# Genetic diversity, structure and gene flow of migratory barren-ground caribou (*Rangifer tarandus groenlandicus*) in Canada

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*Abstract:* Migratory barren-ground caribou (*Rangifer tarandus groenlandicus*) provide an opportunity to examine the genetic population structure of a migratory large mammal whose movements and distribution, in some instances, have not been heavily influenced by human activities that result in habitat loss or fragmentation. These caribou have likely reached large effective population sizes since their rapid radiation during the early Holocene despite cyclic changes in abundance. Migratory barren-ground caribou are managed as discrete subpopulations. We investigated genetic variation among those subpopulations to determine the patterns of genetic diversity within and among them, and the implications for long-term persistence of caribou. We identified three distinct genetic clusters across the Canadian arctic tundra: the first cluster consisted of all fully-continental migratory barren-ground subpopulations; the second cluster was the Dolphin and Union caribou; and the third cluster was caribou from Southampton Island. The Southampton Island caribou are especially genetically distinct from the other barren-ground type caribou. Gene flow among subpopulations varied across the range. Occasional gene flow across the sea-ice is likely the reason for high levels of genetic variation in the Dolphin and Union subpopulation, which experienced very low numbers in the past. These results suggest that for most migratory caribou subpopulations, connectivity among subpopulations plays an important role in maintaining natural genetic diversity. Our analyses provide insight into the levels of microsatellite genetic diversity and patterns of gene flow that may be common to large subpopulations that historically had a continuous distribution across a large continental range. These data can also be used as a benchmark to compare the effects of habitat fragmentation and bottlenecks on other large caribou populations.

**Key words**: barren-ground caribou; Canadian arctic; conservation; dispersal; gene flow; genetic variation; large effective population; microsatellite DNA; population structure; *Rangifer*.

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## Introduction

Migratory barren-ground caribou (*Rangifer tarandus groenlandicus*) provide the opportunity to examine the genetic population structure of a large mammal that, in many instances, still has much of its annual range relatively intact and is not yet known to have been heavily influenced by human activities that result in habitat loss or fragmentation – although this is changing rapidly. In North America, migratory barren-ground caribou have likely reached large effective population sizes since their rapid radiation during the early Holocene (Yannic *et al.*, 2014b). Effective population size estimates range from 1000s to several 100 000s, with regular natural fluctuations in size over a 40- to 70-year period (Gunn, 2003; Hurst, 2004). One reason for the large population sizes of these caribou is that they occur primarily north of 60°N latitude, where agriculture and resource development have lagged behind other regions. Consequently, these caribou have not yet experienced significant habitat changes interrupting their seasonal migrations and their calving and post-calving range. Interruptions or deflections during migrations are a threat to most of the world's long-distance migratory terrestrial mammals (Berger, 2004). Describing dispersal and gene flow among these caribou will be useful for predicting future changes, such as those due to landscape alterations and warmer climates.

In Canada, barren-ground caribou of Yukon, Northwest Territories and Nunavut occur on the continental subarctic tundra, and include Baffin Island and the islands of Hudson Bay (e.g., Southampton, Coats, Mansel, and Prince Charles Islands). Mainland migratory barren-ground caribou typically migrate long distances annually to calve and summer on the tundra and winter within the boreal forest or on the tundra, while the tundra wintering subpopulations remain entirely on the mainland tundra or on islands (Nagy *et al.*, 2011). Due to its distinct phylogeny and migratory and gregarious behaviour, barren-ground caribou are assigned to a single Designatable Unit DU3 based on criteria outlined by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2011). The caribou that calve and summer on Victoria Island but winter on the continental coastal tundra – the Dolphin and Union herd – are assigned to a separate Designatable Unit DU2 (COSEWIC, 2011).

In close proximity of the continental migratory caribou are two island subpopulations, Victoria Island (Dolphin and Union caribou) and Southampton Island, both of which have experienced historic low numbers and size fluctuations (Nishi & Gunn, 2004; Campbell, 2006; Campbell & Boulanger, 2015). In 1968, 48 caribou were introduced to Southampton Island from nearby Coats Island (Parker, 1975) and by 1997 the population had rapidly increased to an estimated 30 000 caribou (Heard & Ouellet, 1994; Campbell, 2006; Campbell & Boulanger, 2015). The caribou on Southampton Island have declined since 1997, which correlated with an increased prevalence in the pathogen *Brucellosis suis* and a corresponding reduction in pregnancy rates (Ouellet *et al.,* 1996; Campbell & Boulanger, 2015) – and declined to an estimated 7286 caribou by 2013 (Campbell & Boulanger, 2015). There is no direct evidence of movement of caribou onto or off of Southampton Island up until 2013.

Dolphin and Union caribou on Victoria Island formerly were a large subpopulation and recognized as distinct morphologically, being more similar to Peary caribou (*R. t. pearyi*) than barren-ground caribou (Manning 1960). Abundance may have been as many as 100 000 caribou in the late 1800s (Manning, 1960), and was reduced to a possible few 100 in the early 1900s, before recovering to and remaining relatively stable between 1997 and 2007 at about 27 000 (Dumond & Lee, 2013). The 2015 survey and local knowledge indicate that

the Dolphin and Union caribou has declined since 1997 and 2007 (L.-M. Leclerc, unpublished data; M. Tomaselli, unpublished data). These caribou typically migrate annually in the fall across the Dolphin and Union Strait to the coastal mainland, but later timing of sea-ice freeze-up has occasionally delayed such movements (Poole *et al.,* 2010). Despite its apparent stability between 1997 and 2007, the Dolphin and Union is an important focus because the subpopulation may be at risk of negative cumulative effects from a combination of environmental variations (e.g., timing and extent of sea-ice freeze-up), increasing human activity (e.g., mining, resource exploration, marine traffic) and increased predators on their summer range (Dumond *et al.*, 2007; Poole *et al.,* 2010; Dumond *et al.,* 2013; Post *et al.*, 2013).

Migratory barren-ground caribou are managed as discrete subpopulations. Cluster analyses of satellite-collared cows indicate that barren-ground caribou occur as geographically distinct subpopulations (Nagy *et al.*, 2011). The assumption is that female caribou maintain these affiliations with other female caribou through fidelity to a calving ground and throughout the calendar year. Although the relationship between calving associations of cows during the rutting and calving seasons has not been analysed for most subpopulations, there is evidence for that association in some subpopulations (Roffler *et al.*, 2012; Gunn *et al.,* 2013). Male breeding strategies likely differ from those of females and may impose a contrasting effect on population structure among migratory tundra caribou (Roffler *et al.*, 2012).

