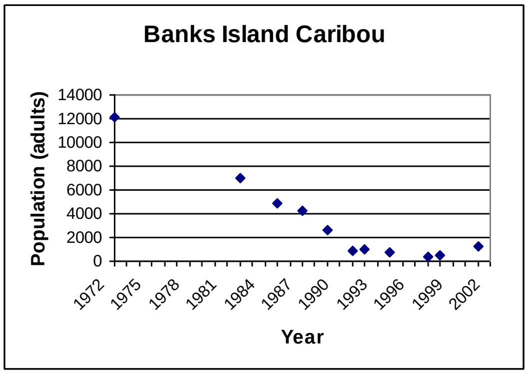

Figure 16. Banks Island population of Peary caribou (Harding, in prep.).

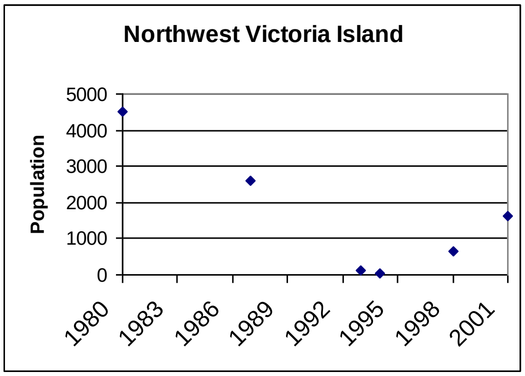

Figure 17. Northwest Victoria Island population of Peary caribou (Harding, in prep.).

DISCUSSION

The last comment about Peary caribou applies generally to all caribou. If different populations have different behavioural or physiological adaptations to certain environments, or that facilitate their adaptation to environmental conditions, then different conservation strategies may be needed. Moreover, the conservation of the genetic diversity that permits such adaptation on evolutionary time scales must be considered a priority. This means both affording protection to populations on the periphery of their ranges – exactly where they are often the most challenged – and avoiding mixing gene pools by translocating inappropriate genotypes. For these reasons, understanding genetic relationships is critical to caribou conservation.

ACKNOWLEDGEMENTS

Don Russell of the Canadian Wildlife Service provided colour maps for the presentation and numbers of herds or populations throughout Canada and Alaska. Anne Gunn of the Northwest Territories Fish and Wildlife Division provided colour maps of caribou distribution for the presentation.

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CARIBOU MORPHOLOGY AND TAXONOMY WITH EMPHASIS ON CANADA'S ARCTIC ISLANDS

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Conservation's goal is to maintain or recover biodiversity. To implement that goal requires us to group caribou for assessment and recovery actions (taxonomic units and geographic population structuring). To conserve caribou biodiversity, groupings have to represent evolutionary relationships as well as current patterns of gene flow and dispersal. The question of what to call caribou groupings has baffled more than a few people. Thus, then to try to integrate those groupings with the requirements of recovery planning and assessment designations as required by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and the Canadian *Species At Risk Act* (*SARA*) becomes even more perplexing. COSEWIC's status report for woodland caribou (Thomas and Gray 2002) and Courtier *et al.* (this proceedings) offers some possible solutions to the nomenclature for woodland caribou.

The current taxonomy is Banfield's (1961) classification of species and subspecies which was based on morphology, the study of form and structure. Banfield based his taxonomy on an extensive review and measurements from 855 skulls representing the circumpolar distribution of *Rangifer*. Although Banfield relied on measuring skulls, he also used information on distribution, pelage color and antler conformation. Now that we have the contemporary tools of DNA analysis and satellite telemetry we have enough information on ecology, movements, and genetic variation to identify incongruence in the current taxonomy. A key point is that those different tools sample variation in caribou over very different time scales ranging from millennia, centuries, and decades to years. Those various time scales is a consideration easily lost when comparing results and evaluating any congruence or incongruence between the groupings resulting from the use of different tools.

To describe caribou evolutionary relationships, we need to quantify variation in a suite of characters. This paper summarizes the contribution of morphology to the question of grouping caribou. The paper's emphasis is biased toward describing the morphology of the caribou on the Canadian High Arctic Islands. It was the concern about the conservation of those caribou that provided the motivation for holding this workshop.

Measuring skulls to describe morphological similarity is based on continuous variation in characters such as skull length or width. In choosing characters to measure, we should assume that they are largely under genetic control and minimally affected by environmental or nutritional conditions. The characters that reveal phylogenetic relationships have to be homologous (common ancestry) rather than homoplastic (similar appearance but not a common ancestor). However, in reality, the selection of useful variables is also influenced by practicality, e.g., ease of preservation and measurement. It is worth emphasizing that using the skull and other bones has the advantage of repeatability of measurements which are easy to take and to standardize so long as the same criteria and procedures are applied in all cases. Although some authors acknowledge that the environment affects skull size and shape, using metric skull characters has persisted in caribou taxonomy (e.g. Manning, 1960; Banfield, 1961; Thomas and Everson, 1982; Hakala *et al.*, 1985; Gunn and Fournier, 1996).

Skeletal growth has both genetic and environmental components. Changes in morphology under the influence of nutrition can be rapid as shown for example by changes in leg length within and over the time scale of decades (Klein *et al.*, 1987). However, as morphology also reflects ecology, leg length will be differentially selected for in different environments. Both Nieminen and Helle (1980) and Klein *et al.* (1987) commented on selection for leg length relative to snow conditions – the advantage of longer legs is energetic efficiency in moving through deeper snow. Nieminen and Helle (1980) also reported that ratios of shoulder height to foreleg length and similar linear ratios were independent of body size and thus are reliable for taxonomy. Hoof width is another morphological variable that reflects snow conditions. Caribou on the Arctic Islands have wide hooves relative to body size compared to mainland barren-ground caribou samples at the time (Manning, 1960; Manning and Macpherson, 1961). However, the functional significance of hoof width has not been investigated, nor has the possible variability in hoof width among barren-ground caribou that consistently winter on the barrens versus those that migrate into the taiga and boreal forest.

Taxonomists such as Manning (1960) were aware of the confounding effect of the environment on skeletal growth and used statistical procedures in an attempt to isolate the effect of skull size when comparing characters. Manning (1960) commented, for example, that skull length and maxillary tooth row were poorly correlated. This condition could mean that the maxillary tooth row has a genetic basis and that the skull length does not, likely being forged more by environmental pressures. Another set of problems arises because the measurement of selected characters was continuous (metric) rather than discrete (non-metric). This condition makes it more difficult to locate and clearly identify the discontinuities, that is, if the resulting continuum does not clearly exhibit measurable separation gaps. Metric characters include the presence or absence of an additional cusp on a tooth or the shape of a skull opening.

Related to finding the discontinuities in continuous data is sensitivity of skull morphological characters to sample size. Caribou are sexually dimorphic and the two sexes mature at different rates with the additional complication that there are skeletal differences in rates of maturity and thus size. All of this means that sample size can rapidly become a factor that limits confidence in taxonomy based on differences in continuous skull characters. Banfield's (1961) total sample size was 855. However, for example, to describe the subspecies *granti*, he used only 4 male and 6 female skulls.

The analyses of skull size and shape did reveal discontinuities, which together with antler and pelage differences together with separation by geographic distribution allowed Banfield (1961) to recognize a hierarchy of groupings above and below the subspecies level. However, he cautiously wrote that the “reindeer and caribou populations do not readily fit into the classical species and subspecies categories” (Banfield, 1961:103). Banfield (1961) followed early descriptions in grouping subspecies as either “tundra” reindeer/caribou (Cylindricornis) or “forest” reindeer/caribou (Compressicornis), based on the horizontal plain cross-sectional shape of the antler’s main beam (cf. Jacobi 1931). Subsequently, Bubenik (1975) commented about the variation in the shape of the horizontal plain cross section of the main beam. Banfield’s (1961) nine subspecies were further divided into geographic populations grouped as demes, although the criteria for grouping the geographic populations (themselves undefined apart from collection location) as demes are not explicit. Although the demes were not supported by significant differences in skull measurements, Banfield (1961) did suggest that the demes would evolve as subspecies.

Manning (1960) has a more detailed account of caribou on Canada’s Arctic Islands and he described a cline in skull absolute length across the Queen Elizabeth Islands through Banks to the Dolphin and Union herd (Victoria Island) onto the mainland. The most abrupt step in the cline was between the Dolphin and Union herd and the caribou that were year-round residents on the mainland. Most other skull characters correlated with skull size except for the length of the anterior skull (nasal bones) which also showed the greatest discontinuity between Dolphin and Union herd and Canadian mainland caribou. Skulls from the Queen Elizabeth Islands had shorter faces (rostral region), with increased skull breadth and height and longer tooth rows relative to skull length. The pairs of measurements that best separated the geographic areas differed for the different areas and mostly offered a percentage nonoverlap of about 80%. Manning (1960), seemingly, implied that the cline in size across the Arctic Islands to the mainland was a “stepped cline” as he identified that the four groups (Queen Elizabeth Islands, Banks Island, Dolphin and Union herd, and caribou restricted to the mainland were each relatively homogenous and semi-isolated. Sample sizes were low as Manning (1960) had 37 specimens from the Queen Elizabeth Islands (5 skulls from Prince Patrick, 1 from Melville, 27 from Ellesmere, 1 from Axel Heiberg, and 3 from the Isachsen area of Ellef Ringnes), 29 from Banks Island and 15 from Dolphin and Union herd (Victoria Island).

Thomas and Everson (1982) also described a stepped cline in skull measurements with the western Queen Elizabeth Islands (55 adult skulls from Prince Patrick, Melville and Bathurst islands) forming a relatively homogenous group compared to 35 adult skulls collected from Prince of Wales and Somerset islands. They and Manning and Macpherson (1961) also collected 5 and 7 larger-bodied, short-legged caribou, respectively, on Prince of Wales Island in the summer. Manning and Macpherson (1961) described their 7 skulls collected in summer 1958 as ultra *pearyi*, based on their larger size and shortened rostrum. However, Thomas and Everson (1982) concluded that the 5 bulls collected in the summer of 1978 (average body weight 203 kg) were different from the other caribou collected during late winter on Prince of Wales and Somerset and further speculated that the 5 bulls were likely visitors from Victoria Island. However,

F. L. Miller (pers. comm., 2003), states that this large ultra *pearyi*-type bull was found on Prince of Wales in both winter and summer (i.e, apparently year-round) and that he had seen them on Somerset Island and Boothia Peninsula in later winter during the late 1970s and early 1980s. Therefore, he believes that those 5 bulls collected by Thomas and Everson (1982), which he actually assisted in obtaining, were more likely year-round residents. He also assumes that the 7 ultra *pearyi* collected by Manning and Macpherson (1961) were also year-round residents on Prince of Wales and Somerset islands and possibly also on Boothia Peninsula in wintertime. At the very least, he questions how Manning (1960:49) identified caribou of the Dolphin and Union herd as intergrades of *R. a. arcticus* [*R. t. groenlandicus*] > *R. a. pearyi* [*R. t. pearyi*] and then identified the 7 ultra *pearyi* on Prince of Wales Island as caribou that exhibited evidence that is “overwhelmingly against intergradation on Prince of Wales Island” (Manning and Macpherson, 1961:227) – if they are indeed the same type of caribou. Given the extremely low numbers on Prince of Wales and Somerset Islands in the mid-1990s (Gunn and Dragon, 1998), the question of whether, based on skull measurements and body size, there were two types of caribou year-round or seasonal immigration from Victoria Island is not likely to be resolved.

Skull measurements and pelage color in the 1970s support the notion that at least two types of caribou occur on Boothia Peninsula (Thomas and Everson, 1982). In 1976-77, caribou collected on northern Boothia Peninsula were similar but slightly larger than caribou from Prince of Wales and Somerset, except for one young bull that was more typical of barren-ground caribou and one cow that was more similar to Prince of Wales and Somerset caribou. The caribou taken on central Boothia Peninsula were predominantly barren-ground caribou being larger, longer-legged and having conspicuously darker pelage.

The statistical analyses that Manning (1960) and Banfield (1961) used in inferring phylogenetic relationships from caribou skull data were relatively simple, and subsequently more powerful statistical procedures might contribute to describing phylogeny. For example, Eger (1990) used Principle component analysis and found that although skull size in the ermine (*Mustela erminea*) correlated with climate, it also exhibited geographic discontinuities consistent with glacial refugia. Other analytical approaches are, for example, the use of cladisitic methods to reexamine skeletal data by McCracken and Sheldon (1998) who compared phylogenies from morphology, behaviour (vocalization) and mtDNA sequencing.

Aside from applying other statistical techniques to existing morphological data from caribou, more could be learned from body form to derive evolutionary relationships by studying variation and change in size and shape (morphometrics). Morphometrics can be further defined as the analysis of biological homology. Homology is similarity in form assuming inheritance from a common ancestor. However, the relevance of morphometrics to phylogeny has been debated over the selection of characters that are homologous and the value of metric relative to non-metric characters. Another potential problem of comparing groups using morphometrics is convergence and differences in evolutionary rates of characters.

In the context of caribou taxonomy, morphometrics has not really been applied. However, for example, molariform teeth could be revealing about intraspecific relationships. Molariform teeth are relatively conservative characters (less molded by environmental variation) and techniques and analyses exist to describe and compare the complex shapes of teeth. There are many techniques ranging from transformation grids to three-dimensional laser scanning to capture data on complex shapes. For example, an optical topometry system reveals high resolution measurements of tooth shape using distance, area, and relief parameters along with wear patterns.

Another application of morphometrics would be to examine the shape of antlers. This follows from Bubenik's (1975) suggestion because antler conformation is shaped through behavioural selection and thus may have a strong genetic component. Currently, the newer techniques to scan three-dimensional shapes and the software to apply transformation grids would provide more refined quantitative descriptions and comparisons.

Manning (1960), Banfield (1961), Manning and Macpherson (1961), and Thomas and Everson (1982) used pelage colour as a taxonomic character. Pelage colour and patterning are inheritable characteristics and coat colour inheritance is well understood in domestic animals. The genes and modifying genes for coat colour have been mapped through gene sequencing. Thomas and Everson (1992) had only late winter skins while Manning (1960) limited his comparisons to late summer hides which would have been breeding pelage. Manning (1960) looked at skins from the Canadian Arctic Islands and the

Canadian mainland and commented that 80% to 90% of the skins could be assigned to the location of origin. He described a cline of increasing darker hair from the Queen Elizabeth Islands to Banks Island to the Dolphin and Union herd and then with the greatest step from the Dolphin and Union herd to mainland caribou. The amount of dark hair on the face, back, and the legs were distinguishing features although subject to individual variation (Figure 1).

Geist (1991) rejected the subspecies classification based on skull morphology; he described skulls as “environmentally plastic”. He argued that pelage patterning (social markings) on the basis that ”social organs” are evolutionarily conservative given the reciprocity of sender and receiver. Pelage patterns and antler size and shape are morphological characters linked through behaviour to the species’ ecology (ecomorphology). Geist (1991) briefly described and concluded that the caribou’s rump patch, extent of the white neck field, mane, flank stripe, belly patch, and facial markings did not comply with Banfield’s (1961) designation of subspecies. For example, on the basis of pelage, Geist (1991) would lump *stoni* and *granti* with *groenlandicus*. The pelage is most patterned on caribou that live in herds with distinct seasonal migrations across the treeline: dark belly stripe contrasting with white belly and shoulder. This group would include barren-ground caribou (*groenlandicus*) but also Northern Mountain caribou in the Yukon and “woodland” caribou in the George River herd. However, there are no quantitative measures of coat patterning taken during the rut and analyzed for the degree of patterning, which could be remedied by a series of digital images. Figure 1 is illustrative rather than analytical but does convey variation in breeding pelage (photographs 1-8), the light velvet and relatively gray brown pelage of the caribou on the Arctic Islands (photographs 9-11), and the short faces with variable amounts of brown of Dolphin and Union cows compared to a barren ground cow. It is worth noting that a systematic collection of photographs showing pelage colour and patterns is currently unavailable.

Antler velvet colour does not follow a cline and instead exhibits a discontinuity in colour between the Arctic Islands and mainland in North America. Manning (1960) described the paler, more slate gray velvet of caribou antlers on the Canadian Arctic Islands compared to the darker and more chocolate brown velvet from the caribou on the mainland. Manning (1960) did not have antler velvet from the Dolphin and Union and Banks Island caribou but my observations are that their antler velvet is pale gray with a scattering of darker grayish hairs. Manning (1960) cautioned that the antler velvet should be examined in small samples, preferably from only two animals at a time and under artificial light. Antlers are densely haired and the hairs have exceptionally large sebaceous glands. Consequently the hairs have a shine in some light conditions, which makes comparing antler velvet from photographs problematic. However, despite this, reindeer from the High Arctic Svalbard Archipelago also appear to have paler grayish antler velvet.

Current patterns of morphological and genetic variation are a consequence of recent and past events. Although some progress is being made with a phylogeographical analysis, less progress has been made with integrating the fossil record. Caribou are an ancient deer as the deer family evolved in Eurasia during the early Miocene (20 million years before present). Some deer during the Pleistocene (2 million years before present) reached the Americas, most likely by using the Bering land bridge. The South American primitive deer moved north, and Harington (1999) has described the earliest North American *Rangifer* fossils, which are in Yukon, dating from the early Pleistocene (1.6 million years before present). Caribou during the Pleistocene evolved during ice age cycles which initially had a periodicity of about 40 ka (thousand years) then lengthened to a periodicity of about 100 ka duration for the last 700 ka.

During the most recent glaciation, the extent of glaciers was less in western Asia which was connected to North America until about 11,000 years ago, although even when separated by a body of water, we cannot rule out ice-crossings by reindeer. About 50% of Alaska was never glaciated by the Laurentide and Cordillarian ice sheets. Part of the unglaciated Beringian area served as a refugium for taiga and tundra plants. Molecular phylogeography of plant species such as *Dryas integrifolia* and *Saxifraga oppositifolia* argue for both a Beringia and High Arctic refugia (Tremblay and Schoen, 1999; Abbott *et al.*, 2000). The presence of those two species is in agreement with recent maps (J. M. Adams and H. Faure, eds. Quaternary Environments Network) which show extensive areas of polar desert and smaller areas of dry tundra in Alaska 18,000 radiocarbon years ago. South of the Cordilleran Ice Sheet (then continuous with the Laurentide Ice Sheet) was a relatively small area of dry tundra on the west coast, which was perhaps a third refugium for caribou. This dry tundra area was isolated by extensive temperate semi-desert and grassland from the eastern areas of open boreal woodland, taiga, and relatively narrow bands of tundra. By about 13,000 radiocarbon years ago, the tundra in Alaska was comparable to the more isolated patches of tundra south of the two ice sheets, between which a corridor was opening up.

Those vegetation patterns as the ice sheets retreated support two findings from mtDNA sequencing (Dueck and Strobeck, in prep.). Firstly, the more extensive areas of tundra in Alaska may have supported greater caribou abundance and hence their dispersal southward. Secondly, the vegetation south of the Laurentide Ice Sheet appears to have been relatively patchy with isolated tundra interspersed by projections of the ice sheet between 18,000 and 13,000 radiocarbon years ago. The patchiness may have been a factor in the possible relatively high rate of evolution in the southern mtDNA clade of caribou.

Some similarities may be argued from the role of postglacial vegetation and the distribution over time that resulted in the genetic variation of the lemmings (*Dicrostonyx* vs. *Lemmus*). For example, although fossil distributions of *Dicrostonyx* and *Lemmus* overlap, *Dicrostonyx* is more associated with colder and drier environments than *Lemmus*, which likely explains their different patterns of mtDNA variation (Fedorov, 1999). *Dicrostonyx* has lower mtDNA diversity; mutation rates are likely similar for the two rodents (similar generation rates) and differences presumably reflect effective population size. The lower mtDNA diversity in *Dicrostonyx* may have been a consequence of regional bottlenecks following the northward expansion of forest communities during interglacial periods, whereas the higher mtDNA variation in *Lemmus* suggests that effective population sizes were not reduced (Fedorov, 1999).

Another example that likely has parallels with caribou is from harbour seals *Phoca vitulina*. Harbour seals, like caribou, are abundant and widespread, and their biogeography and phylogeny reflect expansion and recolonization following glacial retreat (Westlake and Corry-Crowe, 2002). The two subspecies (based on morphometrics) are not supported by mtDNA (no reciprocal monophyly). Intraspecific structure suggests regions of higher and lower dispersal with dispersal between neighbouring subpopulations (steppingstone model of population structure). This could have been a result of patchily dispersed refugia during dispersal and range expansion during glacial retreat.

The current patterns of morphological and genetic variation are also a consequence of recent as well as past conditions. The North American Arctic and subarctic climate is strongly regionalized with east–west and north–south gradients in variables (e.g. snow depth), which is related to probabilities of incursions of Pacific and/or Atlantic maritime air masses (Maxwell, 1981). Annual and seasonal variability is high and unpredictable. Consequently, caribou ranges, especially on the Arctic Islands, comprise a non-equilibrium ecological system with environmental extremes causing unpredictably in relative forage supplies (Caughley and Gunn, 1993; Behinke, 2000). Caribou abundance varies with sporadic and unpredictable die-offs leaving periods of low numbers and extremely low mean overall densities. In such remnant populations, genetic drift leads to genetic differentiation and also in such a system, evolutionary selection will likely be the most intense when survival of the caribou is at its lowest.

The implications of intense selection during and between die-offs for Peary caribou has not yet been investigated. Some information on selection in a variable environment comes from Soay sheep (*Ovis aries*) on a small island off northern Scotland where they undergo frequent die-offs (Milner *et al.*, 1999). It was found that there was strong selection for greater body weight, especially in lambs, where the heavier lambs died at a lower rate. However, despite the strong selection for heavier animals, they could not find, on average, an overall increase in body weights during the study. Either the direction of selection is counteracted by stronger selection factors, or the time period (nine years) was not long enough to detect a fixed selection for heavier animals, including calves. If much more effort was made to investigate die-offs, we probably would be able to track some of the likely changes in bone measurements over decades and character selection as a result of exceptionally severe environmental episodes or series of highly stressful years.

The unpredictably severe environment of the Arctic Islands and its attendant intense selection has led to small-bodied caribou with proportionally shorter legs. Similar characteristics including pelage and antler velvet colour are also apparent for the Dolphin and Union herd on Victoria Island, with the exception that, on average, they are larger in body size. All of the factors at play in determining body size are not yet fully known. However, it seems reasonable to suggest that larger body size in caribou is influenced favorably by a longer plant-growing season that results in a greater plant biomass of relatively high-quality forage. In addition, a drier climate, typical of a more continental climate (Maxwell, 1981), should favour weight retention during most winter and spring maintenance periods over a maritime situation with unpredictably deeper snow regimes and icing events. However, the overlap in the distribution of large-bodied barren-ground caribou and smaller bodied Peary-like caribou on Boothia Peninsula suggests that environmental gradients are not the only explanation.