Genetic differentiation and gene flow patterns have yet to be comprehensively explored among Canadian migratory barren-ground caribou. As the subpopulations are geographically separate during the rut and differ demographically from each other, we might expect genetic differentiation to occur. However, radio-collar studies of female caribou have shown a low level of switching between calving grounds over extended periods of time, and more punctuated high levels of switching at other times when examined over the long term (Heard & Stenhouse, 1992; Bergerud *et al.*, 2008; Campbell *et al.*, 2012). Genetic information should allow us to examine long-term trends of distinction in the migratory barren-ground caribou in Canada as compared to the relatively short-term (~2 to 3 generations) information generated by telemetry.

This study is based on previous work on barren-ground caribou that examined genetic diversity using a set of eight molecular markers, offering less power to detect more subtle genetic structure among subpopulations (Zittlau, 2004). Here, we provide an expanded dataset based on more recently collected samples and a larger suite of 18 microsatellite loci for investigating genetic variation, structure, and gene flow among migratory and island barren-ground caribou subpopulations across western Arctic Canada. Specifically, we test the prediction that genetic structure exists within the entire set of migratory tundra caribou, and we explore the impact of past demographic events and present-day gene flow on genetic diversity patterns among these subpopulations. We explore the implication of these patterns on long-term persistence of caribou. This work provides migratory-scale coverage of genetic structure among barren-ground caribou.

## Materials and Methods

*Sample collection*

Muscle, skin, blood and hair were collected from 256 specimens from 6 subpopulations (Table 1). For the Beverly (BEV) and Ahiak (AH) subpopulation(s), samples were obtained from caribou that calved on the Inland Beverly calving ground (n = 30) and on the Queen Maud Gulf (QMG) calving ground (n = 16). These samples, collected during the early post-calving period, could be from the Beverly

Table 1. Sample characteristics and genetic variation of Canadian migratory barren-ground caribou subpopulations.

| Subpopulation | Year collected | # known males | # known females | # unknown sex | Total sample size (n) | $H_E$[1] | $H_O$[2] | $N_{AR}$[3] | $F_{IS}$[4] |
|---|---|---|---|---|---|---|---|---|---|
| Bluenose-East (BE) | 2008-10 | 11 | 25 | 1 | 37 | 0.86 | 0.84 | 10.7 | 0.030 |
| Bathurst (BAT) | 2009-10 | 0 | 20 | 0 | 20 | 0.87 | 0.86 | 11.6 | 0.015 |
| Qamanirjuaq (QAM) | 2005-06 | 11 | 39 | 2 | 52 | 0.86 | 0.84 | 11.0 | 0.029 |
| Beverly/Ahiak [5] (BEV/AH) | 2007-08 | 0 | 46 | 0 | 46 | 0.87 | 0.88 | 11.3 | -0.005 |
| Dolphin & Union (DU) | 2007 | 6 | 37 | 0 | 43 | 0.83 | 0.83 | 8.9 | -0.007 |
| Southampton Island (SH) | 2004 | 0 | 0 | 58 | 58 | 0.67 | 0.67 | 4.6 | 0.007 |

[1] Expected unbiased heterozygosity
[2] Observed heterozygosity
[3] Allelic richness, based on a minimum sample size of 20 individuals
[4] Inbreeding coefficient
[5] Specimens may be from Beverly and/or Ahiak herds

subpopulation, or the Ahiak subpopulation, or a mixture of both (Nagy *et al.*, 2011; Campbell *et al.*, 2012; Adamczewski *et al.*, 2015). Calving grounds for the mainland subpopulations are shown in Figure 1. Sex information was available for 195 specimens: 167 females from Beverly and/or Ahiak ($n_f$ = 46), Bathurst ($n_f$ = 20), Bluenose-East ($n_f$ = 25), Qamanirjuaq ($n_f$ = 39), and Dolphin and Union ($n_f$ = 37); and 28 males from Bluenose-East ($n_m$ = 11), Qamanirjuaq ($n_m$ = 11), and Dolphin and Union ($n_m$ = 6). Sex information was not used for the Southampton Island specimens.

All laboratory analyses were performed by Wildlife Genetics International, Inc. (Nelson, BC). DNA was isolated using silica spin columns (QIAGEN Inc., Mississauga, ON). Each DNA sample was amplified at 18 microsatellite loci in 8 separate PCR reactions, following Serrouya *et al.* (2012). The microsatellite loci were Rt1, Rt5, Rt6, Rt7, Rt9, Rt24, Rt27 (Wilson *et al.*, 1997); BM4513, BM6506, BM1788, BM745, BL42 (Bishop *et al.*, 1994); FCB193 (Steffen *et al.*, 1993); NVHRT16, NVHRT30 (Røed & Midthjell, 1998); CRH (Moore *et al.*, 1992); and OhemD, OhemQ (Jones *et al.* 2000). Genotypes were analysed using a 310 Automated Sequencer (Perkin-Elmer Biosystems) and ABI Genotyper® 2.0 software (Applied Biosystems, Inc., Foster City, CA). All genotypes met standard thresholds for confidence based on legibility and strength, according to minimum criteria outlined by Paetkau (2003).

To ensure that the suite of 18 microsatellites was sufficiently informative, we assessed all loci for their mean polymorphic information content, according to Botstein *et al.* (1980). We used Hardy-Weinberg exact tests (Genepop Version 4.0; Rousset, 2008) to assess deviations from Hardy-Weinberg Equilibrium (HWE) due to non-random association of alleles from different loci (i.e., linkage disequilibrium) and heterozygote deficits within subpopulations. These assessments can confirm whether genotype probabilities are determined solely by allele frequencies, rather than being influenced

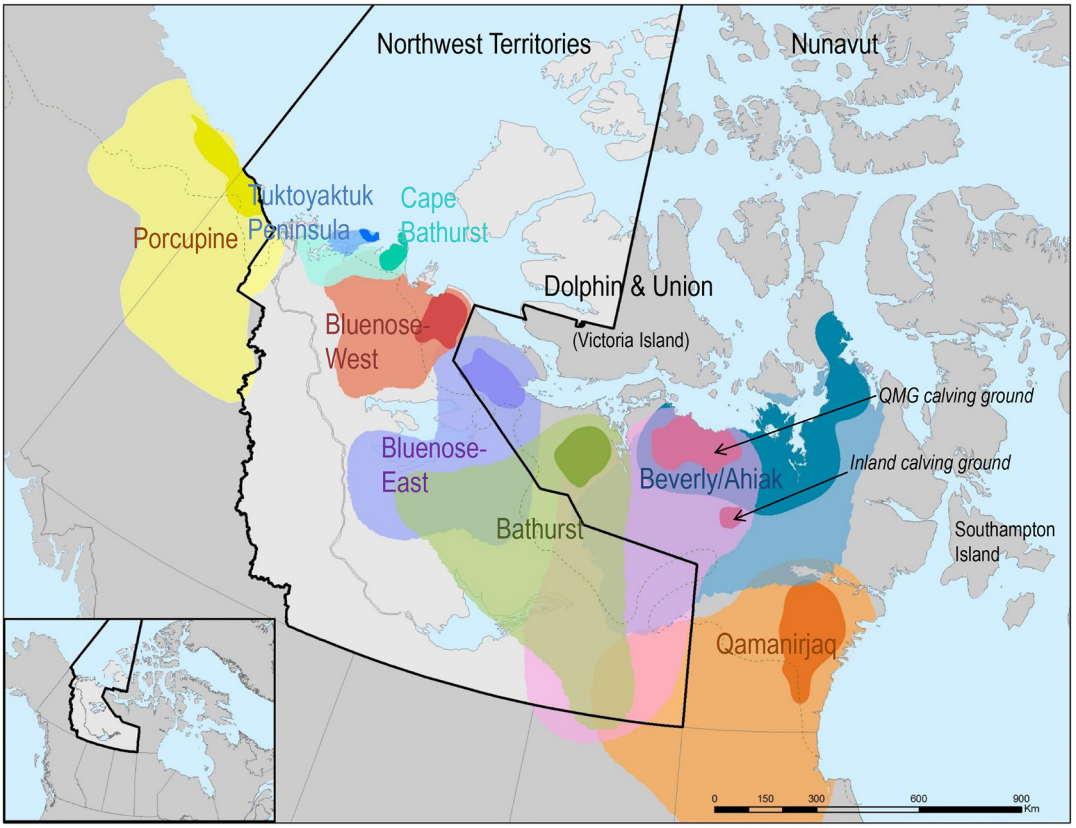


Figure 1. Calving grounds of North American barren-ground caribou subpopulations. Darker shades denote areas used by greater numbers of caribou. There are two major calving grounds within the range of the Beverly and Ahiak subpopulations: the Queen Maud Gulf (QMG) calving ground and the Inland Beverly calving ground. The dark blue shaded area encompasses several calving areas based on 95% utilization distribution for calving caribou across years. The mainland subpopulations from this study include Bluenose-Ease, Bathurst, Beverly/Ahiak (which may include either Beverly or Ahiak caribou, or a mixture of both), and Qamanirjuaq; island subpopulations from this study include Dolphin and Union and Southampton Island. This map was modified from a map of mainland subpopulation calving grounds provided by B. Fournier, Department of Environment and Natural Resources, Government of Northwest Territories.

by other factors such as selection, linkage, or assortative mating. Multiple tests were accounted for using the Bonferroni correction. All data were further analyzed for the presence of null alleles using the online program, MICRO-CHECKER (van Oosterhout *et al.*, 2004).

*Genetic variation*

To measure genetic diversity in the subpopulations of migratory barren-ground caribou, we calculated heterozygosity (observed and unbiased expected; Nei & Roychoudhury, 1974), allelic richness ($N_{AR}$) and inbreeding coefficients ($F_{IS}$) using Fstat Version 2.9.3.2 (Goudet, 2002). Allelic richness provides a measure of allelic diversity that is standardized according to sample size – in this case, n = 20, the smallest sample in our dataset. Inbreeding coefficients test for non-random mating. We used t-tests to determine the potential for significant differences between measures of genetic variation in mainland and island subpopulations.

We tested each subpopulation for evidence of past genetic bottlenecks by using Bottleneck

Version 1.2.02 (Cornuet & Luikart, 1996). Bottleneck compares observed heterozygosity to that expected based on allelic diversity using a Wilcoxon signed-ranks test (Piry *et al.,* 1999). The Wilcoxon test can be powerful for datasets based on more than 10 polymorphic loci, even if sample sizes are not large (n < 40) (Cornuet & Luikart, 1996). We employed a two-phase model of mutation, with 95% of mutations attributed to a stepwise mutation model and 5% attributed to an infinite allele model.

*Genetic structure*

We used Bayesian assignment tests and genetic differentiation measures to determine if genetic structure exists within the entire set of barren-ground caribou.

For the Bayesian assignment tests, we estimated the number of genetic clusters (K) that occur within the dataset, assuming no *a priori* population designation for individuals (Structure; Pritchard *et al.,* 2000). Each chain was run with a burn-in period of 500 000 iterations, followed by an additional 500 000 iterations of data accumulation. K was estimated by performing three independent runs of K = 1 to 10. We identified the main structure of the data by plotting the change in ln likelihood over the range of K (Evanno *et al*., 2005) and we estimated the most likely number of genetic clusters by the value of K that produced the largest mean (± standard deviation) estimated ln probability of data (Pritchard *et al*., 2000). We determined membership to each genetic cluster according to the proportion of individual genotypes assigned to each cluster. To identify finer-scale population structure, a nested analysis of each identified cluster was performed using the same burn-in and run parameters.

Genetic differentiation between pairs of subpopulations was assessed in two ways. First, we calculated standard genetic differentiation measures: $F_{ST}$ (Fstat; Goudet, 2002; Weir & Cockerham, 1984) and Jost's $D_{EST}$ (Jost, 2008; Meirmans & Hedrick, 2011). $F_{ST}$ is the standard estimator of genetic differentiation used in most population genetic studies. However, for populations with high intra-population genetic variation levels, Jost's $D_{EST}$ is more suitable for estimating genetic differentiation (Jost, 2008; Heller & Siegismund, 2009; Meirmans & Hedrick, 2011). Both of these measures should be used with caution when assessing genetic differentiation because values approach zero when gene diversity is high (Jost, 2008). Pairwise genetic differentiation between subpopulations were permutated 1000 times to assess significance. To account for multiple tests, error rates were adjusted using a sequential Bonferroni test (Rice, 1989).

Next, we calculated genetic distances: Nei's genetic distance ($D_S$; Nei, 1972) and average-square distance (ASD; Goldstein *et al*., 1995). Both of these distance measures avoid the biases of $F_{ST}$ and $D_{EST}$ that can lead highly distinct subpopulations to appear to be less distinct than they should (Jost, 2008). Nei's genetic distance is one of the most commonly used measures of genetic distance based on microsatellite markers, and has been shown to increase linearly with time (Nei, 1972; Paetkau *et al*., 1997), permitting its use in estimating divergence patterns. Sun *et al*. (2009) showed that ASD can also be applied to microsatellites to estimate divergence times between populations within the last 2 000 000 years. The use of ASD as a molecular clock requires that values be calibrated for sequence divergence and corrected for inflated estimates (Sun *et al*., 2009). To achieve this for caribou, we applied sequence divergence estimates from Cronin *et al*. (2005) and Eger *et al*. (2009).