In summary, the morphological information was mostly from linear skull measurements (Manning, 1960; Banfield, 1961; Manning and Macpherson, 1961; Thomas and Everson, 1982) and demonstrated a cline in size corresponding to the environmental gradients across the Canadian Arctic Islands. Their data reveal that the cline was stepped with differences between the Queen Elizabeth Islands and the mid-Arctic Islands (Banks, Victoria, Prince of Wales, and Somerset) and that there were also discontinuities in the east–west cline across those mid-Arctic islands. Breeding pelage and antler velvet are discontinuous characters in caribou from the Arctic Islands and the mainland.

Incongruence within morphological characters, such as between skull measurements and breeding pelage patterning may partly reflect incompleteness of the data sets and/or choice of characters selected and the analyses used. Any future review of caribou taxonomy will have to address the question of sample size and selecting characters less responsiveness to environmental variation and that are not homoplastic. Given the new techniques and analyses now available, consideration should be given to reanalyzing existing data, reexamining existing skeletal material for non-metric characters, and describing shape changes in relatively conservative structures such as molariform teeth. A collection of systematically taken images of breeding pelage and its individual variation and its relationship to breeding behaviour would be informative. In some cases, new series of specimens will be necessary given the small sample sizes previously used. In those cases, the specimens should be exposed to the full suite of genetic and morphological sampling and analyses. Such an approach would help to keep the different time perspectives of genetic and morphological sampling in context with each other.

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TOWARDS DEFINING CONSERVATION UNITS FOR WOODLAND CARIBOU IN BRITISH COLUMBIA

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TAXONOMY

Cowan and Guiguet (1956) recognized two subspecies of Woodland Caribou in British Columbia including *Rangifer tarandus montanus* (located south of ~56° latitude) and *Rangifer tarandus osborni* (located north of ~56° latitude). Cowan and Guiguet considered *osborni* to be larger than *montanus*, with antlers that were proportionately larger with long beams between the second tine and crown. They also considered the extinct Dawson's caribou, which formally inhabited Haida Gwaii, an archipelago located 80 km off the coast of British Columbia, as a separate species (*Rangifer dawsoni*).

The definitive taxonomic studies of caribou were done by Banfield (1961) who recognized one subspecies of Woodland Caribou in Canada. Thus, under Banfield's taxonomy, all Woodland Caribou in BC belong to the subspecies *Rangifer tarandus caribou*. Banfield also considered the Dawson's caribou to be a subspecies (*Rangifer tarandus dawsoni*).

Banfield's work has stood, and is still used in BC today, although it has been challenged by Geist (1989). Geist believed that Banfield, as other taxonomists, undervalued the differences in pelage patterns and morphology in favour of statistical treatment of skull measurements. Based on the fall coat of large bulls, Geist suggested that *Rangifer tarandus montanus* should include only the mainland woodland caribou of North America, including the “mountain” caribou of British Columbia, Alberta, and Idaho, while *Rangifer tarandus osborni* should include the larger non-migratory caribou of northern British Columbia and southern Yukon.

Recently, Byun *et al.* (2002) used molecular and ancient-DNA techniques to assess the genetic distinctiveness of *Rangifer tarandus dawsoni*. Their analysis suggests that the Dawson’s caribou was not genetically distinct, and that the unique morphology characterizing this form may have been of recent origin, either from local selection pressures, or from environmentally induced phenotypic plasticity.

ECOTYPES

While only one extant subspecies of caribou is currently recognized in BC, biologists recognize three ecotypes of the woodland subspecies. These ecotypes, which have no formal taxonomic designation, are defined on the basis of distinct patterns of habitat use and behaviour. The ecotypes are known as Mountain Caribou, Northern Caribou and Boreal Caribou (Heard and Vagt, 1998). The distribution of the three ecotypes, as well as the former occupied range (extirpated) of Woodland Caribou, and range of the Dawson’s caribou are shown in Figure 1.

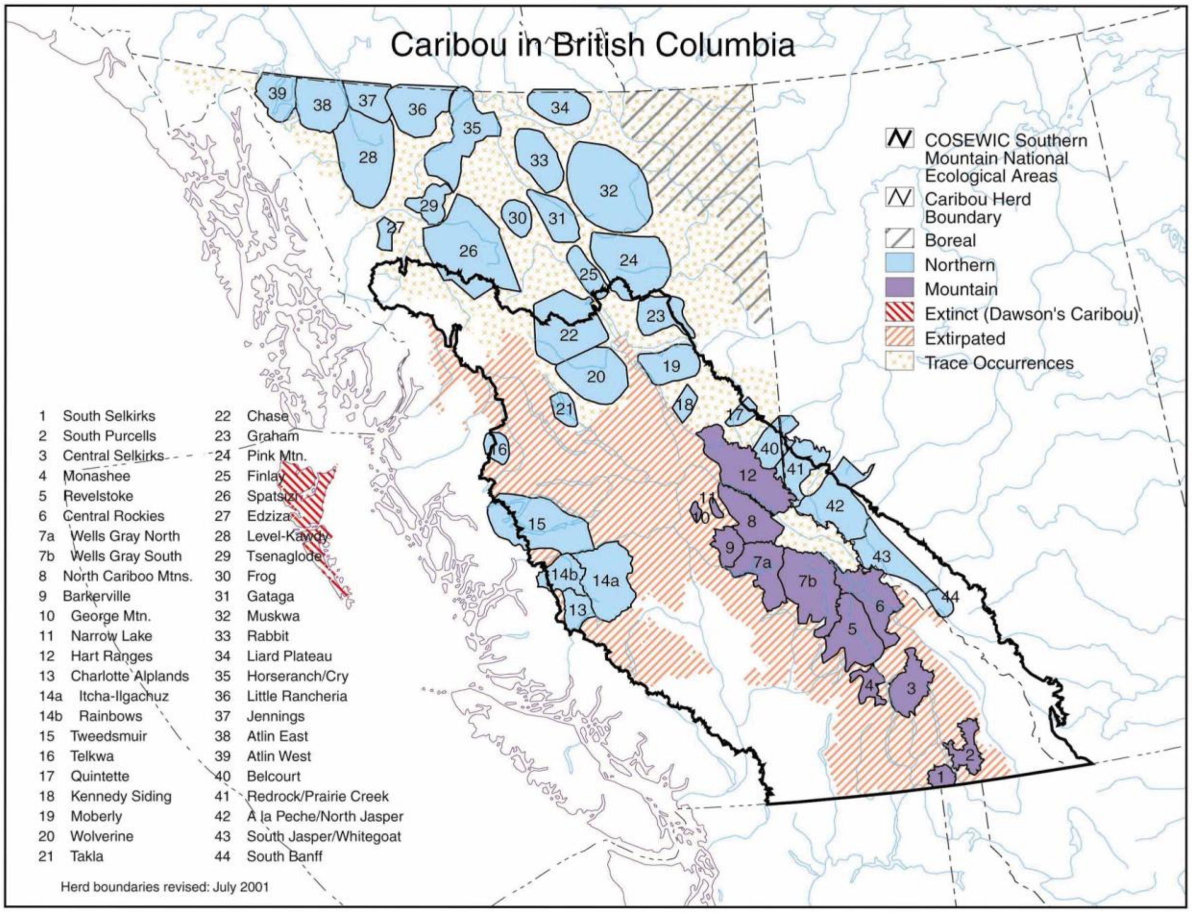

Figure 1. Current and former ranges of Woodland Caribou local populations in British Columbia. The dark line shows the boundary of the COSEWIC SMNEA. Herds located north of the SMNEA line are found in the NMNEA, while the Boreal ecotype occurs in the Boreal NEA. Herds 41-44 occur in Alberta.

DISTRIBUTION

Mountain Caribou in British Columbia occur regularly in portions of the Rocky Mountains’ west slope from the upper Parsnip River to the Morkill River and from the Wood River drainage to the Bush Arm of Kinbasket Lake, although there are sporadic occurrences between the Morkill and Wood rivers. They also occur in the Columbia Mountains, including parts of the Cariboo Mountains, Quesnel Highlands, Shuswap Highlands, Monashee Mountains north of

Whatshan Lake, the Selkirk Mountains, and portions of the Purcell Mountains north of Highway 3.

Northern Caribou in British Columbia occur in the west-central portion of British Columbia, in and around the Itcha, Ilgachuz, Rainbow, and Trumpeter mountains, as well as in and around northern Tweedsmuir Park and Entiako Park and Protected Area. They also occur in the Telkwa Mountains and around the northern part of Takla Lake. Northern Caribou are somewhat contiguous in distribution from the Williston Lake area north to the Yukon border and northwest to Atlin.

Boreal Caribou are found in north-eastern British Columbia in relatively flat boreal forests east of the Rocky Mountain foothills from the Yukon border east of the Liard River as far south as the Wapiti River Drainage, downstream of its junction with the Red Deer River. The western boundary is indistinct but is approximately along the Liard River from the Yukon–Northwest Territories boundary upstream as far as the junction with the Dunedin River, and then generally southeast to Fort St. John. No caribou were likely to have lived or will live in the drier aspen forests along the lowlands near the Peace River, although the occasional transient has been seen in these areas.

LIFE HISTORY

Many components of the life history of the three ecotypes are similar. However, the three ecotypes can be distinguished from each other on the basis of winter diet and seasonal movements, which reflect their areas of occurrence within BC (Table 1).

Table 1. Features of the Mountain Caribou, Northern Caribou and Boreal Caribou ecotypes in British Columbia.

FEATURE	***MOUNTAIN CARIBOU***	***NORTHERN CARIBOU***	***BOREAL CARIBOU***
Occurrence	Mountainous deep-snowpack portion of southeastern BC known as the Interior Wet Belt	Mountainous and adjacent plateau areas with relatively low snowpacks in west-central and northern interior British Columbia	Peatlands (muskeg) in lowland plateau portion of northeastern British Columbia, east of the Rocky Mountains, with relatively low snowpack
Winter diet	Consists almost entirely of arboreal hair lichen, with use of terrestrial lichen and other ground-based foods only in early winter	Consists mostly of terrestrial lichens with use of arboreal lichens dependent on snow conditions	Consists mostly of terrestrial lichens with some use of arboreal lichens
Seasonal movements	Generally involve little horizontal distance but strong elevational shifts	Generally involve both horizontal distance and elevational shifts	Generally involve horizontal distance but no strong elevational shifts although for some local populations, winter and summer ranges may overlap

HABITAT REQUIREMENTS

Table 2 summarizes essential habitat characteristics of Woodland Caribou ranges in British Columbia. All habitat features are required to support viable Woodland Caribou populations. Extensive descriptions of Woodland Caribou habitat requirements are available in numerous government documents and publications including Stevenson and Hatler (1985), Simpson *et al.* (1997), Apps and Kinley (1998), Seip (1998), Poole *et al.* (2000), Apps *et al.* (2001a, 2001b), Stevenson *et al.* (2001), and Youds *et al.* (2002).

Table 2. General habitat requirements for Mountain Caribou, Northern Caribou and Boreal Caribou in British Columbia.

Feature	***Mountain***	***Northern***	***Boreal***
Winter food supply	Access to an adequate supply of accessible arboreal lichen	Access to an adequate supply of terrestrial and arboreal lichens	Access to an adequate supply of terrestrial and arboreal lichens
Snow conditions	Snow conditions that allow caribou to travel on top of the snowpack in subalpine areas where they can access arboreal lichens and where avalanche danger is low	Snow interception by forest canopy to allow movements within the winter range	Snow conditions and frozen ground conditions to allow movements through peat lands
Winter range	Large tracts of winter range where caribou can continue rotating their winter ranges and exist at low densities as an anti-predator strategy		
Calving habitat	Relatively undisturbed high elevation calving habitat where caribou can disperse widely and calve in isolation away from other prey and predators	Relatively undisturbed high elevation calving habitat or low elevation forested calving habitat on islands where caribou can disperse widely and calve in isolation away from other prey and predators	Large tracts of relatively undisturbed peat land complex calving habitat where caribou can disperse widely and calve in isolation away from other prey and predators

METAPOPULATIONS

Mountain and Northern Caribou are considered to occur within metapopulations, groupings of local populations with actual or potential immigration/emigration among them (Thomas and Gray, 2001). These are tentatively identified as the southern metapopulation (Table 3), the north-central metapopulation (Table 4), the west-central metapopulation (Table 5), and the northern metapopulation (Table 6). Currently, there is no information to assess metapopulation structure for the Boreal ecotype.

LOCAL POPULATIONS

Currently, forty-two local populations of Woodland Caribou are recognized in British Columbia. Tables 3 through 7 summarize the current estimate, recent trend, risk status, and density of each local population.

Table 3. Conservation status of Mountain Caribou (southern metapopulation).

Local Population	***Current Estimate***	***Recent Trend[1]***	***Risk Status[2]***	***Range[3] (km^2)***	***Density (#/1000 km^2)***
South Selkirks	35	Declining	EN	1,500	23
South Purcells	20	Declining	EN	2,962	7
Central Selkirks	130	Declining	EN	4,813	27
Monashee	10	Declining	EN	2,082	5
Revelstoke	225	Declining	VU	7,863	29
Central Rockies	20	Declining	EN	7,265	3
Wells Gray N	220	Declining	VU	6,346	35
Wells Gray S	325	Stable	VU	10,381	31
N Cariboo Mtns	350	Stable	VU	5,911	59
Barkerville	50	Stable	EN	2,535	20
George Mtn	5	Declining	EN	441	11
Narrow Lake	65	Stable	TR	431	151
Hart Ranges	450	Stable	VU	10,261	44
TOTAL	**1,905**			**62,791**	**Median=27**

[1] Recent trend defined as trend over last 7 years (1 generation length). Trend based on >20% change.

[2] At risk status based on draft guidelines for quantitative risk assessment of local populations. EN=Endangered; NAR=Not at Risk; TR=Threatened; VU=Vulnerable

[3] Current occupied range.

Table 4. Conservation status of Northern Caribou (North-Central metapopulation).

Local Population	*Current Estimate*	*Recent Trend*[1]	*Risk Status*[2]	*Range*[3] *(km^2)*	*Density (#/1,000 km^2)*
Quintette	200	Unknown	VU	1,421	141
Kennedy Siding	170	Increasing	VU	1,470	116
Moberly	170	Declining	TR	5,115	33
Wolverine	590	Increasing	VU	8,315	71
Takla	100	Unknown	TR	1,850	54
Chase	575	Stable	VU	11,390	50
Graham	300	Declining	TR	4,734	63
Belcourt	100	Unknown	TR	2,045	49
TOTAL	**2,205**			**36,340**	**Median=59**

See Table 3 for footnotes.

Table 5. Conservation status of Northern Caribou (West-Central metapopulation).

Local Population	*Current Estimate*	*Recent Trend*[1]	*Risk Status*[2]	*Range*[3] *(km^2)*	*Density (#/1,000 km^2)*
Charlotte Alps	50	Declining	EN	2,650	19
Itcha-Ilgachuz	2,500	Increasing	NAR	9,457	264
Rainbows	125	Stable	TR	3,804	33
Tweedsmuir	300	Declining	TR	12,811	23
Telkwa	55	Increasing	EN	1,828	30
TOTAL	**3,030**			**30,550**	**Median=28**

See Table 3 for footnotes.

Table 6. Conservation status of Northern Caribou (Northern metapopulation).

Local Population	***Current Estimate***	***Recent Trend[1]***	***Risk Status[2]***	***Range[3] (km^2)***	***Density (#/1,000 km^2)***
Pink Mountain	850	Declining	VU	11,602	73
Finlay	200	Unknown	VU	3,084	65
Spatsizi	2,200	Stable	NAR	16,929	130
Mt Edziza	100	Unknown	TR	1,281	78
Level-Kawdy	1,650	Stable	NAR	12,568	131
Tsenaglode	200	Unknown	VU	3,015	66
Frog	150	Unknown	VU	2,421	62
Gataga	250	Unknown	VU	4,437	56
Muskwa	1,250	Unknown	NAR	16,786	74
Rabbit	800	Unknown	VU	5,936	135
Liard Plateau	150	Stable	VU	5,069	30
Horseranch/Cry	850	Stable	VU	9,499	89
Little Rancheria	1,000	Stable	NAR	7,431	135
Jennings	200	Unknown	VU	4,080	49
Atlin East	800	Stable	VU	7,053	113
Atlin West	350	Stable	VU	4,398	80
TOTAL	**11,000**			**115,590**	**Median=76**

See Table 3 for footnotes.

Table 7. Conservation status of Boreal Caribou.

Local Population	***Current Estimate***	***Recent Trend[1]***	***Risk Status[2]***	***Range[3] (km^2)***	***Density (#/1,000 km^2)***
Boreal Caribou	725	Unknown	VU	51,541	14

See Table 3 for footnotes.

CONSERVATION STATUS

Conservation status of Woodland Caribou in BC is assessed at the local population, provincial, and national levels. Regionally, the local population is the basic unit for conservation. While local population status (“Endangered”, “Threatened”, “Vulnerable”, or “Not at Risk”) carries no formal designation, it is the fundamental unit for recovery actions.

Provincial designations of Woodland Caribou status in BC are conducted by the Conservation Data Centre using NatureServe/Heritage ranking criteria. The conservation unit at this level of resolution is the ecotype (Table 8). Mountain Caribou are on the provincial Red List (S2), while Northern Caribou (S3S4) and Boreal Caribou (S3) are on the provincial Blue List (Table 8). These designations assess risk and help guide conservation priorities.

National designations of Woodland Caribou conservation status within BC are conducted by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) using IUCN Red List criteria. At the national level, the conservation unit for assessing risk is the COSEWIC National Ecological Area (Table 8). Caribou within the Southern Mountain National Ecological Area (SMNEA) include all Mountain Caribou and thirteen local populations of Northern Caribou and are listed as “Threatened”. Caribou within the Northern Mountains National Ecological Area (NMNEA) are comprised of the Northern Caribou ecotype, and are listed as “Special Concern”. Caribou within the Boreal NEA include the Boreal Caribou ecotype, and are nationally listed as “Threatened”.

Tests of genetic distance and similarity (Table 10) suggest very strong differentiation between all Woodland Caribou local populations that have been sampled. The local population in the South Purcells is particularly distinct. In terms of genetic distance, the two populations (Revelstoke and South Purcells) are more similar to several northern ecotype local populations than to each other.

This suggests that these ecotypes may not be monophyletic but rather developed their unique behaviours multiple times as they adapted to local conditions. To date, these analyses have been primarily used to determine the genetic implications of transplanting Northern Caribou to endangered Mountain Caribou populations.

Table 8. Summary of Woodland Caribou conservation status in British Columbia.

Cosewic National Area	***Caribou Ecotype***	***Conservation Status***			
		Global	***Provincial***	***COSEWIC***	***BC Status***
PNEA	Dawson	G5TX	SX	Extinct	Extinct
SMNEA	Mountain	G5T2Q	S2	Threatened	Red
SMNEA	Northern	G5T4	S3S4	Threatened	Blue
NMNEA	Northern	G5T4	S3S4	Special Concern	Blue
BNEA	Boreal	G5T?	S3	Threatened	Blue

GENETIC RELATIONSHIPS

While the importance of genetics and the concept of an “evolutionary significant unit” as the basic unit for conservation is recognized (Ryder, 1986; Pennock and Dimmick, 1997; Waples, 1998), there has been no attempt to employ a genetics-based definition for caribou conservation units in BC.

Recent analysis of microsatellite DNA has provided some information about the genetic variation within and among the mountain and northern ecotypes of Woodland Caribou (Table 9). Heterozygosity within the South Purcells population stands out as uniquely low.

Tests of genetic distance and similarity (Table 10) suggest very strong differentiation between all Woodland Caribou local populations that have been sampled. The local population in the South Purcells is particularly distinct. In terms of genetic distance, the two populations (Revelstoke and South Purcells) are more similar to several northern ecotype local populations than to each other. This suggests that these ecotypes may not be monophyletic but rather developed their unique behaviours multiple times as they adapted to local conditions. To date, these analyses have been primarily used to determine the genetic implications of transplanting Northern Caribou to endangered Mountain Caribou populations.

Table 9. Genetic variation in Woodland Caribou local populations based on eight microsatellite loci. Ecotype: M = Mountain; N = Northern. "Prob. of Identity" is the probability that any two individuals in the local population are genetically identical (from K. Zittlau, Univ. of Alberta, pers. comm.).

LOCAL POPULATION	*ECO-TYPE*	*CURRENT EST. SIZE*	*SAMPLE SIZE*	*AVG. ALLELES*	*HETERO-ZYGOSITY (%)*	*PROB. OF IDENTITY (1 IN)*
South Purcells	M	20	27	4.6	52.7	143,136
Revelstoke	M	225	20	7.1	78.8	2,124,610,670
Itcha-Ilgachuz	N	2,900	17	5.6	73.7	86,915,604
Wolverine	N	400	20	6.6	74.3	246,571,054
Tweedsmuir	N	300	36	7.0	76.1	442,468,694
Finlay	N	200	16	8.3	82.5	41,033,042,665
Atlin East	N	800	24	8.0	82.5	36,563,698,359
Chase	N	700	24	9.3	82.6	112,120,534,461

Table 10. Distinctiveness of the Revelstoke and South Purcells Mountain Caribou populations relative to other Woodland Caribou populations in British Columbia based on Nei's standard genetic distance and frequency of correct assignment. Genetic Distance: small values indicate closely related populations. Assignment Test: distinct populations have a large proportion of individuals assigned to the original population. Sample size was 20 for Revelstoke and 27 for South Purcells. (Data and analysis from K. Zittlau, Univ. of Alberta, pers. comm.).

Local Population	***Genetic Distance***		***Assignment Test***	
	Revelstoke	***South Purcells***	***Revelstoke***	***South Purcells***
Revelstoke	0	0.56	19	0
South Purcells	0.56	0	0	27
Atlin East	0.61	0.69	0	0
Finlay	0.58	0.92	0	0
Itcha-Ilgachuz	0.46	0.70	0	0
Chase/Sustat	0.42	0.58	0	0
Tweedsmuir	0.40	0.79	0	0
Wolverine	0.43	0.70	1	0

RECOVERY PLANNING FOR WOODLAND CARIBOU

The overarching goal for managing Woodland Caribou in BC is to maintain caribou and their habitat in perpetuity throughout their current occupied range. Provincially, recovery planning occurs at the ecotype level. In order to accommodate COSEWIC NEA's within a National Recovery Strategy for Woodland Caribou, separate Recovery Strategies are being prepared for the Mountain Caribou and Northern Caribou within the SMNEA. Locally, Recovery Action Plans are focused on metapopulations, or logical groupings of local populations within a metapopulation (Table 11).

Table 11. Relationship between Recovery Action Plans and Conservation Units.