*Gene flow*

We estimated both historical and contemporary gene flow patterns among the entire set of barren-ground caribou, as well as among only males and only females.

First, we estimated historical gene flow (several hundred years before present) between mainland and island subpopulations using a coalescent-based model (Migrate-N Version 3.6; Beerli & Felsenstein, 2001; Beerli, 2006). Due to their high degree of genetic diversity and low levels of genetic differentiation, we combined the mainland subpopulations of BE, BAT, QAM and BEV/AH into a single grouping so that estimates would reach convergence. For the male-only data, mainland subpopulations included BE and QAM. The separate assessments of male and female gene flow across the sea ice were performed between mainland and DU subpopulations only, because no sex information was available for SH.

Migrate-N aims to reflect biological reality of historical gene flow by allowing for asymmetric dispersal, unequal population sizes, and deviations from Hardy-Weinberg expectations. In our analyses, each chain was run with a burn-in period of 50 000 iterations, followed by 100 000 recorded steps with a sampling increment of 100. Results were averaged across four replicates. We used a Brownian motion mutation model with constant rates across all loci. To eliminate effects from differences in population size, individuals were randomized within populations. We set uniform prior distributions to estimate mutation-scaled parameters θ (range = 0–1000, mean = 100) and M (range = 0–100, mean = 10), with starting values based on $F_{ST}$ calculations. We calculated effective number of immigrants according to $N_em = (\theta\ M)/4$. To confirm convergence, we performed nine independent runs, each with increased run lengths and starting with a different random seed number. Results are reported from the final (ninth) run.

Next, we estimated contemporary gene flow rates using a multilocus assignment approach that estimates gene flow within the last three generations (BAYESASS 3.0.3; Wilson & Rannala, 2003). To provide a comparison with historical rates, we estimated contemporary gene flow between mainland and island subpopulations by combining all mainland caribou into a single grouping, as described above. The separate assessments of male and female gene flow across the sea ice were performed between mainland and DU only, because no sex information was available for SH. We also estimated contemporary gene flow among males and females from individual mainland subpopulations.

BAYESASS also aims to reflect biological reality by allowing for asymmetric gene flow, unequal population sizes and deviations from Hardy-Weinberg expectations. In our analyses, each chain was run with a burn-in period of 1 000 000 iterations, followed by an additional 10 000 000 iterations of data accumulation and a sampling frequency of 100. Mixing parameters were set at 0.50 for allele frequencies, migration rates and inbreeding coefficients for the female-only and all-caribou datasets. Male-only data sets had mixing parameters set to 0.50 (allele frequencies) and 0.70 (migration rates and inbreeding coefficients). To confirm convergence of data, we plotted the trace file using TRACER v1.6 (Rambaut *et al.,* 2014), to ensure that the log probabilities showed regular oscillations around a plateau, and we also conducted three separate runs, each initialized with a different seed number, to ensure that posterior mean parameter estimates showed concordance.

## Results

We obtained 18-locus genotypes for 256 barren-ground caribou from six sample sets (Table 1). Polymorphic information content of the expanded suite of loci was similar to the original set of eight loci, ranging from 0.70 to 0.86. Heterozygote deficiency was not significant in any of the 108 locus-population comparisons (Bonferroni-corrected $p > 0.0005$). Similarly, no null alleles were identified using

MICROCHECKER. Among the locus-locus comparisons, 3 of the 153 comparisons showed significant linkage disequilibrium (RT7/RT6, Fcb193/BL42, BM6506/OhemD). All loci were retained for subsequent analyses.

*Genetic variation*

Among the barren-ground caribou, three distinct levels of genetic variation were observed: SH ($H_E$=67%, $N_{AR}$ = 4.6), DU ($H_E$ = 83%, $N_{AR}$ = 8.9), and the entire group of mainland subpopulations (mean $H_E$=87%, mean $N_{AR}$ = 11.2) (Table 1). Each island subpopulation exhibited significantly distinct levels of variation from each other and the mainland ($p < 0.01$), with SH being the least genetically variable. Inbreeding coefficients did not significantly differ from zero (Bonferroni-corrected $p > 0.0005$). Genetic signatures of past bottlenecks were not detected, as estimated by tests of heterozygosity excess or deficit (Bonferroni-corrected $p > 0.0005$).

*Genetic structure*

Among the entire set of barren-ground caribou, we determined that the main genetic structure was best represented by K = 2, based on the largest ΔK and mean LnP(D), but there was also genetic structure at K = 3, based on the highest mean ln probability of the data (Figure 2). Individual probabilities of assignment to each of the genetic clusters showed that SH was genetically distinct from the mainland and DU subpopulations (Figure 3A). Additional genetic structure was evident between the mainland and DU subpopulations, at K = 3 (Figure 3B). The first genetic cluster (Cluster 1) consisted of caribou from the mainland subpopulations (BE, BAT, QAM and BEV/AH), the second genetic cluster (Cluster 2) consisted of island caribou from DU, and the third genetic cluster (Cluster 3) consisted of island caribou from SH. At K = 4, no additional meaningful genetic structure was evident (Figure 3C). In all cases, assignment probabilities were highest among

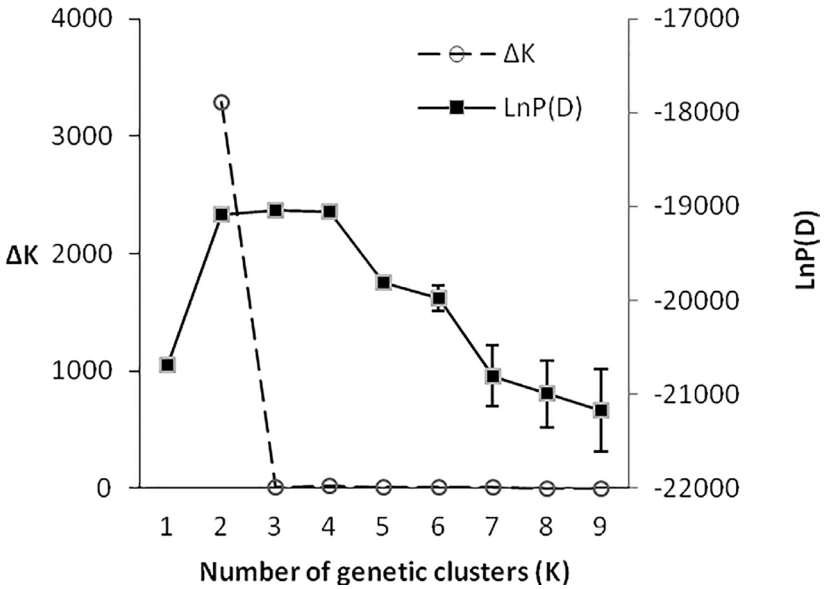


Figure 2. The rate of change in log-likelihood values (ΔK) and the mean (± standard deviation) ln likelihood (LnP(D)) based on the estimated number of genetic clusters (K) among caribou. The largest ΔK value represents the most probable number of genetic clusters, calculated as $\Delta K = m|L''(K)|/s[L(K)]$. Values for K = 1 are invalid (Evanno *et al.,* 2005).

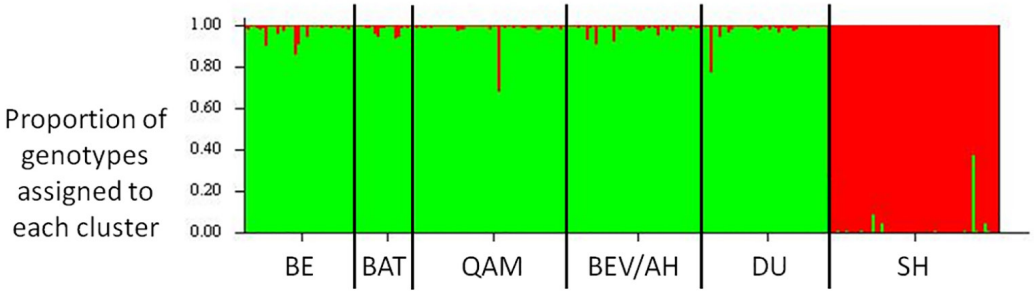


Figure 3A.

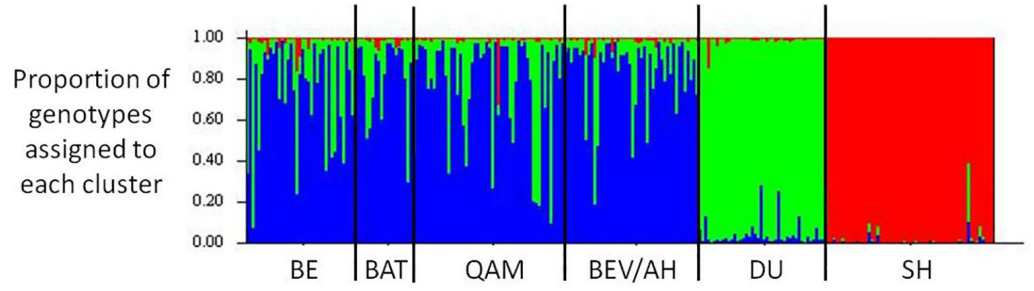


Figure 3B.

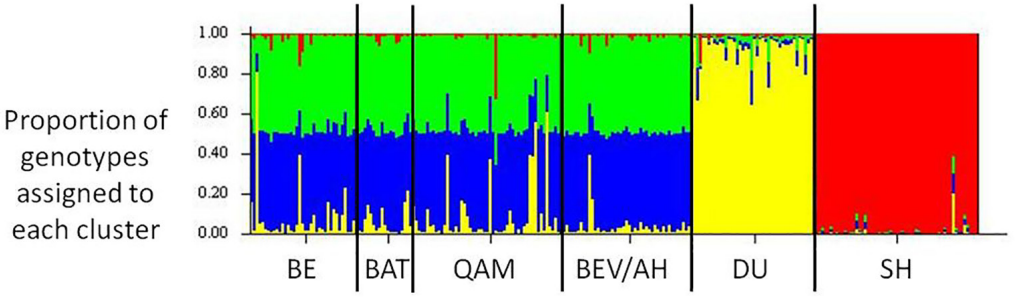


Figure 3C.

Figure 3. Individual inferred assignment probabilities based on STRUCTURE analysis among the entire set of 256 barren-ground caribou for A) K = 2, B) K = 3, and C) K = 4.

individuals assigning to Cluster 3 (SH). The individuals in Cluster 1 (mainland) showed some evidence of mixed ancestry, with small portions of their membership coming from Cluster 2 (DU) (Figure 3B; Figure 3C). Iterative testing of smaller groups of subpopulations did not show evidence of nested population structure among pairs of adjacent subpopulations.

Genetic differentiation measures also identified three genetically differentiated groups of caribou. Significant pairwise $F_{ST}$ and $D_{EST}$ values were measured from SH and DU subpopulations to all other subpopulations; pairwise $F_{ST}$ and $D_{EST}$ values among any of the other subpopulations were not significant (Table 2). For both genetic differentiation and genetic distance measures, largest values were attributed to SH (Table 2; Table 3). Slightly lower, but still significant, values were measured from the DU subpopulation.

*Gene flow*

Across the sea-ice, both historic and contemporary gene flow were estimated to occur at

Table 2. Genetic differentiation between pairs of subpopulation locations. $F_{ST}$[1] above diagonal; Jost's $D_{EST}$[2] below diagonal. Values significantly different from zero are in boldface font (α = 0.05). For explanation of abreviations of studied caribou herds, please see Table 1.

| | BE | BAT | QAM | BEV/AH | DU | SH |
|---|---|---|---|---|---|---|
| BE | | -0.001 | 0.000 | 0.001 | **0.017** | **0.124** |
| BAT | 0.010 | | 0.000 | -0.002 | **0.015** | **0.125** |
| QAM | 0.009 | 0.000 | | -0.001 | **0.018** | **0.129** |
| BEV/AH | 0.038 | 0.007 | -0.004 | | **0.019** | **0.121** |
| DU | **0.067** | **0.048** | **0.061** | **0.059** | | **0.142** |
| SH | **0.498** | **0.482** | **0.527** | **0.497** | **0.436** | |

[1] Goudet (2002)
[2] Jost (2008); Meirmans & Hedrick (2011)

Table 3. Genetic distances between pairs of subpopulation locations. Average-square distance[1] (ASD) is above the diagonal; Nei's standard genetic distance[2] ($D_S$) is below the diagonal. For explanation of abreviations of studied caribou herds, please see Table 1.

| | BE | BAT | QAM | BEV/AH | DU | SH |
|---|---|---|---|---|---|---|
| BE | | 131.4 | 115.7 | 119.5 | 116.8 | 111.0 |
| BAT | 0.12 | | 132.9 | 136.1 | 134.0 | 133.1 |
| QAM | 0.08 | 0.11 | | 120.2 | 112.2 | 120.9 |
| BEV/AH | 0.08 | 0.10 | 0.06 | | 120.9 | 122.5 |
| DU | 0.16 | 0.18 | 0.16 | 0.17 | | 123.6 |
| SH | 0.56 | 0.57 | 0.61 | 0.55 | 0.65 | |

[1] Goldstein *et al.* (1995)
[2] Nei (1972)

low levels (Figure 4; Figure 5). All historical estimates overlapped with each other and had 95% credibility intervals that encompassed zero at their lower limits. Male and female rates did not differ. The highest estimates of historic per-generation migrants ($N_e m$) and contemporary proportions of migrants (m) were found to occur between the mainland subpopulations and DU. Only contemporary male gene flow from DU to the mainland significantly differed from zero, based on 95% confidence intervals. These migrants were predominantly second-generation (i.e., hybrid offspring of migrant individuals), rather than first-generation migrants (i.e., individuals that immigrated from a source population).