RECOVERY ACTON PLAN	ECOTYPE	COSEWIC NEA	METAPOPULATION	LOCAL POPULATIONS
Southern Mountain	Mountain	SMNEA	Mountain	1 - 2
Central Mountain	Mountain	SMNEA	Mountain	3 – 6
Northern Mountain	Mountain	SMNEA	Mountain	7 – 12
West Central	Northern	SMNEA	West Central	13 – 16
North Central	Northern	SMNEA	North Central	20 – 22
Central Rockies	Northern	SMNEA	North Central	17 – 19, 23, 40
Boreal	Boreal	BNEA	unknown	unknown

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POPULATIONS, METAPOPULATIONS, ECOTYPES AND SUBSPECIES OF CARIBOU IN QUÉBEC-LABRADOR: AN EXPLORATORY DISCUSSION

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The goal of this paper is to summarize historical trends (1880–2002) of caribou ecology and demography in the Québec-Labrador Peninsula, particularly the evolution of the migratory caribou herds. In doing so, this exploratory discussion aims at fostering an exchange of ideas on some caribou ecology concepts like herd or population, metapopulation, ecotype, subspecies, phenotypic variations and emigration.

Based on fragmented information sources, it is likely that the Québec and Labrador migratory caribou reached a population peak at the end of the 19th century (Low, 1896) before declining rapidly during the first decades of the 20th century (Elton, 1942). Thereafter, caribou remained at a very low density until the 1950s with some biologists even predicting the local extinction of the species

(Rousseau, 1951; Banfield and Tener, 1958; Bergerud, 1967). In the first aerial survey of the northern Québec-Labrador peninsula, Banfield and Tener (1958) reported a population of about 6,000 caribou for the region. If we analyze their census figures with our current knowledge of the herd space use, their estimate for the George River caribou Herd (GRH) was about 5,000 caribou. It was the first written observation that identified the GRH as a distinct group. For reasons still unknown, the GRH has literally erupted during the 1960s and 1970s. By the late 1980s and early 1990s, GRH was considered the largest *Rangifer* population in the world (Williams and Heard, 1986) reaching an estimated population size of 775,000 caribou (Couturier *et al.*, 1996). From the last census done in 2001, it appears that the GRH has declined (Québec Gov., Newfoundland & Lab. Gov., unpubl. data). Although we cannot predict when the decline will stop, caribou users and managers worry about the caribou's future as a reliable resource.

After the mid-1980s, Québec-Labrador caribou users, native and non-native, observed that caribou body condition was poor and deteriorating. As caribou is not only a food staple but also carries an important cultural value to native peoples, aboriginal users want to know more about caribou diseases, parasites, meat safety and causes of population decline. Hunting and ecotourism outfitters want to know about the future of their industry. On the other hand, wildlife managers look at fat and protein body reserves to detect and understand changes in pregnancy and natality rates, calf survival, recruitment, and ultimately, herd demographic trends. Experts on all sides have the same goal: the long-term conservation and sustainable use of caribou.

Since the 1950s, North American caribou herds have been defined and named based on their calving ground locations (Gunn and Miller, 1986). As most censuses are conducted at or near calving time, this herd definition is still appropriate for short-term management decisions. However, over larger time and space scales, the herd or population may not be the most effective conservation unit. The metapopulation theory may prove to be useful for long-term caribou conservation. Metapopulation is a system of geographically or ecologically isolated populations whereby there is sufficient exchange among populations to have a significant impact on either the demography or genetic profile of each component population (Hanski and Gilpin, 1997).

In western North America, throughout the large mainland area west of Hudson Bay, caribou herd ranges overlap in a continuum of varying caribou abundance; small-scale exchanges may occur between neighbouring herds. The ranges of the migratory and sedentary caribou ecotypes also overlap, a fact that requires study of the ecological factors involved, and more importantly, of the long-term conservation effects on the fragile sedentary ecotype. East of Hudson Bay, on the Québec-Labrador Peninsula, a similar caribou population continuum exists but on a smaller spatial scale where different ecotypes overlap.

Based on preliminary analysis, it seems that emigration–immigration (EI) played an important role in the Québec-Labrador migratory caribou herd dynamics following two different processes. EI must then be clearly defined and distinguished from short-term winter mixing that does not affect herd demography. One must remember that most of the census techniques for migratory caribou are performed on the calving or post-calving range. Caribou from two overlapping migratory herds that mix on the rutting or the winter range and later move to or near their neighbouring herd's calving ground, would represent the first type of EI process. The mixing may begin on the winter range, but more often it seems to start on the rutting range. The calving ground is the key element in the EI definition. Female caribou that spend winter with another herd are not emigrants as long as they come back to their former calving ground during calving. The role of males is not clear in this emigration process that maybe driven mostly by females.

Secondly, EI can also occur through small-scale annual changes to calving ground locations involving gradual overlapping shifts followed by fragmentation. The final result of this spatial trend seems to be binary and could lead either to the creation of a new herd or to the permanent abandonment of a calving ground. In the 1970s, the GRH used two major (Ford River and Champdore Lake) and one minor calving ground near Harp Lake in Labrador. We speculate that this may have been a slow process of calving ground shift and fragmentation into three subunits. In early 1970s, less than one thousand females were located in June on the Harp Lake calving ground, but after 1980 no calving has been reported in the area. The Lac Champdore calving ground, located 250 km southwest of the Ford River, was progressively abandoned from 1975 to 1979, probably because of natural flooding (Juniper, I., pers. comm.). At the same period, the Leaf River Herd (LRH) was discovered when Le Henaff (1976) observed 21,000 calving caribou in June 1975 about 500 km west of the

Ford River calving ground. In 1983, Le Henaff (1983) estimated that 33,000 females were present on the LRH calving ground. The herd size was later estimated at 106,000 caribou in 1986 and at about 260,000 in 1991 (Québec Gov., unpubl. data). Based on the 2001 post-calving photo-census, the LRH is now larger than the GRH. Together, these two herds still add up to about one million caribou (Québec Gov. & Newfoundland & Lab. Gov., unpubl. data). Emigration from the GRH through calving ground shifting and fragmentation may have led to the creation of the LRH in the 1970s. Throughout history in Québec-Labrador, some observations suggest that caribou herds fit in the source-sink metapopulation concept, whereby one source population, typically large in size or occupying prime habitat (i.e. the GRH), produces an excess of individuals that disperse to smaller sink populations in less than optimal habitats (i.e. the LRH). Little is known about the genetics of Québec-Labrador caribou, and it should be investigated further to understand better the gene flow between the groups and the herds as well as within the supposed metapopulation.

Satellite monitoring data have recently confirmed emigration of caribou from the GRH to the LRH involving the first process described earlier (mixing on the rutting, winter, and calving ranges). Space use data also confirmed that after a fourfold increase in annual range size, from 1971 to 1993, the GRH contracted its range by 40% from 1994 to 2001. The LRH calving ground, first reported in 1975, gradually shifted north, so that by 1992 it had moved 400 km, from low altitude landscape south of the treeline to a 530-metre-high tundra plateau-habitat. Since 1993, this herd has used the same area for calving with little annual variability. As revealed by Inuit traditional knowledge, the current (1993 to 2002) LRH calving ground was used in the late 1880s when caribou were abundant. Gunn and Miller (1986) also reported that the Beverly Herd calving ground shifted to the northeast between 1957 and 1982. Few calving ground shifting and fragmentation leading to the creation of a new herd have been reported for migratory caribou.

Bergerud (1988) first suggested avoiding the caribou subspecies distinction between woodland and barren ground proposed by Banfield (1961). He suggested instead to use different ecotypes, sedentary and migratory, to discriminate between populations. Bergerud (1996) defined sedentary animals as those who stay south of the treeline and disperse or space out from each other at calving. On the other hand, migratory caribou move north of the treeline and aggregate at calving. According to Bergerud (1996), migratory caribou move as far as possible from the treeline where wolf densities are higher, but at the same time they select areas for calving where their calves can remain cryptic on brown substrate (<75% snow cover at calving). Later, Mallory and Hillis (1998) retained Bergerud's ecotype distinction and described two other ecotypes: insular and montane. Unfortunately, they used for their ecotypes the same designation, barren-ground and woodland, formerly proposed by Banfield (1961) for the subspecies. Confusing designation of subspecies and ecotypes can lead to misinterpretation like in this sentence from the abstract of their paper: "in North America, the woodland caribou subspecies (genotype) forms the largest barren-ground ecotype herd in the world and is not endangered nor at risk". The authors were referring to the 775,000 GRH caribou having accepted Banfield’s (1961) taxonomic analysis which stated that all caribou in Québec and Labrador belonged to the “woodland subspecies (genotype)”.

In his extensive revision of caribou taxonomy, Banfield (1961) recognized six barren-ground and three woodland subspecies. Most of his analysis was based on skull measurements. Variation in body size and sexual dimorphism are highly dependent on environmental conditions and some differences observed by Banfield (1961) may be more range-related than genotypic. Body size of GRH caribou changed as herd size has increased from the early population growth period (1960s) to the latest peak (late 1980s). Lower jaw length decreased by 1.3 cm for females and 1.5 cm for males between the period 1963 to 1965 (Bergerud 1967) and 1986 (females) to 1987 (males) (Couturier *et al.* 1989). Banfield (1961) collected his skull samples in the same period when Bergerud (1967) collected his lower jaw samples. Bergerud (1967) presented data on lower jaw lengths suggesting that the GRH caribou from both sexes were larger than those from the Mealy Mountains group, a small endangered sedentary caribou group living at the southern edge of the GRH range. To the contrary, caribou users and biologists now believe that GRH caribou are clearly smaller than sedentary caribou living in their overlapping range (Québec Gov., Newfoundland & Lab. Gov., unpubl. data). These phenotypic variations suggest that the Banfield (1961) subspecies status based on skull measurements for Québec-Labrador caribou is invalid. Another skull study conducted in the mid-1980s could have provided different outcomes given that lower jaw of the GRH, and therefore the skull, had decreased in size by then.

As a hypothesis to be tested, we suggest, like Allen (1914), Couturier *et al.* (1990), and Geist (1998), that our migratory ecotype caribou living in high densities between the tundra and the taiga could be considered a distinct subspecies: the Québec-Labrador caribou, *Rangifer tarandus caboti* (scientific name first suggested by Allen 1914). Some genetic evidences suggest that the GRH and the LRH are different from other sedentary or montane populations or groups living in southern Québec. Røed *et al.* (1991) have shown from transfer in variation that the GRH and the LRH are close genetically but that they are different from the Gaspé population, a montane ecotype found south of the St. Lawrence River that has been isolated for many decades. More recently, Courtois *et al.* (2001) studied microsatellite DNA variation in the GRH, the Gaspé population and five sedentary groups south of the treeline. They suggested that the three ecotypes found in Québec are genetically distinct with the largest genetic distance (and also geographic distance) recorded between the migratory ecotype (GRH) and the montane ecotype (Gaspé).

Clarification of the caribou taxonomic status must continue and new genetic studies are needed. Nevertheless, an unequivocal classification of the Québec-Labrador caribou should also include along with the genetic methods, an analysis of genotypic criteria like the coat colouration method proposed by Geist (1998), the study of life-history traits, body measurements, distribution, and range use (also suggested by Courtois *et al.*, 2001).

We should continue to use the ecotype nomenclature, but we suggest that naming conventions be reviewed. The four ecotypes described by Mallory and Hillis (1998) should be used, with some modifications. Instead of “barren-ground” and “woodland”, we suggest using “migratory–tundra” and “sedentary–boreal”, respectively (Bergerud, 1988; 1996). Two other ecotypes, insular and montane, should continue to be used to describe the ecological conditions in which many caribou are also found. If needed, sub-ecotype could be defined for montane caribou with various ecological constraints and foraging behaviour. As some populations in the High Arctic do not fit the previous ecotype definitions, we suggest adding one specific ecotype for the *Rangifer* populations living in the Arctic Archipelago.

The herd or population concept (sensu Caughley, 1977) does not apply very well to the sedentary–boreal groups where caribou show low densities without clear evidence of population cohesiveness. Radio-collaring telemetry data from Labrador suggest that the separation between populations formerly known as Lac Joseph, Red Wine, and Mealy Mountains are very small or maybe nonexistent. Radio-collared caribou movements confirm exchanges during the rut in winter and during the spring (Newfoundland & Lab. Gov., unpubl. data). Caribou distribution in the boreal forest may have been more continuous one century ago, but recent anthropogenic disturbances in the sedentary–boreal ecotype range has led to habitat fragmentation and thus “insularization”, isolation, and perhaps disappearance of many of these caribou groups.

Sedentary–boreal groups do not often fulfill population concept requirements permitting the use of population dynamics tools. Many of these sedentary–boreal groups are simply breeding units that may be closed or not. The failure to recognize true population status probably explains why the first genetic study results on this ecotype has been difficult to interpret. In Québec-Labrador, the sedentary–boreal ecotype may be functioning as a metapopulation of local breeding units. Courtois *et al.* (2001) have shown that the different populations of sedentary-boreal ecotypes in southern Québec are very close genetically and behave like a metapopulation. They suggested maintaining exchanges between local breeding units of the metapopulation to stabilize their precarious status.

The herd concept for the migratory–tundra ecotype seems to fit correctly the animal population definition and is therefore valid for management decisions following population dynamic analysis. “Herd” and “population” are then synonymous. The herd identification convention based on calving ground use is still appropriate for management purposes. Although migratory–tundra caribou herds are clearly distinct units, managers could perhaps learn more about the herd or population ecology by looking at them at a metapopulation scale.

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DEFINING HERDS WITHIN THE RANGE OF ‘BLUENOSE’ BARREN-GROUND CARIBOU IN CANADA’S NORTHWEST TERRITORIES AND NUNAVUT

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ABSTRACT

Barren-ground caribou (*Rangifer tarandus groenlandicus*) that occupy the northern portion of the Northwest Territories and western Nunavut have been considered to be part of the Bluenose herd. Analyses of distribution information documented during surveys done between 1966 and 1993 using a computerized geographic information system (GIS) indicated that there were three distinct calving and two rutting areas within that range. Caribou herds have been identified based on their fidelity to calving grounds. As a result we hypothesized that there were two, and possibly three, herds within this range. The results of satellite tracking and genetic studies conducted between 1996 and 2003 support the hypothesis that there are three herds that use different seasonal ranges

(calving and especially rutting) and are genetically distinct. For convenience we refer to these as the Cape Bathurst, Bluenose-West, and Bluenose-East herds. They are genetically different from Porcupine and Bathurst caribou. The subspecific designation of Porcupine caribou should be reconsidered.

GENETIC DIVERSITY AND HISTORY OF PEARY CARIBOU (*RANGIFER TARANDUS*) IN NORTH AMERICA

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ABSTRACT

Prompted in part by a decline in populations of Peary caribou (classified in 1991 as "Endangered"), we needed to determine the evolutionary history and biogeography of North American caribou using data derived from sequencing mitochondrial DNA (mtDNA). Current classification recognizes four subspecies of caribou in North America: *Rangifer tarandus caribou*, *R. t. granti*, *R. t. groenlandicus*, and *R. t. pearyi.* These subspecies are distinguished morphologically, behaviourally, and ecologically. We sequenced 184 *Rangifer* from 16 localities in Alaska, the Canadian arctic, southern Yukon, Ontario, Quebec, and imported sequences for six Newfoundland caribou from GenBank. The data set was reduced to 103 haplotypes. Phylogenetic analyses of the haplotypes indicate that caribou from Ontario, Quebec, and Newfoundland are closely allied to each other and notably distinct from remaining populations. Analysis of molecular variance indicates that subspecific designations traditionally used within *Rangifer* do not best represent the pattern of genetic variation observed, and that the woodland caribou, *R. t. caribou*, as defined by Banfield (1961), is not monophyletic. Seventeen samples were reduced to thirteen with pooling. A coalescent analysis was used to estimate divergence times for population pairs. The coalescent analysis indicates four distinct groups of caribou: Alaska and the Yukon, central arctic, southeastern North America, and Bathurst Island. The Yukon population was recently derived from Alaska. Populations from the central arctic appear to be derived from a Banks Island refugium. Populations in Ontario, Quebec, and Newfoundland constitute an old lineage, separated from most other caribou by 80,000 years. There is strong evidence for a second old lineage in the High Arctic, represented in this study by animals from Bathurst Island. The current designation of subspecies of caribou does not reflect phylogenetic history but is the result of post-Wisconsin natural selection on the phenotype.

INTRODUCTION

Peary caribou (*R. t. pearyi*) of the Queen Elizabeth Islands in the Canadian High Arctic have declined by some 90% since the early 1960s (Miller 1990, Gunn *et al.* 2000). This decline led the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) to classify the Peary caribou of the High Arctic Islands (Eglinton, Melville, Prince Patrick, Banks, and Bathurst Islands) as “Endangered” in 1991, and those of Victoria Island as “Threatened” in 1994. To draft a recovery plan for the Peary caribou, we needed to determine whether *R. t. pearyi* is phylogenetically distinct from other subspecies of *Rangifer* and to clarify the genetic relationships of the populations of Peary caribou.

The purpose of this study was to investigate the genetic variability and evolution of maternal lineages of caribou in North America using nucleotide sequence analysis of the mtDNA control region. Mitochondrial DNA analysis is a powerful technique for studies of animal evolution. Mitochondrial DNA is maternally inherited and evolves at a relatively rapid rate (compared to most nuclear DNA sequences) and is therefore useful as a genetic marker for studies of matrilineal gene flow, the biogeographic history of a species, and the dynamics of hybrid zones (Moritz *et al.* 1987). It has been used in numerous studies of intraspecific variation in mammals (Cronin, 1992; Stewart and Baker, 1997; Walpole *et al.*, 1997; Lee *et al.*, 1996; Gravlund *et al.*, 1998; Flagstad and Røed, 2003).

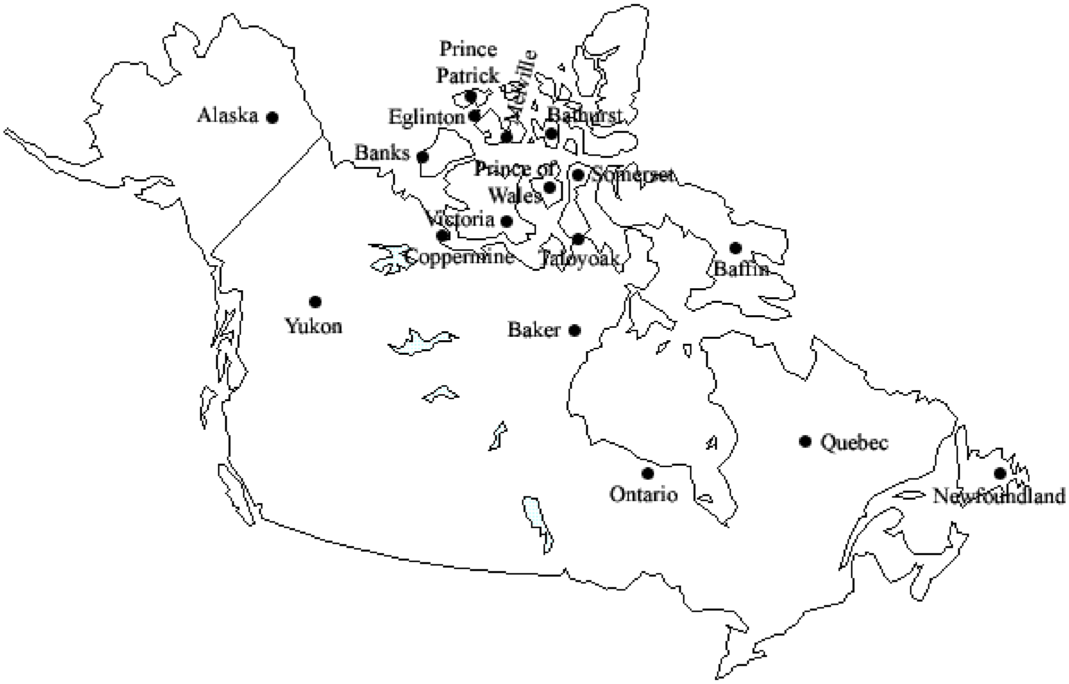

Figure 1. Sample sites of North American caribou (*Rangifer tarandus*) used in this study.

MATERIALS AND METHODS

Samples

In the late 1980s, we opportunistically collected solid tissue samples (muscle or liver) from 200 caribou from 16 sites in North America. Sampling sites encompass most of the North American caribou range and include four of the currently recognized subspecies (Figure 1; and see acknowledgments). We also used sequences of six caribou from Newfoundland and one out-group sample of *Alces alces* obtained from GenBank (accession nos. AF096426-30, AF096440, and U12866). Sample sites of caribou groups (the term population will be used in this paper to refer to the 17 sites) are given in Figure 1, and sample sizes and associated subspecies designations are indicated in Table 1.

Table 1. Collection localities of *Rangifer tarandus* with sample sizes, abbreviations and subspecies designations.

Locality	***N***	**Abbr.**	**Subspecies***
Watson Lake, YT	20	YUKN	*R. t. caribou*
Sachs Harbour area, Banks Island. NT	30	BNKS	*R. t. pearyi*
Prince Patrick Island , NT	3	PPAT	*R. t. pearyi*
Eglinton Island, NT	6	EGLI	*R. t. pearyi*
Coppermine area (Bathurst herd). NT	33	COPP	*R. t. groenlandicus*
Melville Island, NT/NU	4	MELV	*R. t. pearyi*
Cambridge Bay, Victoria Island, NU	16	VICT	*R. tarandus* Dolphin Union Herd
Bathurst Island, NU	10	BATH	*R. t. pearyi*
Prince of Wales Island, NU	7	PWAL	*R. t. pearyi*
Baker Lake, NU	7	BAKE	*R. t. groenlandicus*
Somerset Island, NU	2	SOME	*R. t. pearyi*
Taloyoak, NU	17	TALY	*R. t. groenlandicus*
120 km. E Peawanuck,ON	6	ONTA	*R. t. caribou*
Clearwater/Netilling Fiord, NU	6	BAFF	*R. t. groenlandicus*
Lake Deberg, QC	3	QUEB	*R. t. caribou*
Porcupine Herd, AL	5	ALSK	*R. t. granti*
Newfoundland	6	NFLD	*R. t. caribou*

* Subspecies names based on Banfield, 1961 and Manning, 1960

PCR Amplification and Sequencing of mtDNA

Total DNA was isolated from 200 samples of caribou. DNA was prepared using standard proteinase K digestion/phenol extraction (Sambrook *et al.*, 1989). Primers used for PCR and sequencing are given in Table 2. Caribou mtDNA control regions were amplified as single fragments using the versatile primers H00651 and L15926 (Kocher *et al.*, 1989). These primers anneal to sites in the 12S rRNA and tRNA^{thr} genes, respectively, and amplify the intervening control region. Amplified fragments were excised from 2% agarose gels following electrophoresis and purified by binding to silica beads (Geneclean®, Bio101). In some cases fragments were purified by digesting agarose slices with Gelase® (Epicentre Biotechnologies) followed by precipitation in isopropanol. Two internal control region primers were designed using caribou sequence as a reference. All sequences were generated manually using double-stranded sequencing with Sequenase® (United States Biochemical). Primers L15926, L234 and L533 were used as sequencing primers; in most instances, sufficient PCR product was generated in a single amplification for three sequencing reactions. Approximately 924 base pairs (bp) of control region sequence was obtained for each animal plus 66 bp from the flanking genes.