Across their continental range, contemporary gene flow rates and patterns differed between males and females (Figure 6A; Figure 6B), as determined by non-overlapping 95%

confidence intervals. Female gene flow among the mainland subpopulations occurred in a westward direction, out of QAM. All female migrants were first-generation migrants. Bidirectional male gene flow was detected between BE and QAM. Male migrants were a mixture of first- and second-generation migrants.

## Discussion

We identified three distinct genetic clusters of caribou across the barren-ground caribou range: the largest cluster consisted of the continental barren-ground caribou subpopulations (BE, BAT, QAM and BEV/AH), the second cluster consisted of caribou from the Dolphin and Union subpopulation, and the third cluster was caribou from Southampton Island. This genetic structure is characterized by variable gene flow patterns.

Our data provide insight into common uncertainties and apparent contradictions about caribou population structure. Recent analyses of telemetry data suggest that spatial affiliations of females across annual seasonal ranges and fidelity to calving grounds is a relatively robust basis for subpopulation designation (Nagy *et al.*, 2011), while recognizing that fluctuations in abundance can change spatial affiliations (Hinkes *et al.*, 2005; Gunn *et al.*, 2012; Adamczewski *et al.*, 2015). However, previous population genetic data suggest homogeneous population structure across the range (Zittlau, 2004). The findings from this study support all of these aspects and reveal subtle influences of gene flow.

### *Gene flow patterns*

Based on gene flow patterns, caribou dispersal across the sea-ice occurs infrequently and at low levels (Figure 4; Figure 5). According to our estimates, this pattern of movement has likely been consistently low over time. However, we recognize that these data house a degree of uncertainty as they are based on a single sampling period, which may neglect to identify key elements of punctuated gene flow, if it had occurred.

Among continental caribou, female spatial affiliations form the basis for recognizing caribou subpopulations, and this basis is well-supported by telemetry data (Nagy *et al.,* 2011) and genetic studies of *R. t. granti* (Roffler *et al.,* 2012). Our estimates of contemporary gene flow (which we take to be about the past 21–27 years prior to sample collection, assuming an average caribou generation time of about 7–9 years), suggest that occasional female dispersal occurs across the continental tundra, with the highest levels of recent movements occurring in a westward direction (Figure 6A). All of the contemporary migrant females were first-generation migrants, suggesting those westward movements occur infrequently, as very few hybrid offspring of migrant caribou were detected within the sample. Long-distance eastward movements were not detected between females from any group of adjacent subpopulations. If movements occurred more regularly, we would expect to see higher proportions of second-generation migrants (i.e., hybrids). However, as indicated above, one single sampling period is less likely to capture punctuated movements than multiple sampling years. Similarly, one single sampling period may also not have captured punctuated eastward movements.

In contrast to female movements, male dispersal may be more regular and frequent across the mainland range, as revealed by a combination of first- and second-generation male migrants. Contemporary male dispersal was bidirectional across the mainland (Figure 6B). As with the females, these data are also based on a single sampling period, which may neglect to identify key elements of punctuated gene flow. While the sex-biased differences in gene flow are interesting, we view these results as preliminary and approach conclusions with caution, as these gene flow patterns occur within a system

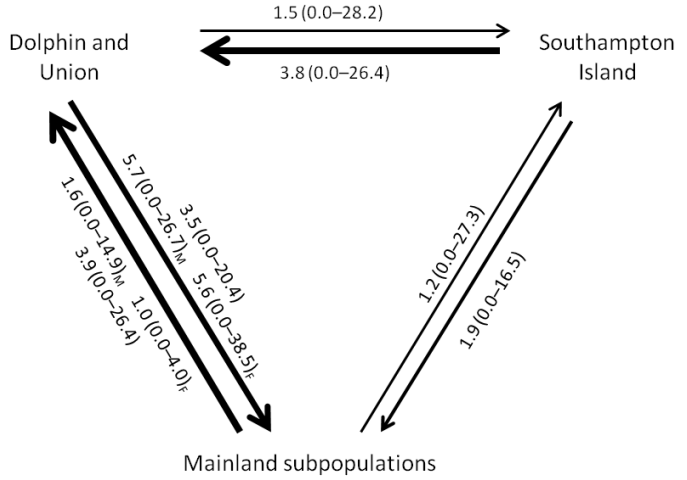


Figure 4. Historical gene flow estimates ($N_e m$) between the mainland and island subpopulations. 95% credibility intervals are indicated in parentheses. Arrow thickness is scaled according to values. Values reflect estimated number of migrants per generation among all migratory barren-ground caribou, unless indicated by the subscripts "M" (male-only data) or "F" (female-only data). Mainland subpopulations include BE, BAT, QAM and BEV/AH for estimates based on the entire dataset and the female-only data; for the male-only data, mainland subpopulations include BE and QAM. Estimates into and out of Southampton Island include both males and females, as no sex information was available for SH.

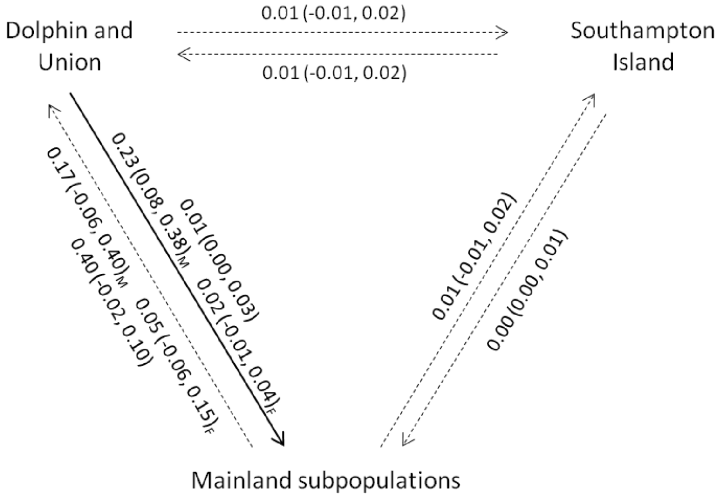


Figure 5. Contemporary gene flow rates (m) between the mainland and island subpopulations. 95% confidence intervals are in parentheses. Dashed arrows indicate values that do not significantly differ from zero based on 95% confidence intervals. Mainland subpopulations include BE and QAM for males (indicated by the subscript 'M'), and BE, BAT, QAM and BEV/AH for females (indicated by the subscript 'F'). Estimates into and out of Southampton Island include both males and females, as no sex information was available for SH. Male migrants were a mixture of first- and second-generation migrants.

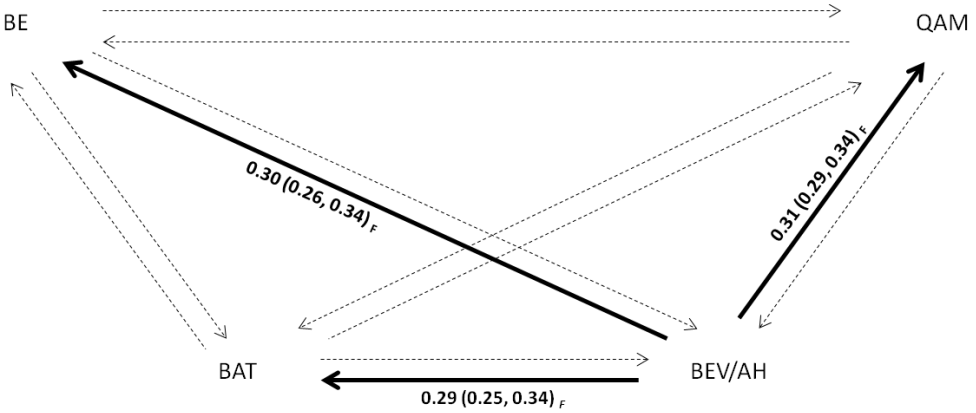


Figure 6A.

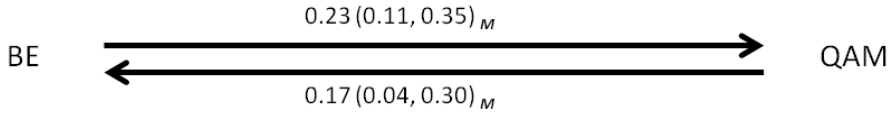


Figure 6B.

Figure 6. Contemporary gene flow rates between individual mainland subpopulations. Values indicate the proportion of migrants (m) from each subpopulation. 95% confidence intervals are in parentheses. Dashed arrows indicate values that did not significantly differ from zero based on 95% confidence intervals (all non-significant values were measured to be m = 0.01, with 95% confidence intervals that fell within -0.01, 0.04). A) Females-only. All female migrants were first-generation migrants. B) Males-only. Male migrants were a mixture of first- and second-generation migrants. Male gene flow into and out of BAT and BEV/AH was not examined because male samples were not available for those subpopulations.

that does not exhibit evidence of genetic structure (see Figure 3A). Also, because estimates of migrant ancestries are closely associated with allele frequencies, results based on the small male-only sample sets should be interpreted with care. Future studies with larger male-only and female-only datasets may reveal more insight on sex-biased gene flow across this region. These patterns of gene flow make it unlikely that genetic variation patterns of barren-ground caribou would correspond to management units. According to ear-tag and telemetry data, approximately <5% of cows may annually alter calving fidelity, without influencing overall subpopulation structure or management units (Parker, 1972; Adamczewski *et al.,* 2009; Roffler *et al.,* 2012). From a genetic perspective, immigration or emigration of only one migrant per subpopulation per generation is sufficient to homogenize gene pools (Mills & Allendorf, 1996). Even occasional or unidirectional dispersal would provide sufficient gene flow to homogenize gene pools across the mainland tundra range. These findings do not contradict the subpopulation structure for female caribou delineated through telemetry data, and confirm the genetic homogeneity of mainland barren-ground caribou.

An interesting finding was the moderate rates of historical dispersal between the mainland and Dolphin and Union subpopulations (Figure 4). These dispersals were likely caribou that crossed the sea-ice during the annual fall and spring migrations. Overlapping distribu-

tion of the smaller Dolphin and Union caribou with larger mainland caribou during winter has been reported by hunters from Inuit communities like Cambridge Bay (on Victoria Island), as the Dolphin and Union caribou are relatively distinct in appearance. This movement pattern appears to occur only occasionally, because historical rates have broad 95% confidence intervals that encompass zero, suggesting that during some years dispersal may not have occurred (Figure 4). During contemporary time periods, mostly first-generation migrants were identified, again suggesting that movements occur infrequently. These gene flow patterns reiterate the genetic structure of the data, which shows that Dolphin and Union caribou share genetic similarities with the mainland subpopulations, yet also maintain their genetic distinctness (Figure 2; Figure 3).

Variable gene flow reflects caribou responses to fluctuations and instabilities with respect to demography, environmental conditions, and behavioural modification from anthropogenic disturbance. Changes in dispersal rates do not occur independently from changes in abundance. Population abundance and distribution vary through regular fluctuations, with periods of high and low abundance (Morneau & Payette, 1998; Morneau & Payette, 2000; Zalatan *et al.,* 2006; Bergerud *et al.,* 2008), which likely influences dispersal and colonization of unoccupied ranges. Some of the annual variation in gene flow likely reflects caribou movement when population sizes were high and the likelihood of dispersal was greatest. Larger herds use larger ranges (Bergerud *et al.,* 2008), increasing the likelihood of overlap between neighbouring herds. When subpopulation abundance is low, rates of first-generation immigration and emigration would be most affected. Our samples were collected when subpopulation sizes were large or at most just beginning to decline (see collection dates in Table 1) – some of the subpopulations have changed in size or distribution during the past decade since our collection occurred. In addition, severe and infrequent environmental phenomena and anthropogenic mechanisms may also cause dispersal. For example, in southwest Yukon, genetic data have shown a partial replacement of caribou populations following the fall-out from the White River volcanic eruption (Kuhn *et al.*, 2010).