This analysis used 564 bp in order to include the Alaska samples that did not sequence readily. Sequence was entered and aligned in the sequence editor Clustal X (Version 1.81, Thompson *et al.*, 1997).

Table 2. Primers used for PCR and sequencing of caribou control regions. H00651 and L15926 are from Kocher *et al.* (1989); numbers refer to positions of the 3' bases in the human mtDNA sequence. Primers 234 and 533 were designed using caribou control region sequence as reference. The numbers refer to positions of the 3' bases in the caribou control region sequence.

Primer	**Sequence**
H00651	5'-TAACTGCAGAAGGCTAGGACCAAACCT-3’
L15926	5'-TCAAAGCTTACACCAGTCTTGTAAACC-3’
L234	5'-AGTACATTAAATTATATGCCCCATGC-3’
L533	TCCTCTTAAATAAGACATCTCGATG-3’

Data Analysis

We used PAUP* software, Version 4.0 beta (Swofford 2001) to construct neighbour-joining trees (unweighted pair group method using arithmetic averages and maximum likelihood trees) to select haplotypes and reduce the data set to unique haplotypes only. We used PAUP to further reduce the haplotypes according to phylogenetic relationships. We analyzed the sequence data using the neighbour-joining method with pairwise deletion of missing sites (Saitou and Nei, 1987).

Heterogeneity in substitution rates among branches was modeled by using a gamma distribution. The gamma distribution was estimated using Modeltest, Version 3.06 (Posada and Crandall, 1998), which indicated the HKY + I + G model of substitution (gamma value) best fits the data. The hierarchical components of mtDNA variation were computed using Arlequin Version 2.0 software, Analysis of Molecular Variance (AMOVA) (Excoffier *et al.*, 1992). This program calculates the amount of total molecular variance contained within and among populations and between sub-specific groups. This procedure was used to evaluate whether the subspecific designations traditionally used within *Rangifer* best represent the pattern of genetic variation observed.

We used a program that simultaneously estimates divergence times and migration rates between two populations (MDIV) developed by Nielsen and Wakeley (2001) to obtain maximum-likelihood estimations of divergence times between caribou populations and for estimating the relative effects of migration and isolation on genetic diversity in pairs of populations using DNA sequence data. Most models of population genetics assume that populations have been exchanging migrants at a constant rate (equilibrium migration) or that populations are descended from a common ancestral population and have since diverged without gene flow (isolation or historical association). MDIV uses a coalescent framework to estimate maximum-likelihood estimators of the divergence times ($t = T \times N_e \times 2.5$, where T = divergence time and N_e = effective population size), theta, θ (mutation parameter), for population pairs, non-equilibrium-based estimates of migration rates between population pairs (M) and the time to most recent common ancestor (TMRCA) of population pairs. We reduced the seventeen samples to thirteen with pooling of geographically proximate populations because some locality samples were too small (Eglinton, Prince Patrick, and Melville [EGLI], Ontario and Quebec [ONTA], and Prince of Wales and Somerset [PWAL]). We used the HKY (Hasegawa *et al.*, 1985) model that takes into account the possibility of multiple hits at each nucleotide site, differences in nucleotide frequencies, and the presence of a transition/transversion bias. The method estimates the likelihood function of the demographic parameters θ, T, and M, the number of migrants per generation between two populations. We calculated from the estimated θ_{ML} using the formula $N_e = \theta_{ML} \div 2\mu$, where μ = 0.39/site/1 million years per generation. We then used N_e values to convert T values, scaled by N_e and the assumed generation rate (7.7 years). Flagstad and Røed (2003) used a substitution rate of 0.16% based on humans (George and Ryder, 1986; Vigilant *et al.*, 1991). Sigurdardottir *et al.* (2000) estimate a much faster substitution rate of 0.32% but for this study we have used the former, more conservative, substitution rate. This methodology considers the importance of gene flow in determining the genetic structure of caribou populations and the construction of population genetics to better fit the demographic history of the species. Finally, we used the program NTSYSpc (Rohlf, 2000) to construct a tree (single linkage clustering method) to summarize the divergence history using distances between populations based on estimated divergence time ($t = T \times N_e \times 7.7$) among the thirteen groups of caribou.

RESULTS

We sequenced approximately 1,000 base pairs for 184 caribou. However, because we had problems sequencing the Alaska samples, we used 564 base pairs of mtDNA sequenced from the 5' end of an area of the control region that is most variable. There were 103 haplotypes among the 17 geographic populations of *Rangifer*. Comparison of the haplotypes indicated 67 variable nucleotide positions. Nucleotide composition of the sequenced region was: C, 22.5%; T, 31.4%; A, 32.3%; and G, 13.8%. There were 58 transitions and nine transversions (6.44 transition/transversion ratio). The pattern of variation within the control region is similar to that found in many other vertebrate species – a highly conserved central block with the ends being more variable. Most of the 103 haplotypes were unique to single animals. Twenty-two haplotypes (24%) were shared among two or more individuals (Appendix 1). The most frequent haplotype, haplotype 65, represented 26% of the haplotyped individuals including animals from the Arctic Islands (Banks, Prince of Wales, Victoria, Somerset, Melville, and Eglinton) as well as the Boothia Peninsula and a single individual from Coppermine on the mainland. The next most frequent haplotype, 86, represented 19% of individuals haplotyped and were from Victoria, Prince of Wales, Eglinton, and Somerset Islands, Boothia Peninsula, and five individuals from Coppermine. Haplotype 102 was found in 10% of individuals and represents individuals from Banks, Eglinton, Melville, Prince Patrick, and Victoria Islands and one individual from Coppermine. The distribution of haplotypes over localities is given in Appendix 1. A neighbour-joining (NJ) tree of haplotypes gave little phylogeographic information and is not shown here.

The AMOVA results indicate that there is virtually no relationship between subspecies designations and mtDNA differentiation. When localities were ordered by subspecies (*pearyi*, *groenlandicus*, *granti*, *and caribou*), among-group variance explained only 7.62% of the total variance. When seventeen locales were analyzed, among-group variance explained 19.32% of the total variance. When the seventeen locales were divided into two groups – eastern Canada (Ontario, Quebec, and Newfoundland) and northern North America – among-group variance explained 38.53% of the total variance.

Although computationally intensive, we used thirteen populations of *Rangifer* to calculate the maximum-likelihood estimators of the divergence times ($t = T \times N_e \times 7.7$) (Table 3), the mutation parameter θ (Table 4), and the migration rate M (Table 5). The modes of divergence times among these populations range from just a few decades to greater than 100,000 years; upper confidence limits range from about 2,400 to 270,000 years. Population divergence time is greatest between the eastern populations (Ontario/Quebec and Newfoundland) and the Arctic populations whose times range from 25,000 to more than 100,000 years. Within the Arctic populations, population divergence times are recent among the central Arctic populations (Prince of Wales, Victoria, Eglinton, and Banks Islands, Coppermine, and Taloyoak) but Bathurst Island caribou appear to have diverged at a much earlier date. The two eastern populations, Ontario/Quebec and Newfoundland, have diverged recently from each other. The Yukon population has diverged most recently from Alaska and shows earlier divergence from the central arctic populations.

Table 3. Caribou genetic coalescent analysis. Values represent computed time (t) to coalescence, based on an assumed mutation rate of 0.000668 and an assumed generation time of 7.7 years.

	ALAS	BAFF	BAKE	BANK	BATH	COPP	EGLI	NEWF	ONTA	PWAL	TALY	VICT	YUKO
ALAS	0												
BAFF	20844	0											
BAKE	19834	15535	0										
BANK	29697	11388	21987	0									
BATH	61875	6735	11309	50280	0								
COPP	18756	144	22467	2205	47808	0							
EGLI	14518	12821	23044	6325	49522	1420	0						
NEWF	72184	76757	82900	46669	79200	102899	67992	0					
ONTA	84406	69437	82525	29484	61985	91415	25052	81	0				
PWAL	7108	5437	2511	7560	37499	905	3404	78301	80761	0			
TALY	17419	3621	17823	17963	41305	1934	1511	54848	78823	33	0		
VICT	24460	11380	10245	2582	49625	1071	1240	90959	34089	1379	8536	0	
YUKO	4590	23410	17766	26366	57503	19563	22515	95000	48164	15325	27084	26153	0

Mutation rates differ within Arctic populations (Table 4), being high between Alaska, Yukon, and the remaining populations except Prince of Wales, and low between Prince of Wales and all other populations.

Table 4. Estimates of mutation parameter (θ) between population pairs of *Rangifer*.

	ALAS	BAFF	BAKE	BANK	BATH	COPP	EGLI	NEWF	ONTA	PWAL	TALY	VICT	YUKO
ALAS	0.000												
BAFF	11.158	0.000											
BAKE	17.200	10.363	0.000										
BANK	12.119	9.273	11.917	0.000									
BATH	11.249	5.310	9.430	9.562	0.000								
COPP	17.489	12.520	14.540	12.749	13.120	0.000							
EGLI	10.320	7.220	12.490	7.836	7.738	12.310	0.000						
NEWF	18.092	11.802	19.430	12.045	11.641	20.373	10.740	0.000					
ONTA	18.118	12.314	18.710	11.675	10.970	18.653	10.058	14.070	0.000				
PWAL	5.314	3.833	8.540	6.070	4.262	9.810	4.072	7.850	8.541	0.000			
TALY	12.433	8.263	12.880	10.050	10.176	12.900	7.707	12.890	13.020	5.670	0.000		
VICT	13.597	8.657	12.340	7.720	8.340	10.930	8.269	13.600	13.561	5.980	9.870	0.000	
YUKO	16.586	15.616	22.010	15.243	16.138	19.500	15.496	22.387	21.310	13.290	18.790	16.435	0.000

The migration rate (*M*; Table 5) is high between Coppermine and other central Arctic populations, namely Baffin, Banks, Eglinton, Prince of Wales, and Victoria Islands, and Taloyoak. It is high between Taloyoak and Prince of Wales and Eglinton Islands, high between Victoria and Prince of Wales Islands, high between Newfoundland and Ontario/Quebec, high between Alaska and Yukon, and low between Bathurst Island, Alaska, Yukon, Baker Lake, and most other populations. The migration rate between Alaska and Yukon is relatively high whereas migration rates between Alaska and Yukon and the central Arctic populations are low, giving the different divergence times. The Alaska population and the eastern Canada populations are greatly divergent from the Canadian arctic populations and from each other.

Table 5. Estimates of migration rates (*M*) between population pairs of *Rangifer*.

	ALAS	BAFF	BAKE	BANK	BATH	COPP	EGLI	NEWF	ONTA	PWAL	TALY	VICT	YUKO
ALAS	0.0000												
BAFF	1.610	0.0000											
BAKE	1.440	1.680	0.0000										
BANK	0.032	1.200	0.588	0.0000									
BATH	0.015	0.800	1.720	0.024	0.0000								
COPP	0.084	11.400	2.190	5.100	0.205	0.0000							
EGLI	0.627	1.470	0.050	1.200	0.020	9.720	0.0000						
NEWF	0.210	0.250	0.170	0.180	0.140	0.245	0.270	0.0000					
ONTA	0.300	0.290	0.350	0.312	0.252	0.354	0.366	8.040	0.0000				
PWAL	1.110	0.840	0.690	1.440	0.012	5.920	2.400	0.174	0.312	0.0000			
TALY	0.600	4.480	1.400	3.900	0.010	5.600	5.566	0.336	0.510	14.650	0.0000		
VICT	0.532	1.350	1.160	3.600	0.204	6.600	2.820	0.165	0.264	3.660	1.400	0.0000	
YUKO	4.960	1.630	1.320	0.720	0.368	1.116	0.500	0.280	0.500	1.400	0.040	1.120	0.0000

The single linkage clustering of distance values (Sneath and Sokal, 1973) between and among caribou groups based on estimated divergence times (Figure 2) reveals three distinct clusters. Caribou from eastern Canada are the most divergent. The second most divergent group is a cluster representing Alaska and Yukon. The third cluster encompasses the remaining populations with Bathurst Island the most divergent population. Alaska and Yukon are separate from the central Arctic localities which comprise two groups: Coppermine, Baffin Island, Taloyoak, and Prince of Wales Island in one cluster and Victoria Island, Eglinton Island, Banks Island, and Baker Lake in a following chain. Bathurst Island is part of this chain but highly differentiated from the other populations.

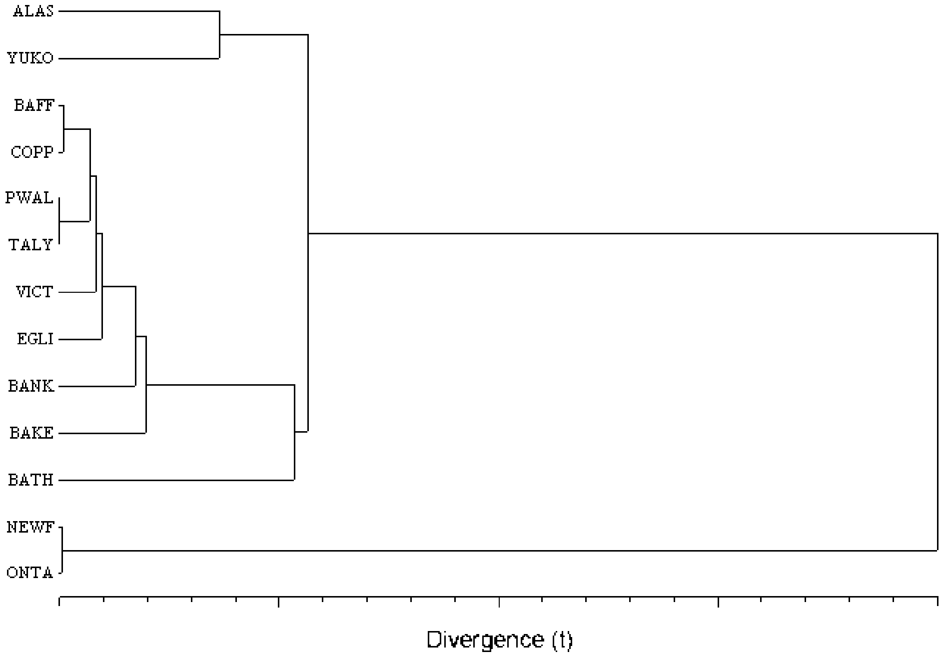

Figure 2. Single linkage cluster diagram of estimated divergence time (t) among thirteen samples of *Rangifer tarandus*.

DISCUSSION

Our results using coalescent analysis of sequences of the mtDNA control region of 190 caribou reveal: the complete isolation of eastern Canada populations from the remaining populations of caribou in Alaska, Yukon, and the Canadian Arctic; differentiation of the Alaska and Yukon populations from the central Arctic populations; and isolation of the Bathurst Island caribou from central Arctic populations. This pattern of variation can be explained by differentiation that has taken place during last 100,000 years as a result of the last glaciation. The most recent glaciation in North America – the Wisconsin – began approximately 70,000 years before present (ybp) and climaxed 18,000 to 20,000 ybp (Pielou, 1991). While much of northern North America was covered by ice during the Wisconsin, there were several refugial areas where Arctic animals and plants survived. Beringia – defined as the area encompassing eastern Siberia, the Bering land bridge, Alaska, and Yukon – is the largest and best known with a strong fossil record (Pielou, 1991). However, there is also fossil evidence of caribou in refugia in northeastern Greenland, in areas south of the Cordilleran and Laurentide Ice Sheet, and evidence of a refugium on Banks Island (Kurtén and Anderson, 1980; Harington, 2003). Isolation in these refugia during the Wisconsin probably produced the patterns found in these data. The estimated divergence times vary from more than 100,000 years of separation time between northern North America and eastern Canada to less than 100 years separating Newfoundland from Ontario and Quebec.

The multiplicity of haplotypes and the apparent lack of phylogeographic structuring within the caribou haplotypes supports Flagstad and Røed's (2003) suggestion that the haplotype distributions in *Rangifer* result from historical division and recolonization of the species rather than from present day relationships. The widespread distribution of several haplotypes found in the central Arctic suggests substantial recolonization and historical gene flow among the populations of caribou in the central Arctic Islands and nearby mainland. Alternatively, it is possible that considerable mixing occurred after the Wisconsin, but given the estimated divergence times (Table 3), this seems unlikely. Genetic studies using microsatellite DNA analyses have detected only low levels of gene flow among the caribou populations in the central Arctic (Zittlau, these proceedings; Zittlau, 2004). As microsatellite DNA has a more rapid mutation rate than mtDNA (Schlötterer, 2000), these genetic differences reflect a more recent time scale (<10,000 years) (Paetkau *et al.*, 1997). Thus, major gene flow and significant dispersal events have not likely occurred recently.

As summarized by Manning (1960), and Banfield (1961; 1974), there are four subspecies of caribou in North America, which represent three ecological forms. Occurring south of the tundra in the boreal forest are: the woodland caribou (*Rangifer t. caribou*), a large dark subspecies with short, heavy antlers; the tundra caribou, a paler subspecies with larger, more slender antlers, represented by *Rangifer t. groenlandicus* and *R. t. granti*; and the small caribou of the High Arctic, the Peary caribou (*Rangifer t. pearyi*). However, the observed mtDNA differentiation is not consistent with the currently accepted subspecies of caribou or with the three ecological types. Dueck (1998), Flagstad and Røed (2003), and Cronin *et al.* (2005) also failed to find a relationship between mtDNA phylogeography and subspecies designation. The Banfield (1961) and Macpherson (1965) theory that morphological variation as exemplified by subspecies description developed in allopatry during the Wisconsin is not substantiated by the results of this study.

The ecological differentiation is likely caused by post-Wisconsin natural selection. Evidence supporting this idea comes from the study of Gravlund *et al.* (1998) who investigated the origin of three small-bodied, High Arctic subspecies: *R. t. peary* (the Canadian archipelago); *R. t. eogroenlandicus* (east Greenland, extinct since 1900); and *R. t. platyrhynchus* (Svalbard). They concluded that these three subspecies were polyphyletic and that the small-bodied High Arctic caribou represent ecotypes that evolved convergently in similar High Arctic environments.

However, allopatric isolation does explain variation in divergence times between populations of caribou. Based on the coalescent analysis, we can say that at the end of the Wisconsin, caribou recolonised Canada from at least four refugial areas: Beringia, Banks Island, the High Arctic, and the southeast. The data are consistent with the eastern Canada caribou originating in a southern refugium and their subsequent recolonization of eastern North America. The patterning of vegetation south of the ice sheets likely influenced the distribution of caribou during the Wisconsin (Gunn, these proceedings) and this distribution in turn would have influenced the dispersing caribou as they followed the retreating ice sheets. Beringia is a proven refugial area for caribou (Pielou, 1991). Banks Island supported both muskoxen (*Ovibos moschatus*) and mammoth (*Mammuthus primigenius*) in the mid-Wisconsin (Harington, 1986; as summarized in Harrington, 2003) and therefore likely a refugium for caribou also. Caribou on Banks Island would have been isolated from Beringian caribou about 30,000 years ago. Banks Island was isolated from Beringia to the south and Prince Patrick, Eglinton, and Melville Islands to the north until 12,000 ybp by large ice shelves (Dyke and Prest, 1986). As the Laurentian Ice Sheet receded from around Banks Island, caribou were able to colonize Prince Patrick, Eglinton, and Melville Islands to the north (approx 6,300 ybp) and Victoria Island to the east (approx. 3,000 ybp), proceeding to Coppermine on the mainland (approx. 3,000 ybp). As the ice sheet continued to recede, Prince of Wales and Somerset

Islands were also colonized from Victoria Island (approx 1,500 ybp). Still using divergence times (Table 3) it appears that Taloyoak and Baffin were colonized by animals moving east along the mainland. The coalescent analysis supports the idea of a High Arctic refugium in the north during the Wisconsin as represented by the caribou sampled from Bathurst Island. Haplotypes of animals from Bathurst Island are unique and not shared with any other geographic population that we sampled. We assume that Bathurst Island caribou originated in a refugium to the north but we were unable to sample Peary caribou from the eastern High Arctic Islands. Figure 3 summarizes the hypothesized the routes of recolonization from the four refugia into Canada. Supporting evidence for the Wisconsin isolation of animals sampled from Bathurst Island comes from Federov and Stenseth (2002), who conclude that there is evidence for localized High Arctic refugia based on mtDNA variation in the collared lemming, *Dicrostonyx groenlandicus*.

Figure 3. Hypothesized routes of post-Wisconsin recolonization of *Rangifer tarandus* from Wisconsin refugia.

The current study provides evidence of long divergence times of caribou populations from eastern Canada, followed by Bathurst Island, then Alaska and Yukon, and finally the central Arctic populations the most recently derived. Caribou were present in North America as early as the Aftonian interglacial Kansan glacial periods of the middle Pleistocene (Kurtén and Anderson, 1980) in Beringia. Caribou remains have been reported from Illinoian Stage deposits near Fairbanks but the majority of fossils have been found in Wisconsin and Holocene deposits in Alaska and Yukon as well as some found south of the Wisconsin ice in western, central, and eastern North America (Kurtén and Anderson, 1980; Harington, 2003). The relative divergence times of the four groups suggest the following scenario: populations of *Rangifer* survived in southern refugia during the Wisconsin glaciation and the herds of caribou in eastern Canada today are derived from a southeastern refugium. There was a High Arctic refugium during the Wisconsin from which the Bathurst Island population is likely derived – perhaps northern Ellesmere Island. A second northern refugium, Banks Island, was the source of caribou of the central Arctic and the caribou of the central Arctic have not been isolated from each other. Woodland caribou of the southern Yukon are recently derived from Beringia, the largest and best known refugium of the Wisconsin.

Conservation implications for Peary Caribou

This study was undertaken to assess whether or not Peary caribou of the Canadian High Arctic constitute a monophyletic subspecies that could be labelled as an endangered subspecies. Our analyses of mtDNA suggest that Peary caribou is a High Arctic ecotype that has evolved within the last ten thousand years and does not represent a monophyletic lineage. The apparent isolation of Bathurst Island is surprising and of potential concern. However, the relationship of Peary caribou on Bathurst Island cannot be considered in isolation of the eastern islands of Devon, Ellesmere, and Axel Heiberg Islands as we did not have samples from those islands. Peary caribou do not share a more recent common ancestor with each other than with individuals outside the "subspecies". Even individuals from a single island such as Eglinton Island are not monophyletic. The process of population subdivision and speciation is known to produce polyphyletic relationships that progress over time to paraphyletic and then to monophyletic relationships (Crandall *et al.*, 2000). The simplest explanation is that there has been ecological and morphological divergence within *Rangifer tarandus* that is not reflected in the genetic data produced in this study.

Crandall *et al.* (2000) recommend that management should preserve adaptive diversity and evolutionary processes across the geographic range of a species and to preserve the natural network of genetic connections between populations rather than just the distinct populations within that network. This ensures that the processes that maintain adaptive diversity and evolutionary potential are conserved. To preserve adaptive diversity, the population network that best samples functional diversity within the species should be given high priority for conservation. Restoration should rarely be considered if isolation or mixing result from natural processes such as postglacial environmental change rather than anthropogenic change. Maintaining separate management units is the tendency in conservation but it is necessary to consider that continued isolation could compromise the future viability and evolutionary potential of a population. Applied to the Peary caribou, we recommend that caribou of the central Arctic be maintained as a population network. A necessary step is to sample Peary caribou from the eastern High Arctic Islands to evaluate the distinctiveness of the Peary caribou from Bathurst Island.

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Appendix 1. Haplotypes of *Rangifer tarandus*.

Haplo- type	AL SK	BA FF	BA KE	BN KS	BA TH	NF LD	CO PP	EG LI	ME LV	ON TA	PP AT	PW AL	QU EB	SO ME	TA LY	VI CT	YU KN	Total
1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
2	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	1	-	3
3	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
4	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
7	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	4
10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
13	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1
14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
15	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
16	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2
20	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
21	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1
22	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
23	-	1	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	4
24	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	2
25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
27	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1
28	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	3
29	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	2
30	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
31	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
32	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
33	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
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35	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
36	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
37	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	3
38	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
39	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
40	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	2
41	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	2
42	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	2

Haplotype	ALSK	BAFF	BAKE	BNKS	BATH	NFLD	COPP	EGLI	MELV	ONTA	PPAT	PWAL	QUEB	SOME	TALY	VICT	YUKN	Total
43	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
44	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
45	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
46	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1
47	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1
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49	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
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52	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1
53	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
54	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1
55	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
56	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1
57	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
58	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1
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61	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Alces 62	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0
63	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
64	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
65	-	-	-	13	-	-	1	1	1	-	-	4	-	1	5	1	-	27
66	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
67	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	-	3
68	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
69	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
70	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
71	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	2
72	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	2
73	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
74	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1
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83	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1
84	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1
85	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1

Haplo-type	AL SK	BA FF	BA KE	BN KS	BA TH	NF LD	CO PP	EG LI	ME LV	ON TA	PP AT	PW AL	QU EB	SO ME	TA LY	VI CT	YU KN	Total
86	-	-	-	-	-	-	5	1	-	-	-	3	-	1	3	7	-	20
87	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
88	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
89	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
90	-	-	-	2	-	-	-	-	-	-	-	-	-	-	1	-	-	3
91	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
92	-	3	-	-	-	-	2	1	-	-	-	-	-	-	-	-	-	6
93	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	2
94	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
95	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	3

GENETIC DIVERSITY AND RELATEDNESS AMONG CARIBOU POPULATIONS IN NORTH AMERICA

INTRODUCTION

The purpose of this paper is to discuss the genetic relatedness and diversity within and among caribou herds across northwestern North America. Three specific objectives are addressed here. In Part 1, the genetic diversity within the *R. t. pearyi* subspecies is examined to demonstrate that the use of subspecies to define conservation units may not be appropriate if there is much biodiversity below this level. A level at which conservation efforts should be directed is recommended and suggestions are offered for how subdivisions should be made for this subspecies. Part 2 of this paper deals with the genetic diversity of the barren-ground caribou (*R. t. groenlandicus*) herds from the mainland Northwest Territories and Nunavut. The genetic diversity of the barren-ground caribou is compared to that of the Porcupine (*R. t. granti*) caribou and the degree of relatedness among the herds is discussed. Part 3 describes the genetic variation and relatedness among herds of woodland caribou (*R. t. caribou*) from Yukon and British Columbia, as well as among herds of Grant's caribou (*R. t. granti*) from Alaska. In addition, genetic diversity between *R. t. caribou* and *R. t. granti* are described and compared to results from Parts 1 and 2. It is important to note that Parts 1, 2, and 3 are draft papers and are by no means complete.

PART 1. DO SUBSPECIFIC DIVISIONS MAKE GOOD CONSERVATION UNITS?

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ABSTRACT

Wildlife conservation should target the maintenance of biodiversity and the use of biological resources in a sustainable manner. Although conservation units are often applied at the subspecies level, many wildlife species have substantial biodiversity within their subspecific divisions. Genetic differentiation can identify the finer scale population dynamics that exist, allowing us to define units that would be appropriate for targeting conservation. In this study, we demonstrate, using caribou (*Rangifer tarandus*) as an example, that the use of subspecies to define conservation units may not be appropriate for species that have considerable biodiversity below this level. We used microsatellite DNA analyses to assess genetic diversity and describe the relationships within and among caribou populations from the western and central Canadian Arctic Islands and Boothia Peninsula. Expected heterozygosity ranged from 0.66 to 0.84, which is lower than most other tundra caribou populations. We show that the island populations are more genetically differentiated than mainland populations

because of their small sizes, low levels of genetic variation, recent population bottlenecks, and the strong selection pressures in the High Arctic. As the caribou from the Canadian Arctic Islands and Boothia Peninsula are highly adapted to their unique environments, conservation and management efforts should ensure that the present levels of genetic diversity are maintained. We conclude that the current subspecific divisions of caribou are insufficient to represent the diversity that exists within this species. We identify five conservation units to which conservation efforts should be directed. Furthermore, we recommend that the Queen Elizabeth Island and the lower Arctic island populations be recognized as unique from each other as well as from mainland animals.

INTRODUCTION

Wildlife conservation should target the maintenance of biodiversity and the use of biological resources in a sustainable manner. Appropriate conservation units must be identified to maintain biodiversity of threatened or endangered wildlife. Conservation units, however, are not easily identified and there have been many debates about how they should be defined. In 1986, the term “Evolutionary Significant Unit” (ESU) was developed to specify the foremost focus of conservation efforts (Ryder, 1986). An ESU was originally defined as a population that shows significant adaptive variation by a number of different techniques. Since its inception, the definition of an ESU has become increasingly restrictive, such that it is only useful for wildlife species or subspecies that are reciprocally monophyletic (Moritz, 1994). Many wildlife subspecies do not fit this criterion. The term “management unit” (MU) was developed to describe populations that are differentiated based on their allele frequency distributions (Moritz, 1994). However, MUs are typically recommended for short-term management issues, rather than as units toward which to direct conservation efforts (Moritz, 1994). Although conservation units are often applied at the subspecies level, many wildlife species have substantial biodiversity below the subspecific rank.

Caribou (*Rangifer tarandus*) on the Canadian Arctic Islands are an example of a wildlife species for which conservation units should be established below the subspecies level. All caribou populations that occur solely on the Canadian Arctic Islands are currently classified as the subspecies *R. t. pearyi* (Banfield 1961). The Dolphin and Union herd, which splits its annual range between the mainland and southern Victoria Island, is classified as *R. t. groenlandicus* along with all Canadian mainland tundra caribou. Geographic and environmental variation in the Canadian Arctic has resulted in much regionally specific morphological diversity within the caribou that occupy the range, and several ecotypes of caribou occur across this region (Manning, 1960; Banfield, 1961; Thomas and Everson, 1982). Although managers and residents in the Arctic regions recognize different caribou ecotypes and populations, conservation efforts are often directed at the subspecific level (Miller, 1990). Recently, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) revised their guidelines and currently recognizes two of the groups within the *R. t. pearyi* subspecies. However, there is still considerable unrecognized biodiversity within the caribou on the Canadian Arctic Islands. Furthermore, caribou on the Canadian Arctic Islands and Boothia Peninsula have experienced a series of population fluctuations over recent years (Gunn *et al.*, 2000a). The extent of the fluctuations, as well as their causes, varies from population to population. As a population fluctuates in size, variability can be lost and the population's potential for recovery may decrease (Gilpin & Soulé, 1986; Goodman, 1987).

The two primary considerations in establishing conservation units for any organism should be to determine the level at which the conservation efforts should be directed and to identify how the subdivisions should be made. Most importantly, the conservation units should be naturally occurring. Genetic differentiation can identify the finer scale population dynamics that exist, allowing us to define units that would be appropriate for targeting conservation. In this study, we demonstrate that the use of subspecies to define conservation units may not be appropriate for species that have considerable biodiversity below this level. Caribou were sampled from sites within the western and central Canadian Arctic Islands. Microsatellite DNA analyses were used to assess genetic diversity and describe the relationships within and among caribou on those islands. We identify the level at which conservation efforts should be directed and demonstrate how we believe subdivisions should be made for this species. Also, we compare the levels of gene flow and variation to those determined previously for mainland tundra caribou (J. Nagy and K. Zittlau, unpublished data) to evaluate the genetic differences between the mainland and island arctic ecosystems.

METHODS

Study Area

Caribou were sampled from eight populations on seven Canadian Arctic Islands and Boothia Peninsula (Figure 1). In this study, the High Arctic island populations refer to the caribou on Melville Island (42,149 km^2) and within the Bathurst Island complex (Bathurst Island (16,042 km^2) and its satellite islands: Vanier (1126 km^2), Cameron (1059 km^2), Alexander (484 km^2), Massey (432 km^2), and Marc (56 km^2). The terms Canadian High Arctic Islands and Queen Elizabeth Islands are interchangeable. The lower Arctic island populations refer to caribou on the islands south of 74°N but north of the Arctic Circle. The western low Arctic includes Banks (70,028 km^2) and Victoria (217,291 km^2) Islands, whereas the central low Arctic includes Prince of Wales (33,339 km^2) and Somerset (24, 786 km^2) Islands. Victoria Island contains two caribou populations: the Minto Inlet population and the Dolphin and Union population. The Dolphin and Union population spends part of its annual migration on the mainland. Boothia Peninsula (32,715 km^2) lies just several kilometers south of Somerset Island and runs southward to Boothia Isthmus (ca. 69°N latitude). Boothia Peninsula is the most northerly extension of the Canadian mainland and is unique in that from three to five caribou ecotypes can occur there seasonally or year-round (Thomas and Everson, 1982). Two ecotypes of caribou that are intermediate forms between Arctic Island and mainland caribou, together with the Canadian form of barren-ground caribou (*R. t. groenlandicus*), are known to have adjacent calving areas and rutting areas on Boothia Peninsula (Gunn *et al.*, 2000b). This study does not include caribou from the Baffin Island region and the islands in Foxe Basin and Hudson Bay.

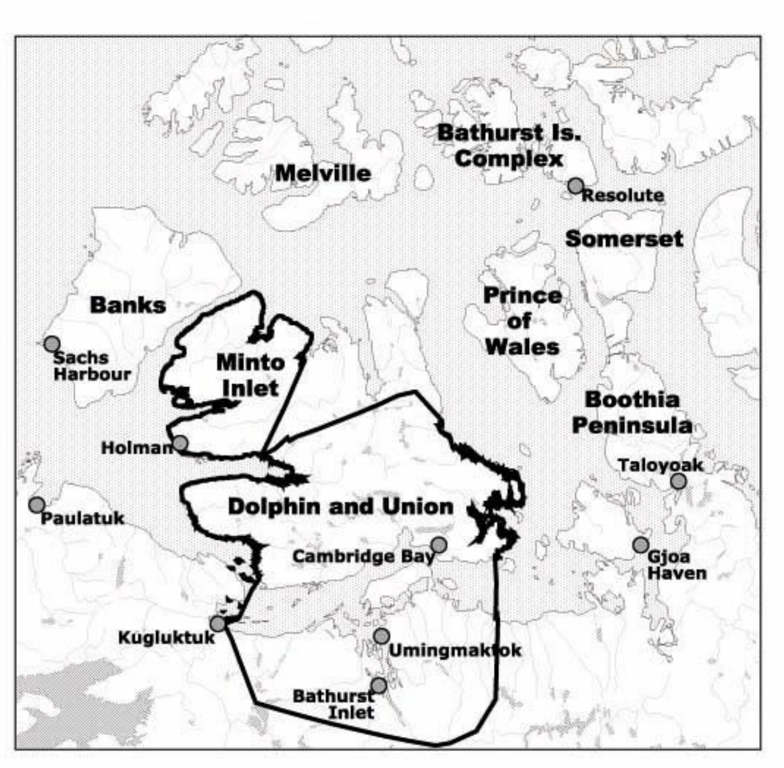

Figure 1. Canadian Arctic Islands and Boothia Peninsula where caribou samples were collected.

Sample collection

Recently, cast antlers were collected from caribou on the calving areas on Melville Island (n=31) and Minto Inlet, Victoria Island (n=12). Skeletal remains or muscle tissue samples were collected from caribou that were harvested by local residents on Banks Island (n=64) and Dolphin and Union, Victoria Island (n=38). Cast antlers and skeletal remains were also collected from caribou that died of natural causes within the Bathurst Island complex (n=129). The cast antlers were collected from rutting areas (males) and calving areas (females). Samples collected within the Bathurst Island complex from skeletal remains represent animals that died during the three annual winter and spring die-offs from 1994–

97. Two batches of samples were obtained from Prince of Wales Island. The older group, which we obtained from the National Museum of Canada, consisted of tissue and bone specimens collected by T. H. Manning and A. H. Macpherson during the summer of 1958. The newer samples from Prince of Wales and Somerset Islands, as well as samples from Boothia Peninsula, were from shot specimens obtained between 1974 and 1977 (Thomas and Everson, 1982) and from an Inuit hunter (T. Manik, Resolute Bay).

Molecular Techniques

DNA was isolated using QIAamp spin columns (QIAGEN Inc.) with either 25 mg of muscle tissue or 500 µL of marrow from bone and antler cores (obtained by drilling into the sample). Each DNA sample was amplified at eight microsatellite loci (RT1, RT5, RT6, RT7, RT9, RT24, RT27, Wilson *et al.*, 1997; BM4513, Bishop *et al.*, 1994) using the polymerase chain reaction (PCR). One primer from each pair was fluorescently labeled. Cycling conditions were 1 min at 94°C, followed by 3 cycles of 30 s at 94°C, 20 s at 54°C, and 5 s at 72°C, followed by 33 cycles of 15 s at 94°C, 20 s at 54°C, and 1 s at 72°C, and then 30 min at 72°C. Allele sizes were determined by analysis of PCR products after polyacrylamide gel electrophoresis on 373A and 377 Automated Sequencers (PE Biosystems) using ABI Prism™ Genescan™ 2.0.2 and Genotyper® 2.0 software.

Analytical Techniques: Hardy-Weinberg Equilibrium And Genetic Variation

The eight loci were tested for Hardy-Weinberg equilibrium (HWE) in each population using a Markov chain algorithm in GENEPOP version 3.1 (Raymond and Rousset, 1995). Each locus was tested for heterozygote deficiency and all locus pairs within a population were tested for linkage disequilibrium. Error rates were adjusted to 0.05 using the Dunn-Sîdak correction to account for the number of comparisons performed. The mean number of alleles per locus (*A*), unbiased expected heterozygosity (H_E; Nei and Roychoudhury, 1974), and unbiased probability of identity (*p*I; Paetkau *et al.*, 1998) were used to estimate genetic diversity for each population. A Wilcoxon's signed ranks test was used to show significant differences in *p*I among populations ($\alpha = 0.05$) (Sokal and Rohlf, 1995).

To determine if the island populations have recently lost genetic diversity, the *M*-test for population bottlenecks was performed (Garza and Williamson, 2001). The bottleneck coefficient, *M,* was calculated from the allele distributions in each population. Several assumptions must be made about the mutation model of the microsatellite alleles examined for this method to be applicable. This method assumes that the alleles obey a one-step mutation model and that multistep mutations only occur occasionally and should not be incorporated into the model. Allele frequency distributions in each population were examined, and it was found that only two-nucleotide repeats occurred. As no odd-sized alleles were found, there is no reason for us to assume that these loci do not obey the one-step mutation model that is recommended for this method (Garza and Williamson, 2001). Furthermore, only the alleles that fell within two standard deviations of the mean allele size were used in the calculation. This avoids bias from extreme outliers that could result from an occasional mutation. *M* could only be calculated in populations for which we had sufficiently large sample sizes; if the sample size is more than twice the number of alleles at the most variable locus it is assumed that most alleles are represented in the sample (Garza an Williamson, 2001). Consequently, the Minto Inlet and the 1958 Prince of Wales Island populations could not be analysed using this method due to the small sample sizes. Significant differences among the *M*-values were examined using an ANOVA. Garza and Williamson (2001) state that an *M*-value below 0.7, derived from seven microsatellite loci, suggests the recent occurrence of a bottleneck. Each of the *M*-values calculated in our study was derived from eight microsatellite loci and we determined a threshold *M*-value for caribou based on large caribou populations that have not experienced a recent bottleneck.

We also performed the one-tailed Wilcoxon's signed ranks test (Piry *et al.*, 1999) from BOTTLENECK version 1.2.02 software (Cornuet *et al.*, 1996). We used the Wilcoxon's signed ranks test as it is the most powerful and robust test for bottlenecks when less than 20 loci are examined. A significant result indicates an excess of heterozygosity compared to that expected at mutation-drift equilibrium. Although Piry *et al.* (1999) recommend the use of the Two Phase Mutation model (TPM) with a 95% Stepwise Mutation Model (SMM) and 5% multistep mutations, the proportion of single step mutations cannot be accurately estimated for microsatellite loci without the sequence of each allele being known. Therefore, we chose not to use the TPM option and instead we used both the SMM, which provides a conservative estimate, and the Infinite Allele Model (IAM), which provides a more extreme estimate. The microsatellite loci examined likely fall between the SMM and IAM models.

Analytical Techniques: Genetic Heterogeneity

The genetic differentiation within and among populations was examined using several measures. First, a G-test for heterogeneity was used to detect differences in allele frequency distributions among populations (Sokal and Rohlf, 1995). The G-test was also used to confirm that caribou from the satellite islands and the multiple rutting and calving areas within the Bathurst Island complex form a homogeneous population. Second, the Doh assignment test calculator was used to determine if a population is genetically distinct (Paetkau *et al.*, 1995). The assignment test was calculated using a program from the website http://www2.biology.ualberta.ca/jbrzusto/Doh.php. The assignment test can identify migrants between populations. The test was also used to determine if there are genetic differences at the regional level or even below the population level. Caribou from the High Arctic, western low Arctic, and central low Arctic island regions were examined for genetic distinctness from Boothia Peninsula, Dolphin and Union, and mainland populations. Absent alleles were adjusted according to Titterington *et al.* (1981). Next, Nei's standard genetic distance (D_S; Nei 1972) and F_{ST} were calculated between pairs of populations to indicate the degree of relatedness among them. An unrooted neighbour-joining tree (Saitou and Nei, 1987) was created using PHYLIP version 3.573 (Felsenstein, 1995) to show D_S among all island and mainland populations. F_{ST} was calculated using GENEPOP version 3.1 (Raymond and Rousset, 1995).

RESULTS

Hardy-Weinberg Equilibrium (HWE) and Genetic Variation

The only locus-population pairs that deviated from HWE due to heterozygote deficiency were RT9 in the Bathurst Island complex and BM4513 within the Bathurst Island complex and Banks Island populations. Null alleles are not expected to be present since no locus showed heterozygote deficiency in all populations. However, it is possible that BM4513 contains null alleles at very low frequencies. Linkage disequilibrium was not detected between any pair of loci across all populations.

Our results showed that unbiased expected heterozygosity (H_E) in caribou populations from the Canadian Arctic Islands was almost 70% or higher (Table 1). The allelic diversity (*A*) in each population ranged from 5.25 to 10.63 alleles per locus (Table 1). The lowest H_E and *A* values were found in the Melville Island, Bathurst Island complex, and Prince of Wales–Somerset Island populations, including the 1958 Prince of Wales population (H_E=0.66 to 0.70; *A*=5.25 to 7.63). Similarly, those populations also had the highest probabilities of identity (pI=1.9×10^{-7} to 2.5×10^{-7}), which also suggests low diversity. The Dolphin and Union and Minto Inlet populations had the highest values of H_E (H_E=0.83 to

0.84) and the lowest *p*I values (*p*I=1.3×10^{-11} to 2.2×10^{-11}). The Wilcoxon's signed ranks test indicated that *p*I values differ significantly ($p<0.05$) between the High Arctic and the western low Arctic island populations, as well as between the central and western low Arctic island populations. The *p*I values also differed significantly between the island and mainland populations.

The bottleneck coefficients ranged from M=0.347 for the Prince of Wales–Somerset Islands population to M=0.472 for the Banks Island population (Table 2). All *M*-values calculated in this study were below Garza and Williamson's (2001) threshold of M=0.7 and our calculated threshold of M=0.5 that were deemed indicative of a population bottleneck (Table 2). *M*-values for each population were not significantly different from one another at the 5% level. Using the BOTTLENECK program, the IAM mutation model suggested that all populations, except Boothia Peninsula and the 1958 Prince of Wales population, showed a significant excess of heterozygosity at $p<0.05$ (Table 2). Under the SMM mutation model, none of the populations examined showed an excess of heterozygosity from mutation-drift equilibrium (Table 2).

Table 1. Genetic variation in caribou populations from the Canadian Arctic Islands and Boothia Peninsula. Mainland tundra caribou populations are included for comparison (J. Nagy and K. Zittlau, unpublished data).

Population	**n** [a]	***A*** [b]	**H_E** [c]	***p*I** [d]
Canadian Arctic Islands				
Bathurst island complex	129	7.63	0.70	1.9×10^{-7}
Melville Island	31	6.25	0.69	2.5×10^{-7}
Banks Island	64	10.13	0.80	7.3×10^{-9}
Minto Inlet	12	7.75	0.83	1.3×10^{-11}
Dolphin and Union	38	10.63	0.84	2.2×10^{-11}
1958 Prince of Wales Island	15	5.75	0.66	2.0×10^{-7}
Prince of Wales-Somerset Islands	14	5.25	0.69	2.0×10^{-7}
Boothia Peninsula	25	9.25	0.79	6.2×10^{-9}
Mainland				
Porcupine	75	14.50	0.88	5.6×10^{-12}
Cape Bathurst	40	12.50	0.87	2.6×10^{-12}
Bluenose-West	62	13.38	0.87	2.7×10^{-12}
Bluenose-East	66	12.88	0.86	1.2×10^{-12}
Bathurst	52	14.00	0.87	5.2×10^{-12}

[a] n = sample size
[b] *A* = mean number of alleles per locus
[c] H_E = unbiased expected heterozygosity
[d] *p*I = unbiased probability of identity

Table 2. Bottleneck *M*-values from Garza and Williamson (2001) test and *p*-values from BOTTLENECK software (Cornuet *et al.* 1996) for caribou populations from Canadian Arctic Islands and Boothia Peninsula.

			BOTTLENECK (*p*-value)	
Population	***M*** [a]	**Variance** [b]	**IAM**	**SMM**
Bathurst Island complex	0.405	0.0061	0.00391	0.98047
Melville Island	0.397	0.0107	0.02734	0.875
Banks Island	0.472	0.0022	0.00195	0.99609
Minto Inlet	n/a [c]	n/a [c]	0.00586	0.32031
Dolphin and Union	0.433	0.0028	0.00195	0.72656
1958 Prince of Wales Island	n/a [c]	n/a [c]	0.52734	0.99414
Prince of Wales-Somerset Island	0.347	0.0075	0.02734	0.84375
Boothia Peninsula	0.444	0.0067	0.09766	0.99414

[a] Mean *M* across all loci in each population.
[b] Variance of *M* across all loci in each population.
[c] Sample size was too small to accurately calculate *M* for Minto Inlet and the 1958 Prince of Wales Island populations.

Genetic Heterogeneity

The G-test for heterogeneity revealed that differences in allele frequency distributions among neighbouring populations are significant ($p<0.05$). Similarly, the assignment test showed that individuals were more often self-assigned to the population from which they were sampled than cross-assigned to a different population (Table 3). The only exception was that caribou from Minto Inlet assigned most frequently to the Banks Island population (58%), which is possibly an artifact of the small sample size from Minto Inlet. The Melville Island caribou showed an equal proportion of assignments (39%) to the Melville Island population as they did to the Bathurst Island complex. The Dolphin and Union population was the most genetically distinct, with 87% of the caribou self-assigned to the population from which they were sampled. The majority of cross-assignments occurred among neighbouring populations, with the exception that the caribou from the Prince of Wales-Somerset Islands complex cross-assigned more often to the Bathurst Island complex population (29%) than they did to the more geographically proximate Boothia Peninsula population (7%). When the populations were divided into regional groups, the assignment test showed that most individuals self-assigned to populations within the region from which they were sampled. Both the G-test and the assignment test (Table 3) indicated that the samples collected from Prince of Wales Island in 1958 have significantly different allele frequencies than those collected from the Prince of Wales-Somerset Islands population during the 1970s.

Table 3. Assignment test results among caribou populations. Source populations are along the left-hand column; sink populations are across the top row. Values indicate the percentage of caribou assigned to each potential sink population. Bolded values indicate largest percentage of assignments for each source population. Shaded area represents data from mainland tundra caribou (J. Nagy and K. Zittlau, unpublished data).

	BIC	Mel	BI	MI	DU	BP	PW58	PWS	P	CB	BW	BE	Ba
BIC	**58**	21	5	1	1	1	5	8	0	0	1	0	0
Mel	**39**	**39**	10	0	0	3	3	6	0	0	0	0	0
BI	8	6	**58**	6	2	3	0	3	0	2	6	3	3
MI	0	0	**33**	0	8	8	0	8	8	0	0	17	17
DU	3	0	0	0	**63**	0	3	0	3	11	3	5	11
BP	4	0	4	4	8	**36**	8	4	4	0	12	8	8
PW58	7	7	7	0	0	7	**40**	27	0	0	7	0	0
PWS	36	7	0	0	0	7	7	**43**	0	0	0	0	0
P	0	0	1	0	3	0	0	0	**64**	11	3	8	11
CB	0	0	0	2	2	2	0	0	27	**33**	13	13	7
BW	0	0	4	4	5	1	4	0	5	16	**26**	21	14
BE	0	1	6	3	3	0	1	0	14	25	15	**28**	4
Ba	0	0	2	2	5	2	0	0	22	15	13	4	**36**

Abbreviations are BIC: Bathurst Island Complex, Mel: Melville Island, BI: Banks Island, MI: Minto Inlet, DU: Dolphin and Union, BP: Boothia Peninsula, PW58: 1958 Prince of Wales Island, PWS: Prince of Wales-Somerset Island, P: Porcupine, CB: Cape Bathurst, BW: Bluenose-West, BE: Bluenose-East, Ba: Bathurst.

In this study, the F_{ST} values showed comparable trends to the D_S values (Table 4). As F_{ST} and D_S are calculated in different ways but show similar patterns of results, we will discuss only D_S. D_S values ranged from 0.03 to 0.66 (Table 4). Among the island populations, the greatest D_S values were those involving the Dolphin and Union population (D_S = 0.22 to 0.52). Caribou from Minto Inlet were also quite genetically distant from all island populations (D_S = 0.20 to 0.35), with the exception of the Banks Island population to which it was closely related (D_S = 0.12). A large D_S value occurred between the Minto Inlet and Dolphin and Union populations (D_S = 0.26), even though the populations occur on the same Arctic island. The smallest D_S values were measured between the two samples collected from Prince of Wales Island at different time points (Prince of Wales, 1958; and Prince of Wales-Somerset Islands, 1970s; D_S = 0.03) and between the two High Arctic island populations (Bathurst Island complex and Melville Island; D_S = 0.04). Despite the geographic distance between them, the caribou sampled from both Prince of Wales populations appeared to be most closely related to the Bathurst Island complex and Melville Island populations (D_S = 0.09 to 0.11). The Boothia Peninsula and Banks Island populations were also closely related (D_S = 0.13). The unrooted neighbour-joining genetic distance tree (Figure 2) shows the relationship of each of the populations to one another.

Table 4. D_S (below diagonal) and F_{ST} (above diagonal). Largest and smallest values are in bold. Shaded area represents data from mainland tundra caribou (J. Nagy and K. Zittlau, unpublished data).

	BIC	Mel	BI	MI	DU	BP	PW58	PWS	P	CB	BW	BE	Ba
BIC	-	0.005	0.033	0.054	0.087	0.058	0.026	0.018	0.110	0.084	0.070	0.088	0.092
Mel	0.04	-	0.031	0.053	0.089	0.054	0.015	0.017	0.105	0.080	0.061	0.079	0.084
BI	0.11	0.11	-	0.004	0.034	0.018	0.049	0.042	0.048	0.027	0.020	0.027	0.026
MI	0.24	0.25	0.12	-	0.020	0.016	0.077	0.061	0.026	0.013	0.007	0.013	0.011
DU	0.35	0.40	0.22	0.26	-	0.045	0.110	0.100	0.029	0.019	0.021	0.023	0.016
BP	0.21	0.21	0.13	0.20	0.30	-	0.055	0.064	0.053	0.034	0.024	0.030	0.035
PW58	0.11	0.09	0.18	0.35	0.52	0.21	-	0.027	**0.120**	0.098	0.072	0.092	0.103
PWS	0.09	0.10	0.18	0.33	0.51	0.28	**0.03**	-	0.109	0.086	0.072	0.092	0.099
P	0.52	0.54	0.32	0.29	0.26	0.37	**0.66**	0.64	-	0.009	0.016	0.013	0.012
CB	0.33	0.35	0.18	0.21	0.19	0.24	0.46	0.44	0.12	-	0.003	**0.001**	0.005
BW	0.25	0.24	0.13	0.18	0.20	0.17	0.30	0.35	0.17	0.09	-	0.004	0.007
BE	0.36	0.34	0.17	0.20	0.20	0.20	0.41	0.48	0.13	0.06	0.08	-	0.007
Ba	0.39	0.38	0.17	0.20	0.16	0.24	0.49	0.54	0.15	0.10	0.11	0.10	-

Abbreviations are defined in Table 3.

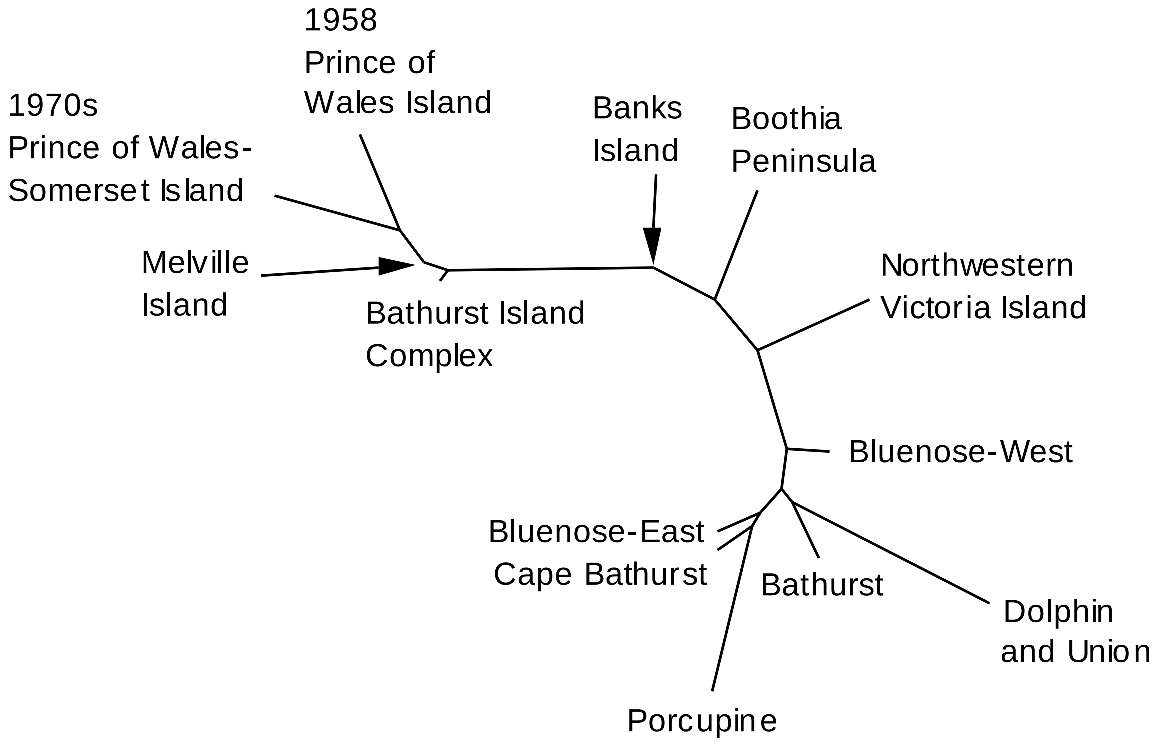

Figure 2. Unrooted neighbour-joining tree of Nei's standard genetic distance (D_S).

DISCUSSION

Genetic diversity

Our results indicate that caribou possess higher levels of genetic variation than many other ungulate populations. The caribou populations from the Canadian Arctic Islands and Boothia Peninsula have an average H_E of 0.75, whereas wapiti (*Cervus elaphus*), moose (*Alces alces*), muskoxen (*Ovibus moschatus*) and bison (*Bison bison*) populations each have an average H_E of less than 0.53 (Polziehn *et al.*, 2000; Broders *et al.*, 1999; Holm *et al.*, 1999; Wilson and Strobeck, 1999). These estimates are considerably lower than those calculated in our study. In other studies, white-tailed deer populations have an average H_E of 0.72 (Anderson *et al.*, 2002), semidomestic Norwegian reindeer have an average H_E of 0.66 (Røed and Midthjell; 1998), and a recent study revealed an average H_E of 0.435 to 0.536 in Alaskan and Canadian caribou and 0.041 to 0.714 in domestic reindeer (Cronin *et al.*, 2003). Some of the microsatellite loci examined in the study by Cronin *et al.* (2003) were linked on the same chromosome, while others were potentially linked to functional genes. Consequently, those loci would not be inherited neutrally and selection pressures could significantly reduce the genetic diversity. Caution should be taken when comparing genetic diversity estimates from neutrally inherited microsatellite loci to loci that are non-neutral and linked. When our results are compared to previous surveys of caribou using the same microsatellite loci (Zittlau *et al.*, 2000, J. Nagy and K. Zittlau, unpublished data), it is evident that caribou on the Canadian Arctic Islands are significantly less variable than woodland caribou and mainland tundra populations (Table 1). The Minto Inlet and Dolphin and Union caribou have the highest levels of variation, yet the average H_E values are 10% lower and the *p*I values are one magnitude lower than the mainland tundra caribou. The Bathurst Island complex, Melville Island, 1958 Prince of Wales, and 1970s Prince of Wales-Somerset Islands populations have the lowest levels of genetic diversity of all caribou populations examined in this study.

The demographic history of the caribou populations on the Arctic Islands suggests that the lower variation may be indicative of a reduction in the effective population size (N_E). While island populations of many species often show low levels of variation (Frankham, 1998), this may be exacerbated in the populations examined in this study as they are relatively small, experience frequent bottlenecks, and have slow recoveries under unfavourable conditions. With each bottleneck, alleles are lost and genetic variation may be reduced. The results of the *M*-test confirm that each population for which *M* could be calculated has undergone a recent reduction in N_E, as all *M*-values are below the bottleneck thresholds of $M = 0.5$ (for caribou) or $M = 0.7$ (from Garza and Williamson, 2001) (Table 2). The 1970s Prince of Wales-Somerset Islands population experienced the most severe bottleneck, followed by the Melville Island and Bathurst Island complex populations, although these differences were not significant. Significant bottlenecks were also detected for all populations, with the exception of Boothia Peninsula and the 1958 Prince of Wales caribou, with the IAM mutation model of the BOTTLENECK program ($p < 0.05$). The SMM did not detect bottlenecks in any of the examined populations, but heterozygosity excess is not always detectable for the SMM (Piry *et al.*, 1999). The BOTTLENECK program is typically useful when examining more than twenty loci (Piry *et al.*, 1999), whereas the *M*-test is more effective when fewer than twenty loci are examined (Garza and Williamson, 2001). As we examined eight loci in our study, we will focus our discussion on the results of the *M*-test.

A reduction in N_E is an important concern due to its potential to reduce genetic variation and threaten biodiversity. If genetic variation is reduced, there is an increased risk of inbreeding depression as well as a loss of adaptive potential (Lacy, 1987; Lacy, 1997; Saccheri *et al.*, 1998). This could result in a decrease in the population's ability to adapt to shifts in environmental conditions. Furthermore, with every decline, a population's recovery to a healthy state may become increasingly difficult, as genetic variation will be lost. If a population is reduced to a critically low size (often identified as an N_E of fewer than fifty individuals; Franklin, 1980), the population may enter an extinction vortex due to increased susceptibility to demographic, environmental, and genetic stochasticity (Gilpin and Soulé, 1986; Goodman, 1987). The island caribou populations have already experienced a number of declines and may not be able to adapt to changes in their environment if their genetic diversity is not preserved.

Conservation units

There are several problems involved with defining conservation units for caribou on the Canadian Arctic Islands and Boothia Peninsula. To begin with, these caribou occur across two territorial jurisdictions and two land claim regions, as well as a national park, a natural wildlife area, and three areas proposed for territorial and national parks. To complicate matters, the Northwest Territories–Nunavut territorial border runs through the middle of both Melville Island and Victoria Island. Each territory and land claim region has different harvesting goals and regulations. Currently, wildlife co-management boards that are established under land claim agreements manage the caribou populations in Canada. Caribou are managed at the population level in order to maintain the current range of occupancy. We believe that conservation efforts should be directed at the same level as management endeavors.

Our results show that much genetic diversity exists below the subspecies level for caribou on the Canadian Arctic Islands and Boothia Peninsula. All of the populations examined are genetically differentiated from each other, with the exception of the Banks Island and Minto Inlet populations. This is likely due to the small sample size that we used for the Minto Inlet caribou. Moreover, migratory and dispersal movements of caribou have occurred between Banks Island and Minto Inlet. Residents of Sachs Harbour, Banks Island and Holman, Victoria Island reported caribou movements between those islands during the 1980s (A. Carpenter and P. Esau, pers. com.). The degree of genetic differentiation among the island populations is significantly greater than that detected among mainland caribou populations (Figure 2; Tables 3 and 4). Two subspecies of tundra caribou occur on the Canadian mainland (*R. t. groenlandicus* and *R. t. granti*). Interestingly, the *R. t. pearyi* populations from the lower Arctic Islands are more genetically differentiated than the mainland *R. t. groenlandicus* and *R. t. granti* subspecies are from each other. In addition, the *R. t. pearyi* on the lower Arctic Islands are highly differentiated from both the *R. t. pearyi* on the High Arctic Islands and the barren-ground caribou on the mainland. The Dolphin and Union caribou (*R. t. groenlandicus*) are also distinct from the *R. t. groenlandicus* that occur on the mainland year-round.

The island populations are more differentiated than mainland populations because of their small sizes, low levels of genetic variation, recent population bottlenecks, and the strong selection pressures in the High Arctic. The caribou on the Arctic Islands are specifically adapted to their unique environment. Caribou on the Queen Elizabeth Islands have the whitest pelage, broadest hooves, and shortest legs of the tundra caribou (Manning, 1960). These adaptations allow them to survive the encumbering snowfall and harsh weather of the High Arctic. Caribou on Banks Island and Minto Inlet, Victoria Island exhibit slightly darker pelage and narrower hooves than the Queen Elizabeth Island caribou. The Dolphin and Union caribou, which occupy range on both southern Victoria Island and the mainland, are larger than the other island caribou, but are significantly smaller and lighter in colour than the mainland barren-ground animals (Manning, 1960). The smaller size of the Dolphin and Union caribou, in comparison to the mainland barren-ground animals, has enabled them to exist on the poor forage that is insufficient for the larger mainland caribou. The extreme selection pressures that are unique to the Arctic Islands limit the opportunity for gene flow from less harsh environments, as many immigrating caribou will not survive. Therefore, particularly in the High Arctic Islands, the minimal levels of diversity are maintained as well as their genetic uniqueness due to a lack of gene flow with the mainland that would act to decrease genetic drift. Furthermore, after a population decline, recovery is often slow to occur and these populations become increasingly distinct.

One of the most significant genetic divisions among the Arctic Island populations is the distinctness of the Dolphin and Union population. These caribou are genetically more related to the adjacent mainland caribou than to those that occur on the same island (Minto Inlet caribou). Radio-collar data show that the Dolphin and Union caribou on Victoria Island travel on the sea ice at least twice annually (spring and fall) across the Dolphin and Union Strait from and to the mainland (Wright *et al.*, 2002). In fact, *pearyi*-type caribou were harvested near Rendezvous Lake, northeast of Inuvik, during the last four to five years (B. Jacobson, pers. com.). These are likely Dolphin and Union caribou that did not return to Victoria Island. Nonetheless, the Dolphin and Union caribou are also more differentiated from any of the populations examined than either the *R. t. granti* or *R. t. groenlandicus* caribou are from each other (Figure 2; Tables 3 and 4). The distinctness of the Dolphin and Union caribou may be due to a severe population bottleneck that is believed to have occurred in the early 1900s (Manning, 1960). Furthermore, the Dolphin and Union caribou rut on Victoria Island before they cross over the sea ice to winter on the mainland. Consequently, although the Dolphin and Union caribou spend much of their time on the mainland, only limited gene flow occurs between them and the mainland barren-ground caribou.

Also interesting is the differentiation between the caribou from Prince of Wales–Somerset Islands and those from Boothia Peninsula. Several caribou populations have been reported to occur within the Prince of Wales–Somerset–Boothia Peninsula complex, but the relationships among the populations have not been identified. Movement data and observations from local residents suggest that the caribou on Prince of Wales–Somerset Islands and Boothia Peninsula function as an inter-island population (Miller *et al.*, 1982). Some of those caribou use adjacent, if not overlapping, calving grounds, which suggests that they should be closely related, if not a homogeneous population. Yet, all measures of genetic differentiation indicate that there are significant differences between the caribou we examined from Prince of Wales–Somerset Islands and those on Boothia Peninsula. Therefore, despite existing in contemporaneous time and space, those caribou do not interact genetically. The caribou that occur within the Prince of Wales–Somerset Islands complex must occasionally fluctuate in size and distribution, as the samples collected from Prince of Wales Island in 1958 are significantly different from those collected during the 1970s (Figure 2; Tables 3 and 4). Moreover, the 1958 Prince of Wales caribou do not show evidence of a genetic bottleneck, whereas a significant bottleneck was detected for the 1970s Prince of Wales–Somerset Islands population (Table 2). The different samples examined may represent different ecotypes that occur within the Prince of Wales–Somerset–Boothia Peninsula complex. Thomas and Everson (1982) recognized several caribou ecotypes on the Boothia Peninsula. Banfield (1961) reported seeing caribou on Prince of Wales Island that possessed characteristics of *R. t. pearyi* but were of a larger size. Banfield (1961) called these caribou "super" *pearyi*.

We conclude that the current subspecific divisions of caribou are insufficient to demonstrate the level of diversity that exists within this species. Conservation units must reflect this biodiversity and should preserve the uniqueness of each caribou population on the Canadian Arctic Islands. If conservation efforts are targeted at too broad a level, diversity will go unrecognized and may be lost. Accordingly, if the island populations are conserved as a single unit, these genetically differentiated and potentially highly adapted populations may be lost. Also, each conservation unit should be a naturally occurring one. To retain the vast amount of genetic diversity present among the declining caribou on the Arctic Islands, conservation efforts should be targeted below the subspecific level.

We recommend the establishment of at least five conservation units for the caribou on the Canadian Arctic Islands, although additional conservation units may be identified when caribou from the eastern region by Hudson Bay and Baffin Island are examined. The recommended conservation units are based on our goal that each genetically distinct and geographically separated group is conserved separately to preserve the biodiversity within the group. The conservation units that we have identified are: 1) Bathurst Island complex and Melville Island populations; 2) Banks Island and Minto Inlet populations; 3) Dolphin and Union population; 4) Boothia Peninsula population; and 5) Prince of Wales–Somerset Islands population. Furthermore, we recommend that conservation strategies should recognize that the Queen Elizabeth Island and the lower Arctic Island populations are unique from each other and from the mainland animals.

Although the island populations and the conservation units that we have identified are genetically differentiated, there is evidence of some gene flow among them. The assignment test shows that some cross-assignments occur between pairs of populations, suggesting that some animals do move between them. The island populations are not necessarily reproductively isolated from each other; caribou can move freely among the Arctic Islands due to the sea ice that persists for almost ten months of the year. Caribou from Boothia Peninsula are more genetically similar to those from Banks Island than expected, despite the large geographic distance between the populations. This could be a result of breeding between caribou from either of these populations with the caribou on the mainland. Both the Banks Island and Boothia Peninsula populations would therefore possess certain allele frequencies similar to those in the mainland populations, resulting in genetic similarities between them. A large number of Banks Island caribou traveled onto the sea ice south of the island during the severe icing winter of 1952 (A. Carpenter and P. Esau, pers. comm.). *Pearyi*-type caribou were seen on the mainland for a number of years following that event (F. Wolkie, pers. com.). Caribou on Banks Island have also been reported to mix with *R. t. groenlandicus* caribou from the mainland (Banfield, 1961). However, the features of Banks Island caribou are more similar to *R. t. pearyi* than to *R. t. groenlandicus* (Banfield, 1961) and indeed we have shown that the Banks Island caribou are genetically distinct from the mainland caribou. Caribou movements among the Arctic Islands are likely to be "trickle" events, as the observations of movements have been sporadic; constant movements would likely have decreased the genetic differentiation between these populations. Consequently, we speculate that there must have been some intermittent mass movements of animals between populations during the last several hundred generations. Such movements possibly occurred hundreds of years ago, which could explain the lack of movement observations by recent telemetry studies. We must recognize that due to fluctuating population sizes and intermittent gene flow between them, the caribou populations are not static. Therefore, conservation units should not be static either. The conservation units identified by this study may require readjustment if changes occur or if new data are found.

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PART 2. GENETIC DIVERSITY AMONG BARREN-GROUND AND THE PORCUPINE CARIBOU HERDS

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INTRODUCTION

The purpose of this study was to examine genetic diversity among the Porcupine (*Rangifer tarandus granti*) and seven barren-ground (*R. t. groenlandicus*) caribou herds from the mainland Northwest Territories and Nunavut. As in Part 1, we used microsatellite DNA analyses to examine genetic variation and relatedness and to identify population genetic structure among the large, migratory herds. Specifically, we sought three things:

1) To determine the levels of genetic variation present in the large migratory caribou herds;
2) To describe existing population genetic structure among the herds; and
3) To determine if the Porcupine herd is genetically differentiated from the barren-ground herds. This information will be useful for aiding management plans for barren-ground caribou.

METHODS

Study area and sample collection

John Nagy (RWED, GNWT), Anne Gunn (RWED, GNWT), Don Thomas (CWS), and Gustaf Samelius (Environment Canada) collected blood and tissue samples from the Porcupine herd and seven populations of barren-ground caribou that occur on the mainland Northwest Territories and Nunavut. For the Cape-Bathurst, Bluenose-West, Bluenose-East, Bathurst, and Ahiak herds, antler and tissue samples were collected from the calving grounds and likely represent females. For the Beverly and Qamanirjuaq herds, tissue was collected from annual harvests. For the Porcupine herd, blood samples were collected while the animals were handled for ear tagging. Sample sizes from each population are listed in Table 5.

Laboratory techniques

Details of all laboratory techniques are described in Part 1. DNA was isolated from the antler, bone, and tissue samples and subsequently amplified at eight microsatellite loci (RT1, RT5, RT6, RT7, RT9, RT24, RT27; Wilson *et al.*, 1997; and BM4513; Bishop *et al.*, 1994) using PCR. Allele sizes were resolved by polyacrylamide gel electrophoresis.

Statistical analyses

Details about analyses can be found in Part 1. Levels of genetic variation were estimated using three measures: mean alleles per locus, unbiased expected heterozygosity (Nei and Roychoudhury, 1974), and unbiased probability of identity (Paetkau *et al.*, 1998). Unbiased expected heterozygosity is the proportion of the population that is expected to have differently sized alleles at a particular locus. Therefore, a high heterozygosity reflects a high level of genetic variation. Unbiased probability of identity is the probability that two random, unrelated individuals are genetically identical across all loci. Consequently, a low probability of identity reflects a high level of variation within the population. A Kruskal-Wallis test was used to determine if probabilities of identity are significantly different between populations.

Using a G-test for heterogeneity, we compared allele frequency distributions between neighbouring populations to determine if the populations are genetically differentiated (Sokal and Rohlf, 1997). A Dunn-Sîdak correction was used to account for the number of comparisons made with the G-test. Genetic differentiation was also examined using an assignment test (Paetkau *et al.*, 1995). Lastly, Nei's standard genetic distance (D_S) was calculated between all pairs of populations to determine the relatedness among the herds (Nei, 1972).

RESULTS

The populations examined in this study displayed high levels of genetic variation (Table 5). Average alleles per locus ranged from 11.9 (Beverly) to 14.6 (Bluenose-West). Unbiased expected heterozygosity ranged from 86% (Beverly) to 88% (Porcupine), and unbiased probabilities of identity ranged from to

8.9×10^{-12} (Beverly) to 1.0×10^{-12} (Qamanirjuaq). The Kruskal-Wallis test indicated that the eight populations are not significantly different in their levels of genetic variation. When all three measures are taken together, the Porcupine caribou were the most genetically variable and the Ahiak caribou were the least genetically variable.

Table 5. Genetic variation in the Porcupine and barren-ground caribou populations.

Population	**N**	***A***	**H_E**	***p*I**
Porcupine	75	14.5	0.88	5.6×10^{-12}
Cape Bathurst	45	12.6	0.87	2.7×10^{-12}
Bluenose-West	80	14.6	0.87	3.2×10^{-12}
Bluenose-East	79	13.3	0.86	1.4×10^{-12}
Bathurst	55	14.4	0.87	5.2×10^{-12}
Ahiak	40	12.6	0.86	1.1×10^{-12}
Beverly	25	11.9	0.88	8.9×10^{-12}
Qamanirjuaq	46	12.8	0.86	1.0×10^{-12}

Measures of variation are described in Table 1.

The G-test for heterogeneity indicated that the allele frequency distributions significantly differ between most neighbouring populations ($p < 0.05$). The Bathurst and Ahiak populations were not significantly different from each other, nor were the Beverly and Qamanirjuaq populations.

The assignment test also showed that most of the herds are genetically differentiated from each other (Table 6). However, no herd was highly differentiated from the others. The Porcupine herd was the most genetically distinct of the eight herds examined in this study; 56% of the Porcupine caribou were “self-assigned” to their own herd. None of the barren-ground populations exceeded 50% self-assignments; self-assignments for the barren-ground populations ranged from 19% to 33%. Nonetheless, despite being low, the self-assignments composed the largest proportion of assignments in all herds except Ahiak and Beverly. The Ahiak caribou assigned most often (28%) to the Bathurst herd. The Beverly caribou assigned most often (28%) to the Cape Bathurst herd. An equal proportion (19%) of Bluenose-East caribou assigned to Bluenose-West.

Table 6. Assignment test results among mainland tundra caribou populations. Source populations are along the left-hand column; sink populations are across the top row. Values indicate the percentage of caribou assigned to each potential sink population. Bolded values indicate largest percentage of assignments for each source population.

	P	CB	BW	BE	Ba	A	Bev	Q
P	**56**	9	1	5	8	4	8	8
CB	13	**22**	16	11	4	11	11	11
BW	5	14	**30**	19	10	8	4	11
BE	10	16	**19**	**19**	0.04	14	5	13
Ba	15	11	11	0.04	**31**	15	4	11
A	3	10	10	13	**28**	20	10	8
Bev	4	**28**	8	12	8	8	24	8
Q	2	15	7	13	9	11	11	**33**

Abbreviations are defined in Table 3.

Pairwise genetic distances ranged from D_S = 0.059 to 0.168 (Table 7). The smallest D_S occurred between the Bluenose-East and Cape Bathurst populations and the largest D_S occurred between the Porcupine and Bluenose-West populations. The Porcupine herd was the most genetically distinct. Pairwise comparisons involving the Porcupine caribou resulted in genetic distance values ranging from D_S = 0.124 to 0.168. An unrooted neighbour-joining genetic distance tree shows the relationship among all of the herds examined in Parts 1, 2, and 3 of this study (Figure 3).

Table 7. Nei's standard genetic distance (D_S) between mainland tundra caribou populations. Largest and smallest values are shown in bold.

	P	CB	BW	BE	Ba	A	Bev	Q
P	-							
CB	0.124	-						
BW	**0.168**	0.092	-					
BE	0.134	**0.059**	0.076	-				
Ba	0.146	0.104	0.107	0.098	-			
A	0.151	0.095	0.100	0.084	0.072	-		
Bev	0.139	0.106	0.129	0.109	0.147	0.128	-	
Q	0.147	0.091	0.118	0.069	0.079	0.097	0.125	-

Abbreviations are defined in Table 3.

DISCUSSION

The genetic variation among the mainland populations (Table 5) is significantly higher than measures reported for other ungulate species (Broders *et al.*, 1999; Holm *et al.*, 1999; Polziehn *et al.*, 2000; Anderson *et al.*, 2002; Wilson and Strobeck, 1999). In addition, mainland caribou are more genetically variable than other caribou populations (Zittlau *et al.*, 2000; Zittlau, 2004). Among the mainland populations, the levels of genetic variation are similar. This suggests that, despite potential fluctuation in size of some of the populations (e.g. Wakelyn, 1999), genetic variation has not been lost. Evidence from telemetry and radio-collar studies suggest that some herds have been recently established, or at least recently recognized (Nagy *et al.*, unpublished data; A. Gunn, unpublished data). When new populations are established, genetic diversity can be lost due to founding effects or genetic drift. However, the genetic diversity results from this study indicate that these populations have not lost genetic variation.

The results from the G-test for heterogeneity and the assignment test (Table 6) indicate that most of the mainland caribou populations are genetically differentiated from each other, although the degree of differentiation is not great. Because the populations examined have such large sizes, genetic drift is slow to occur, resulting in a minimal degree of differentiation among the mainland herds. Nonetheless, the degree of genetic differentiation differs for each herd. For instance, although most populations are at least slightly differentiated according to G-test and assignment test results, the Ahiak caribou are not significantly different from the Bathurst caribou. Telemetry data indicate that the Ahiak herd may have been recently established from the Bathurst herd (A. Gunn, unpublished data). Based on our results, this separation has not been in existence for a sufficient period of time for the Ahiak herd to become genetically distinct from the Bathurst herd.

The Porcupine herd is the most genetically distinct of the herds examined. Based on the assignment test, over 50% of the Porcupine caribou likely originate from the Porcupine herd (Table 6). However, the D_S results suggest that the Porcupine herd is not much more distantly related to the barren-ground herds ($D_S = 0.124$ to 0.168) than is the Beverly herd to its neighbours (Bathurst, Ahiak, and Qamanirjuaq; $D_S = 0.125$ to 0.147) (Table 7). The Porcupine caribou are not as genetically differentiated from the barren-ground populations as would be expected for a different subspecies.

When genetic drift occurs locally, an isolation-by-distance process can create genetic structure, wherein neighbouring populations would be the most closely related and geographically distant populations would be genetically distinct (Wright, 1943). This occurs because gene flow most often occurs among neighbouring populations, rather than to populations that are more distant. Therefore, we would expect to observe an isolation-by-distance effect among the mainland caribou. Although this has not yet been tested for statistical significance, the trend observed in genetic distance and differentiation measures indicates that this does not occur among the mainland caribou populations. The smallest D_S values were not detected between adjacent herds and cross-assignments were almost equally distributed among all populations, regardless of the geographic distance separating them. In fact, the assignment test and D_S results reveal that the Beverly herd is most closely related to the geographically distant Cape Bathurst caribou (Tables 6 and 7).

The limited population genetic structure observed among the mainland caribou is likely a result of their large population sizes, vast migration routes and overlapping home ranges. Small, isolated populations can become genetically differentiated within only a few generations. For large populations, however, genetic differentiation will be slow to occur. Consequently, the mainland tundra caribou have maintained both genetic diversity and genetic similarity. This is unusual among large mammals today; few populations have maintained such large herd sizes and unfragmented distributions. The results presented in this study provide insight into the levels of diversity that could be common to other mammal populations that historically displayed a continuous distribution and maintained their population sizes. Furthermore, this offers an occasion to follow a precautionary approach to conservation and preserve the existing genetic diversity of mainland tundra caribou.

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PART 3. GENETIC DIVERSITY AMONG WOODLAND AND GRANT'S CARIBOU HERDS

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INTRODUCTION

The purpose of this study was to examine genetic diversity within and between two subspecies of caribou: woodland caribou (*R. t. caribou*) and Grant's caribou (*R. t. granti*). We also examined the genetic diversity within and between the two ecotypes of woodland caribou that occur in British Columbia: the Mountain woodland ecotype and the Northern woodland ecotype. As in Parts 1 and 2 of this paper, we used microsatellite DNA analyses to estimate levels of genetic diversity and the degree of relatedness among herds. The results will be useful for assisting with the management and conservation of several threatened and endangered herds.

METHODS

Study area and sample collection

Samples from 30 woodland and 10 Grant's caribou herds were collected by Rick Farnell (DRR, YGT), Pat Valkenburg (AFG), Trevor Kinley (Sylvan Consulting, Ltd.), Helen Schwantje (WLAP), Scott McNay (Slocan Forest Projects), Jon Almack (WDFW), and Rick Marshall (WLAP). Sample sizes from each population are indicated in Table 8.

Laboratory techniques

Details of all laboratory techniques are described in Part 1. DNA was isolated from the blood, tissue and hair samples and amplified at eight microsatellite loci using PCR (see Part 1 for details). Allele sizes were resolved by polyacrylamide gel electrophoresis.

Statistical analyses

Details about analyses can be found in Part 1. As in Parts 1 and 2, levels of genetic variation were estimated using three measures: mean number of alleles per locus (*A*), unbiased expected heterozygosity (H_E; Nei and Roychoudhury, 1974), and unbiased probability of identity (*p*I; Paetkau *et al.*, 1998). A Wilcoxon's signed ranks test was used to compare levels of genetic diversity between herds, ecotypes, and subspecies examined in Parts 1 and 2 (Sokal and Rohlf, 1995).

Genetic differentiation of herds was examined using an assignment test (Paetkau *et al.*, 1995). An assignment test was also used to identify regional differences within the Alaskan Grant's caribou. Nei's standard genetic distance (D_S; Nei, 1972) was calculated between all pairs of populations to determine the relatedness among the herds.

RESULTS

Genetic variation

Allelic diversity ranged from 4.8 (North Cariboo Mountain) to 12.5 (Hart River) alleles per locus and unbiased expected heterozygosity ranged from 53% (South Purcells) to 88% (Hart River) (Table 8). The probabilities of identity ranged from 1.5×10^{-5} (South Purcells) to 5.3×10^{-12} (Hart River). Based on probabilities of identity and expected heterozygosities, the most genetically variable herds were Hart River, Nelchina, and Fortymile. The least variable herd was South Purcells, followed by Unimak and Itcha-Ilgachuz. Based on a Wilcoxon's signed ranks test, the Mountain woodland ecotype had significantly higher probabilities of identity than those measured for the Northern woodland ecotype ($p < 0.05$). Probabilities of identity were also significantly higher in Grant's caribou compared to the Northern woodland ecotype and coastal Grant's caribou showed significantly higher probabilities of identity compared to interior Grant's caribou located near the Alaska-Yukon border. The genetic variation levels were not significantly different between the Northern woodland ecotype herds and the Yukon woodland herds, nor were they different between the Yukon woodland and Grant's caribou herds.

Table 8. Genetic variation in woodland and Grant's caribou herds.

Ecotype	**Population**	**N**	***A***	**H_E**	***p*I**
Yukon woodland	Aishihik	42	7.9	0.74	3.4×10^{-8}
	Atlin	13	7.3	0.83	6.4×10^{-10}
	Bonnet Plume	19	9.9	0.86	1.1×10^{-12}
	Carcross	18	7.4	0.79	4.1×10^{-9}
	Chisana	51	9.4	0.82	2.5×10^{-10}
	Clear Creek	21	10.5	0.86	1.6×10^{-12}
	Finlayson	20	9.8	0.85	6.3×10^{-11}
	Hart River	38	12.5	0.88	5.3×10^{-12}
	Ibex	20	7.3	0.79	5.4×10^{-9}
	Klaza	10	5.8	0.76	1.6×10^{-9}
	Kluane	21	6.4	0.75	1.5×10^{-8}
	South Nahanni	26	9.6	0.84	1.6×10^{-11}
	Pelly	36	10	0.85	1.9×10^{-11}
	Tay River	20	8.9	0.83	1.1×10^{-11}
	Wolf Lake	29	9.5	0.84	1.0×10^{-11}
Mountain ecotype	North Cariboo Mountains	4	4.8	0.84	5.5×10^{-9}
	Prince George	33	9.4	0.80	9.6×10^{-9}
	Revelstoke	20	7.3	0.79	2.3×10^{-9}
	South Purcells	28	4.9	0.53	1.5×10^{-5}
Northern ecotype	Atlin East	24	8.1	0.83	3.7×10^{-10}
	Cassiar	9	7.6	0.85	2.6×10^{-12}
	Chase	25	9.4	0.83	1.1×10^{-11}
	Finlay	15	8.5	0.83	1.2×10^{-11}
	Itcha-Ilgachuz	17	5.6	0.74	8.7×10^{-7}
	Tweedsmuir-Entiako	36	7	0.76	4.4×10^{-8}
	Wolverine	20	6.6	0.74	2.6×10^{-8}
Grant's	Fortymile	20	10	0.87	2.0×10^{-12}
	Macomb	20	9.5	0.86	1.3×10^{-12}
	Mentasta	32	10.9	0.85	2.8×10^{-11}
	Nelchina	20	10.4	0.86	2.4×10^{-12}
	White Mountain	6	5.5	0.82	5.2×10^{-10}
	Mulchatna	19	8.9	0.85	2.7×10^{-11}
	Nushagak	20	9.5	0.82	1.1×10^{-11}
	North Alaska Peninsula	20	8.4	0.81	4.9×10^{-10}
	South Alaska Peninsula	20	6.9	0.77	5.0×10^{-8}
	Unimak	17	5.8	0.68	2.1×10^{-7}

Measures of variation are described in Table 1.

Genetic relatedness among woodland caribou

The assignment test results indicated that self-assignments for the Yukon woodland herds ranged from 15% (Atlin) to 83% (Aishihik) (Table 9). The majority of the Yukon caribou assigned most often to the population from which they were sampled. The only exceptions were the Atlin, Bonnet Plume, Finlayson, and Tay River caribou. The Atlin caribou assigned most often (38%) to the Pelly herd. The Bonnet Plume caribou assigned equally (32%) to the Hart River herd as they do to their own herd. The Finlayson and Tay River caribou cross-assigned to each other at least as often (20%-25%) as they self-assigned to their own herd. The most genetically distinct herds were the Aishihik (86% self-assignments), Chisana (71% self-assignments), and Kluane (71% self-assignments) herds.

Table 9. Assignment test results among all woodland caribou herds. Source herds are along the left-hand column; sink herds are across the top row. Values indicate the percentage of caribou assigned to each potential sink population. Bolded values indicate largest percentage of assignments for each source population.

	AI	AH	BP	CC	CH	CK	FH	HR	IH	KA	KU	PH	NH	TH	TR	WL	CM	RV	SP	PG	AE	CA	CS	F	II	TE	WO
AI	**83**	-	-	2	5	-	-	-	-	-	5	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	2
AH	-	15	-	-	-	-	-	-	-	15	-	23	8	-	-	-	-	-	-	-	**31**	-	-	8	-	-	-
BP	-	-	26	-	-	11	5	**32**	-	-	-	5	5	-	-	11	-	-	-	-	-	5	-	-	-	-	-
CC	-	-	-	**44**	6	-	-	-	17	-	-	-	-	6	-	6	-	6	-	-	17	-	-	-	-	-	-
CH	-	6	-	-	**71**	2	2	4	-	-	4	4	2	4	-	-	-	-	-	-	2	-	-	-	-	-	-
CK	-	10	5	-	5	**29**	5	19	-	-	10	-	5	-	5	5	-	-	-	-	5	-	-	-	-	-	-
FH	-	-	5	-	-	10	20	5	-	-	-	10	10	-	**25**	-	-	-	-	-	-	5	5	-	-	-	5
HR	3	5	-	3	3	18	5	**21**	3	-	3	3	8	3	8	5	-	-	-	-	3	-	5	-	-	-	3
IH	-	-	5	10	5	-	-	-	**50**	-	-	-	-	-	-	15	-	-	-	-	10	-	5	-	-	-	-
KA	-	10	-	-	10	-	-	10	-	**50**	-	-	-	10	-	-	-	-	-	-	-	-	10	-	-	-	-
KU	14	-	-	-	10	-	-	-	-	-	**71**	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PH	-	-	-	3	6	-	3	6	-	3	-	**36**	11	8	6	8	-	-	-	-	-	3	6	3	-	-	-
NH	-	-	-	-	12	-	8	-	-	-	4	8	**31**	-	23	4	-	-	-	-	4	4	4	-	-	-	-
TH	11	-	-	-	-	6	-	6	6	-	-	11	-	**50**	-	6	-	-	-	-	-	-	6	-	-	-	-

	AI	AH	BP	CC	CH	CK	FH	HR	IH	KA	KU	PH	NH	TH	TR	WL	CM	RV	SP	PG	AE	CA	CS	F	II	TE	WO
TR	-	5	5	-	-	5	**25**	-	-	-	-	-	20	5	**25**	-	-	-	-	5	-	-	5	-	-	-	-
WL	-	3	7	3	-	-	3	3	7	-	-	7	-	7	3	**45**	-	-	-	-	-	3	3	-	-	-	3
CM	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**75**	-	-	-	-	-	25	-
RV	-	-	-	-	-	5	5	-	-	-	-	-	-	-	-	-	-	**65**	-	25	-	-	-	-	-	-	-
SP	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**100**	-	-	-	-	-	-	-	-
PG	-	-	3	-	-	-	-	3	-	-	-	-	-	-	-	-	8	15	3	**56**	-	-	-	3	3	5	3
AE	-	21	-	13	4	-	-	4	-	-	-	4	4	-	-	4	-	-	-	-	**42**	-	4	-	-	-	-
CA	-	-	-	-	-	-	-	11	-	-	-	**33**	22	-	-	-	-	-	-	-	-	-	22	-	-	11	-
CS	-	-	8	8	-	-	-	4	8	-	-	12	-	-	4	4	-	-	-	4	4	-	**44**	-	-	-	-
F	-	-	-	-	-	-	-	27	-	-	-	-	7	-	-	-	-	-	-	-	-	-	13	**53**	-	-	-
II	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	-	-	-	**94**	-	-
TE	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	3	-	3	**86**	6
WO	-	-	-	-	-	-	-	-	5	-	-	-	-	-	5	-	-	5	-	5	-	-	10	-	-	-	**70**

Abbreviations are AI: Aishihik, AH: Atlin, BP: Bonnet Plume, CC: Carcross, CH: Chisana, CK: Clear Creek, FH: Finlayson, HR: Hart River, IH: Ibex, KA: Klaza, KU: Kluane, PH: Pelly, NH: South Nahanni, TH: Tatchun, TR: Tay River, WL: Wolf Lake, CM: North Cariboo Mtns, RV: Revelstoke, SP: South Purcells, PG: Prince George, AE: Atlin East, CA: Cassiar, CS: Chase, F: Finlay, II: Itcha-Ilgachuz, TE: Tweedsmuir-Entiako, WO: Wolverine

Self-assignments for the British Columbia woodland caribou herds ranged from 0% (North Cariboo Mountains and Cassiar) to 100% (South Purcells) (Table 9). The majority of the British Columbia woodland caribou assigned most often to the population from which they were sampled. The exceptions to this were North Cariboo Mountains, which assigned most often (75%) to the Prince George herd, and Cassiar, which assigned most often (33%) to the Pelly herd. Neither the North Cariboo Mountain nor the Cassiar caribou had any self-assignments to the herd from which they were sampled.

Among all woodland caribou herds, Nei's standard genetic distance (D_S) ranged from 0.109 (Tay River-South Nahanni) to 1.182 (North Cariboo Mountains-South Purcells) (Tables 10 and 11). Among just the Yukon woodland herds, D_S ranged from 0.109 (Tay River-South Nahanni) to 0.877 (Klaza-Kluane) (Table 10). Among only the British Columbia woodland herds, D_S ranged from 0.234 (Wolverine-Chase) to 1.182 (North Cariboo Mountains-South Purcells)

(Table 11). An unrooted neighbour-joining genetic distance tree shows the relationship among all of the woodland caribou herds (Figure 3).

Table 10. Nei's standard genetic distance (D_S) between Yukon woodland caribou herds. Largest and smallest values are shown in bold.

	AI	**AH**	**BP**	**CC**	**CH**	**CK**	**FH**	**HR**	**IH**	**KA**	**KU**	**PH**	**NH**	**TH**	**TR**	**WL**
AI	-															
AH	0.457	-														
BP	0.340	0.304	-													
CC	0.331	0.218	0.296	-												
CH	0.336	0.231	0.293	0.366	-											
CK	0.240	0.325	0.165	0.331	0.267	-										
FH	0.322	0.284	0.185	0.307	0.303	0.162	-									
HR	0.302	0.221	0.132	0.260	0.221	0.121	0.187	-								
IH	0.251	0.288	0.213	0.175	0.372	0.275	0.229	0.256	-							
KA	0.811	0.339	0.329	0.367	0.504	0.486	0.527	0.362	0.565	-						
KU	0.411	0.563	0.592	0.587	0.229	0.390	0.491	0.412	0.643	**0.877**	-					
PH	0.277	0.173	0.197	0.220	0.223	0.177	0.165	0.139	0.196	0.355	0.442	-				
NH	0.347	0.275	0.170	0.317	0.236	0.184	0.115	0.166	0.231	0.469	0.461	0.168	-			
TH	0.364	0.278	0.311	0.315	0.340	0.259	0.231	0.213	0.283	0.516	0.531	0.151	0.182	-		
TR	0.335	0.309	0.224	0.350	0.336	0.193	0.145	0.173	0.263	0.641	0.561	0.192	**0.109**	0.201	-	
WL	0.253	0.215	0.179	0.241	0.276	0.200	0.179	0.146	0.162	0.409	0.517	0.118	0.149	0.183	0.180	-

Abbreviations are defined in Table 9.

Table 11. Nei's standard genetic distance (D_S) between BC woodland caribou herds. Largest and smallest values are shown in bold.

	CM	**RV**	**SP**	**PG**	**AE**	**CA**	**CS**	**F**	**II**	**TE**	**WO**
CM	-										
RV	0.441	-									
SP	**1.182**	0.558	-								
PG	0.340	0.312	0.536	-							
AE	0.722	0.605	0.694	0.511	-						
CA	0.690	0.598	1.061	0.590	0.323	-					
CS	0.490	0.418	0.573	0.254	0.299	0.396	-				
F	0.585	0.556	0.902	0.514	0.557	0.620	0.343	-			
II	0.598	0.444	0.706	0.408	0.581	0.497	0.443	0.725	-		
TE	0.518	0.399	0.795	0.268	0.549	0.579	0.373	0.751	0.373	-	
WO	0.550	0.436	0.700	0.348	0.412	0.515	**0.234**	0.371	0.548	0.486	-

Abbreviations are defined in Table 9.

Genetic relatedness among Grant's caribou

Caribou from most Grant's herds were self-assigned to the population from which they were sampled (Table 12). Self-assignments ranged from 15% (Fortymile and Nushagak) to 94% (Unimak). Only the Fortymile and Nushagak herds had more cross-assignments to other populations than self-assignments to themselves. The Fortymile caribou assigned most often to Mentasta (25%) and Macomb (20%), but also assigned frequently to Nelchina, Mulchatna, and White Mountain (10% each). The Nushagak caribou assigned most often (55%) to the North Alaska Peninsula herd. Unimak was the most genetically distinct herd with 94% self-assignments; the other 6% of Unimak individuals cross-assigned to its neighbouring herd, South Alaska Peninsula. The South Alaska Peninsula herd was the second most genetically distinct with 80% self-assignments; the only cross-assignments from South Alaska Peninsula occurred to the neighbouring North Alaska Peninsula herd. The results of the assignment test between coastal and interior caribou showed that herds from the two regions were significantly different ($p < 0.05$).

D_S among the Grant's caribou herds ranged from 0.128 (Mentasta-Nelchina) to 0.934 (Unimak-White Mountain) (Table 13). The genetic relationships among all of the Grant's and woodland herds, based on D_S, are illustrated in Figure 3.

Table 12. Assignment test results among Grant's herds and one woodland herd (Chisana). Source herds are along the left-hand column; sink herds are across the top row. Values indicate the percentage of caribou assigned to each potential sink population. Bolded values indicate largest percentage of assignments for each source population.

	NC	FM	MA	WM	ME	MU	UM	NP	SP	NG	CH
NC	**30**	15	20	-	15	5	-	10	-	-	5
FM	10	15	20	10	**25**	10	-	5	-	-	5
MA	10	20	**40**	-	10	5	-	-	5	5	5
WM	-	**67**	-	33	-	-	-	-	-	-	--
ME	6	9	9	-	**56**	3	-	6	-	3	6
MU	-	11	11	5	16	**58**	-	-	-	-	-
UM	-	-	-	-	-	0	**0.94**	-	0.06	-	-
NP	0.10	0.10	-	-	-	0.05	-	**0.35**	0.15	0.25	-
SP	-	-	-	-	-	-	-	0.20	**0.80**	-	-
NG	-	-	-	-	0.1	0.15	-	**0.55**	0.05	0.15	-
CH	0.08	0.06	-	0.02	0.04	-	-	-	-	0.04	**0.76**

Abbreviations are NC: Nelchina, FM: Fortymile, MA: Macomb, WM: White Mountain, ME: Mentasta, MU: Mulchatna, UM: Unimak, NP: North Alaska Peninsula, SP: South Alaska Peninsula, NG: Nushagak, CH: Chisana

Table 13. Nei's standard genetic distance (D_S) between Grant's caribou herds. Largest and smallest values are shown in bold.

	NC	FM	MA	WM	ME	MU	UM	NP	SP	NG	CH
NC	-										
FM	0.183	-									
MC	0.166	0.135	-								
WM	0.446	0.298	0.391	-							
ME	**0.128**	0.153	0.143	0.409	-						
MU	0.277	0.194	0.238	0.501	0.233	-					
UM	0.820	0.548	0.675	**0.934**	0.658	0.707	-				
NP	0.312	0.205	0.320	0.574	0.283	0.321	0.355	-			
SP	0.585	0.370	0.538	0.693	0.504	0.529	0.370	0.260	-		
NG	0.323	0.219	0.312	0.563	0.295	0.259	0.518	0.145	0.357	-	
CH	0.294	0.185	0.261	0.513	0.219	0.332	0.438	0.328	0.438	0.313	-

Abbreviations are defined in Table 12.

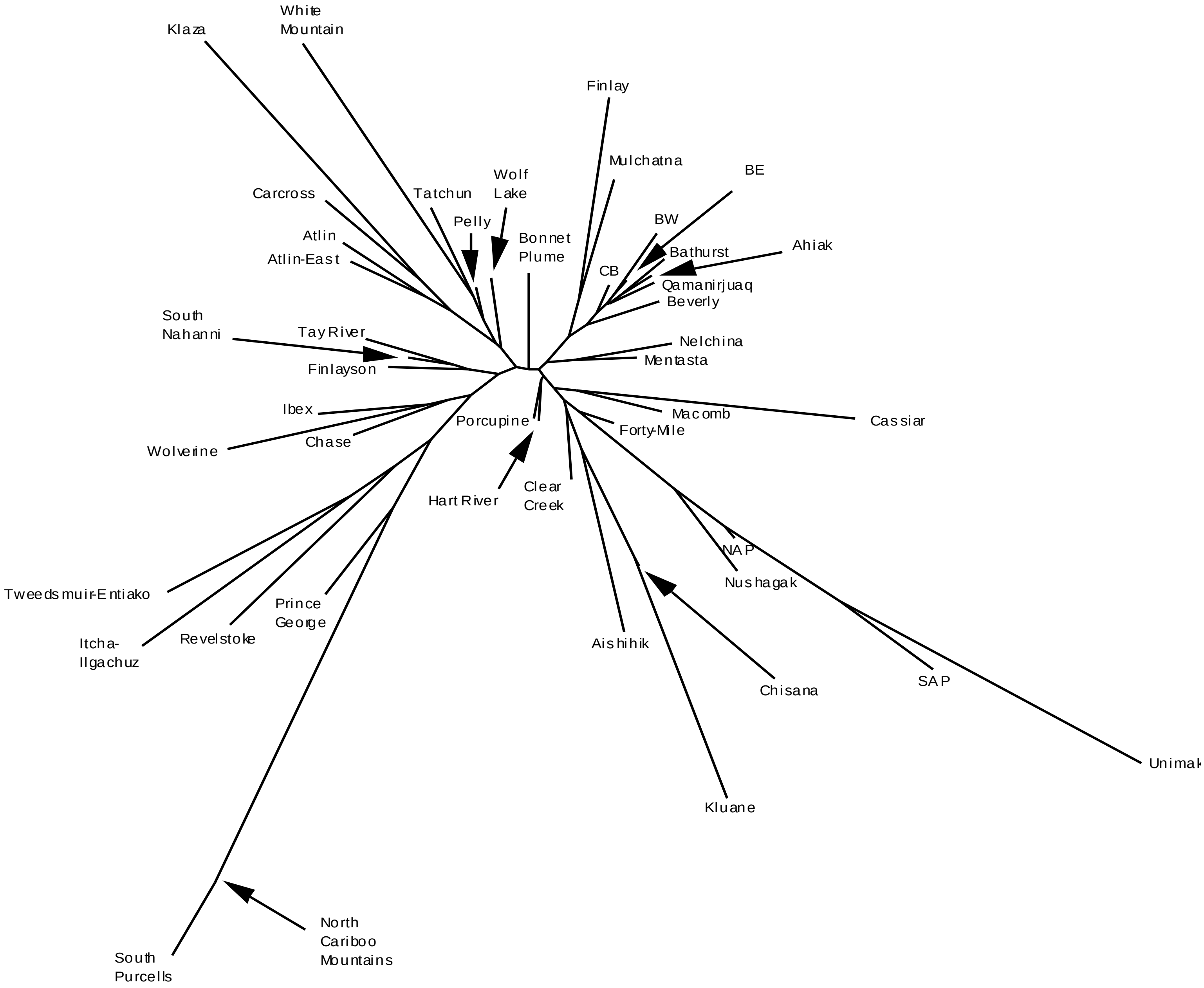

Figure 3. Unrooted neighbour-joining tree reflecting Nei's standard genetic distance (D_S) among woodland, Grant's and barren-ground caribou herds.

DISCUSSION

Genetic variation

The levels of genetic diversity measured in the woodland and Grant's caribou herds are highly variable (Table 8). Variation ranged from extremely low levels (A = 4.9, H_E = 53%, $p\mathrm{I} = 1.5\times10^{-5}$) in the potentially inbred South Purcells herd to very high levels that resemble those in the large, migratory herds. A high H_E and low pI reflect high levels of variation. Both these measures showed higher variation in the woodland and Grant's herds than reported for populations on the Canadian Arctic Islands (Part 1, this study; Zittlau *et al.*, 1999), but lower variation than that reported for the mainland barren-ground and Porcupine herds (Part 2, this study; Nagy *et al.*, 1999).

In many instances, levels of genetic variation reflect current population trends (i.e. stable, increasing, or decreasing) and/or differences in population size. For example, herds belonging to the Mountain woodland ecotype are significantly less variable than those of the Northern woodland ecotype. Their low levels of diversity likely reflect of the extensive habitat fragmentation within their range. These herds are small in size and potential for dispersal among them has become reduced (Spalding 2000). Therefore, genetic variation has been lost over time due to genetic drift. This effect has been exacerbated by the genetic bottlenecks that many of the Mountain woodland herds have experienced (K. Zittlau, unpublished data). In contrast, much less fragmentation has occurred within the Northern ecotype range and these caribou exhibit considerable gene flow among herds. Furthermore, the Northern woodland herds are much larger in size than Mountain woodland herds (Heard and Vagt, 1998) and, as would be expected for larger populations, they have not lost genetic variation at the same rapid rate as the Mountain woodland caribou. Comparisons among Grant's caribou show a similar pattern. Many Interior Alaskan herds are significantly more variable than many Coastal Alaskan herds. The Coastal herds are generally smaller in size and often have limited gene flow among them, which has likely led to a decrease in their genetic diversity.

Nonetheless, in contrast to the examples described above, a correlation between genetic diversity and population trends and/or size does not apply to all herds. The Chisana herd in the Yukon Territory has higher levels of genetic variation than would be expected from its declining status. The Chisana herd has been decreasing in size over recent years due to extremely low calf recruitment rates as a result of wolf predation (Yukon Fish and Wildlife Branch, 1994). As mostly young individuals are affected by wolf predation, the gene pool of the population is not largely influenced; adult caribou still exist within the population and their alleles will not be lost from the population until they die. Genetic diversity is only lost between generations. Consequently, the genetic variation of the herd has not changed because only the age structure within the population has shifted while the gene pool has remained constant. Nonetheless, unless recruitment rates are improved, the population will continue to age, mortality rates will similarly increase, and the herd will begin to rapidly lose genetic diversity. A captive-rearing program is currently being established to reduce the effects of wolf predation on the herd and to consequently increase the calf recruitment rate.

Genetic relatedness among woodland and Grant’s caribou

The woodland and Grant's caribou herds are more genetically differentiated than the barren-ground populations described in Part 2. Based on assignment test results, the Aishihik, Kluane, and Chisana herds are the three most genetically distinct of the woodland herds (Table 9). The Kluane and Chisana herds are distinct from each other because they are physically separated by Kluane Lake. However, the Aishihik and Kluane herd ranges are adjacent and may even overlap at certain times of the year. Consequently, these herds must be maintaining strict fidelity to their calving and rutting grounds to reflect such minimal gene flow between them.

Many of the Bonnet Plume and Hart River caribou cross-assigned to each other (Table 9). Both of these populations overlap with the Porcupine range, so it is possible that gene flow occurs among the three herds. The D_S tree shows that Porcupine and Hart River caribou are closely related, with the Bonnet Plume caribou positioned not too distantly from that node.

The North Cariboo Mountain and Cassiar caribou did not self-assign to their own population (Table 9). This is likely a factor of their small sample sizes (n = 4 and *n* = 9, respectively). However, it may alternatively reflect historic or current patterns of gene flow. Caribou from the North Cariboo Mountains most often assigned to the neighbouring Prince George herd. Gene flow may have, or may still be occurring among these populations, thereby maintaining genetic similarity among them. As these herds are geographically close, we suspect that these results are not an artefact of small sample size. Nonetheless, these results must be taken with caution and a further examination should be conducted. The Cassiar caribou most often assigned to the Pelly population, but also frequently to the South Nahanni and Chase herds. Possibly, high levels of gene flow occur into and out of the Cassiar herd due to the metapopulation dynamics of Northern woodland caribou. If levels of gene flow are high, the nine individuals examined from the Cassiar herd will likely not be representative of the entire herd.

Based on D_S, most Northern ecotype herds are more closely related to the Yukon woodland caribou than they are to the Mountain ecotype caribou in southern British Columbia (Figure 3). This relationship exists despite several of the Northern ecotype herds being more closely genetically related to the Mountain herds (i.e. Itcha-Ilgachuz and Tweedsmuir-Entiako). The Itcha-Ilgachuz and Tweedsmuir-Entiako herds occur within Mountain ecotype range and are as closely related to the Mountain ecotype herds as the Mountain herds are to each other.

Genetic regional differences exist among the Grant's herds in Alaska. Coastal herds are significantly differentiated from the interior herds. The small D_S values and the high number of cross-assignments reveal that many of the interior Alaskan herds were derived from the Fortymile herd. Likewise, the North Alaska Peninsula and the Nushagak herds have had substantial genetic interactions in the past. Several caribou from North Alaska Peninsula were transplanted to the

Nushagak herd about 15 years ago. The D_S suggests a stepwise pattern of genetic relatedness among the Grant's herds along the Alaska Peninsula. The pattern suggests that gene flow occurs primarily between neighbouring herds and that most movements occur in a southwest direction from the Alaskan interior toward the tip of the peninsula; the Unimak herd was derived from the South Alaska Peninsula herd, which originated from the North Alaska Peninsula herd. Furthermore, the Unimak herd is the most genetically distinct, suggesting that gene flow is limited across False Pass.

The regional differences in Alaskan Grant's caribou, in concert with the variable levels of genetic diversity and the varying degrees of interaction among many woodland and Grant's herds should all be considered when management decisions are made. In the past, several herds were managed together, yet based on our results, we suggest that woodland and Grant's caribou be managed as discrete populations to preserve their genetic distinctness.

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CONCLUSIONS OF THE WORKSHOP

The workshop culminated with a discussion of the information provided by the various position papers. The moderator, Dr. David Shackleton, invited all participants to address three main questions:

1) What information do genetic studies of caribou reveal?
2) How can current research be used to define conservation units for long-term caribou preservation, especially for arctic island caribou?
3) Where are the gaps in our knowledge?

What information do genetic studies of caribou reveal?

The genetic studies of caribou can reveal the degree of genetic diversity in populations and provide a method to describe caribou “groupings”. In addition, mitochondrial DNA (mtDNA) results may suggest that Peary caribou (*R. t. pearyi*) were not isolated in northern refugia during the last glaciation and that they migrated from other areas to populate the north. However, this position based on mtDNA data is not completely clear. Nuclear DNA analyses (microsatellites) should be more reflective of caribou recent history as these markers are neutrally inherited and often have high mutation rates. Therefore, we should concentrate more on nuclear DNA analyses to describe current groupings (conservation units) and use mtDNA to reveal longer-term relationships and evolutionary history.

Based on the analysis of nuclear DNA, patterns of genetic differentiation do not necessarily conform to existing caribou taxonomy. Grant’s caribou (*R. t.*

granti) are not distinct from other barren-ground caribou (*R. t. groenlandicus*). Woodland caribou, on the other hand, are genetically distinct from barren-ground caribou (*R. t. groenlandicus*). Various levels of genetic differentiation within the Peary caribou subspecies have also been identified.

The classification of the Dolphin and Union population should also be reconsidered. The inclusion of the Dolphin and Union population with barren-ground caribou could be disputed on the grounds of antler velvet colour; based on velvet colour, Dolphin and Union should be grouped with Peary caribou. However, according to all other evidence, including nuclear DNA analyses, the Dolphin and Union population warrants being considered as a unique entity in the caribou world. It does not fall clearly into either the *pearyi* group or the *groenlandicus* group, but shares characteristics from each. The population's genetic makeup, distinctive morphology, ecology, and physiological, physical, and behavioural adaptations to its environment make a distinct contribution to the biodiversity of caribou in Canada that warrants recognition and protection.

How can current research be used to define conservation units for long-term caribou preservation, especially for arctic island caribou?

Several participants agreed that nuclear DNA provides the best available data to work with but that groupings should not be based entirely upon the genetic analyses. It is recommended that we consider all of the existing evidence (e.g. nuclear DNA, distinctions in morphology, ecology – spatial and temporal range-use patterns – and physiological and behavioural adaptations forged by the environment) for defining conservation units. Furthermore, distinct units should also be based upon population size and degree of heterozygosity. This collective consideration would provide the soundest approach for maximizing the maintenance of biodiversity among these caribou, which, when followed, would lead to their division into at least four ecological units on the Canadian Arctic Islands and Boothia Peninsula.

Most importantly, it is paramount to have ongoing monitoring of all populations and that all populations, except the Dolphin and Union population, should be surveyed and analyzed as a “complex” (or geographical eco-unit) for data integrity. The Dolphin and Union population stands by itself as a distinct genetic entity.

It is important to note that discord exists between how the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) views designatable units and how nuclear DNA data “suggests” designatable units. This discord could negatively impact some northern caribou populations. This concern introduced two additional questions:

a) Which criteria should be used to develop the “groupings”?

One of the objectives of the workshop was to deal with the issue of how caribou groupings should be structured in the context of COSEWIC and under the Species at Risk Act (SARA).

According to nuclear DNA results, five groupings of caribou should be recognized on the Canadian Arctic Islands:

1) Bathurst Island complex and Melville Island populations
2) Banks Island and Minto Inlet populations

3) Dolphin and Union population
4) Boothia Peninsula population
5) Prince of Wales-Somerset Islands population

Potentially, these groupings based on nuclear DNA data would work for the purposes of population “status designation” and “harvest”. However, it is unclear what these groups would mean within a management context. If populations were managed effectively, the genetic diversity and relationships should not be an issue.

Unfortunately, these five groups do not, in fact, meet the criteria outlined in the COSEWIC guidelines document. COSEWIC tends to “lump” populations until there is sufficient evidence that requires them to “split” the populations. The IUCN/COSEWIC status of “Threatened” may be met even when “lumping” caribou from different populations.

Nonetheless, recent population trends also support these groupings. Some populations have declined by 50% to 85% in a single year. More importantly, the overall decline has been continual during the last four decades of the 20th century. These cataclysmic die-offs merit smaller designatable conservation units than are currently recognized to preserve the distinct biodiversity that remains within each of the separate caribou complexes. Smaller designatable units could allow for the continued contribution of those caribou to the biodiversity of caribou in Canada.

b) What should the groupings be called?

Following the debate concerning the identification of appropriate caribou groupings, a short discussion ensued relating to the use of the term “meta-populations”. Alternative names for caribou groupings include:

- Conservation Units
- Nationally Important Conservation Units
- Ecological Populations

Although there was concern with the how the term “ecotype” is being used, no alternatives to this term were suggested.

Where are the gaps in our knowledge?

The panel discussions revealed that several gaps exist in our current knowledge about caribou classification. The following areas need to be addressed for a complete assessment of caribou conservation.

1) Banfield’s (1961) taxonomy, which was based mostly on skeletal material, should be re-examined and its relationship to molecular taxonomy for caribou should be assessed.
2) Mitochondrial DNA data is incomplete. Additional mtDNA sequence data is required from all populations and preferably from different time points in history to provide a comprehensive view of longer-term relationships and evolutionary history of caribou.
3) The congruity between mtDNA and nuclear DNA data needs to be improved. To date, the different molecular tools have been used to examine different populations. An examination of the same populations

with the different tools should broaden our knowledge of caribou relationships.

4) A phylogenetic analysis based on nuclear DNA data should be constructed.
5) Trait loci responsible for adaptation to different environments should be identified.
6) Data collection and sampling design should be synchronized among government agencies and universities for future studies.

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