*Variation and population structure*

The pattern of genetic variation observed across the mainland migratory barren-ground caribou range is best explained by high levels of individual genetic variation. Migratory barren-ground caribou show greater microsatellite variation than most other North American large mammal species (e.g., boreal caribou (*R. t. caribou*; McLoughlin *et al.*, 2004), wapiti (*Cervus canadensis*; Røed & Midthjell, 1998; Polziehn *et al.,* 2000), pronghorn (*Antilocapra americana;* Sawyer *et al.*, 2005), moose (*Alces alces;* Røed & Midthjell, 1998; Broders *et al.,* 1999), muskoxen (*Ovibos moschatus*; Holm *et al.,* 1999), bison (*Bison bison*; Wilson & Strobeck, 1999), and white-tailed deer (*Odocoileus virginianus*; Anderson *et al.*, 2002; DeYoung *et al.*, 2013). The high heterozygosities and allelic richness values reflect the large effective population sizes and the lack of genetic drift and inbreeding within these subpopulations. The level of genetic diversity observed in the Canadian mainland barren-ground caribou is high even with respect to other ruminants that are relatively numerous and widely distributed. For example, African antelope species – topi (*Damaliscus korrigum*), eland (*Taurotragus oryx*), hartebeest (*Alcelaphus buselaphus*), Grant's gazelle (*Nanger granti*), and impala (*Aepyceros melampus*) – exhibit mean expected heterozygosities ranging from the topi at 60% to the eland at 76% (Eblate *et al.*, 2011). On the other hand, blue wildebeest (*Connochaetes taurinus*) in Tanzania, which reach higher numbers and are also strongly migratory, show similar levels of expected heterozygosity

as reported here for migratory tundra caribou (Røed *et al.*, 2011).

Occasional gene flow from the mainland to Dolphin and Union (Table 4; Figure 4) has reduced the genetic impact of the severe Dolphin and Union subpopulation decline from the early 1920s. Indeed, the peaks at K = 2 on the plots of ΔK and LnP(D) (Figure 2) indicate the occasional gene flow between mainland barren-ground caribou and the Dolphin and Union subpopulation. In comparison, genetic drift and isolation have limited the genetic recovery of the Southampton Island caribou from the low numbers of introduced caribou; Southampton Island caribou remain insular, and exhibit low genetic diversity as a result (Table 1). As a further consequence of genetic drift and isolation, the Southampton Island caribou have also become significantly genetically differentiated from other barren-ground type caribou (Figure 3). Examination by haplotype analyses would reveal further insight on their distinctness.

The lack of significance from genetic bottleneck tests, despite demographic histories that suggest otherwise, may be related to the population expansions of the Dolphin and Union and Southampton Island subpopulations. In general, caribou have high reproductive capacity and behavioural plasticity that could have enabled rapid expansions. If rapid expansions had occurred for the early Dolphin and Union and Southampton Island subpopulations, loss of diversity via genetic drift may be below the detectable levels by bottleneck tests. Some cervid populations have similarly shown a minimal loss of genetic diversity as a result of rapid expansion following a population bottleneck (Baker & Hoelzel, 2013; DeYoung *et al.*, 2013). The sensitivity of bottleneck signature methods depends on rates of genetic drift and may be limited beyond about 4Ne generations (Cornuet & Luikart, 1996; Luikart & Cornuet, 1998; Luikart *et al.*, 1998), which could also contribute to the lack of significant past genetic bottlenecks in these island subpopulations.

To put these diversity levels in context, among caribou expected heterozygosities of less than 80% are typically characteristic of insularity, a past bottleneck, and/or founder effect (Zittlau, 2004). Low heterozygosities are observed among many subpopulations of Peary caribou (*R. t. pearyi*) in the Canadian High Arctic, woodland caribou (*R. t. tarandus*) in Yukon Territory and British Columbia that experience limited gene flow due to geographic barriers, or past population bottlenecks due to habitat fragmentation (Zittlau *et al.,* 2000; Serrouya *et al.,* 2012; McFarlane *et al.,* 2014). Alternatively, there are woodland and Grant's subpopulations that have not experienced these influences and have heterozygosities exceeding 80%, (Roffler *et al.,* 2012; Weckworth *et al.,* 2012; Colson *et al.,* 2014). In light of this, subpopulations of tundra caribou with low diversity (e.g., < 70%) warrant close examination by wildlife managers. For subpopulations with low allelic richness values, the adaptive potential may become an area of concern if the subpopulation is isolated.

An important consideration pertaining to caribou subpopulation structure is the different lengths of time required for geographic or genetic differentiation to become apparent. Caribou exhibit behavioral plasticity (Gunn *et al.,* 2013; Hinkes *et al.*, 2015), which increases the likelihood that geographic and demographic distinctions between subpopulations develop quickly, whereas genetic evidence of such distinction by neutral genetic markers may take considerably longer. Theimer *et al.* (2012) suggest that the result of geographic separation may take a significant amount of time to become genetically evident and as of yet we lack any effective timeline for how long it takes in order to see these effects.

Our work complements past findings based on mitochondrial DNA studies. Numerous

studies have examined mitochondrial DNA to show that genetic variation patterns observed among North American caribou are best explained by genetic differentiation that occurred as a result of the last glaciation (Dueck 1998; Flagstad & Røed, 2003; Cronin *et al.,* 2005; Eger *et al.,* 2009; Weckworth *et al.,* 2012; Yannic *et al.*, 2014b). Mitochondrial DNA reflects longer time periods because mutation rates are slower (~10-6, compared to ~10-2–10-4 for microsatellites; Weber & Wong 1993; Schlötterer, 2000; Driscoll *et al.,* 2002; Sun *et al.,* 2012) and, therefore, mitochondrial DNA markers are often used for phylogenetic analyses, examining deep genetic differences on the order of 10s of 1000s of generations. Understandably, phylogenetic studies of mitochondrial DNA cannot examine recent gene flow and its influence on genetic subpopulation structure. Alternatively, genetic differences among microsatellite alleles reflect a fairly recent time-scale (<10 000 generations; Feldman *et al.*, 1997; Paetkau *et al.,* 1997), similar to the time frame we are examining in this study. This time scale allows us to examine gene flow and post-glacial relationships among subpopulations.

Our microsatellite analyses align with the hypothesis that caribou recolonization of the northern tundra involved large populations with admixture, because the migratory barren-ground caribou show very high levels of genetic variation and an absence of genetic signals for past population bottlenecks or trends toward isolation-by-distance. Neighbouring subpopulations are not necessarily more closely related than more geographically distant subpopulations. In contrast, if subpopulation structure had been maintained during glacial retreat, we would expect to see increased genetic differentiation among present-day subpopulations. It is assumed that there were few geographic barriers to gene flow during population expansion across their continental range, a scenario supported by the inability of our historic gene flow measures to reach convergence when estimating rates among individual mainland subpopulations. We could expect that under similar demographic scenarios as contemporary times, similar levels of occasional sex-based gene flow would have occurred across the mainland during post-glacial retreat, as well.

Phylogenetic data based on mitochondrial DNA suggest that the subpopulations of Dolphin and Union and Bathurst diverged from each other approximately 1000 ybp (Eger *et al.,* 2009). We can build on this knowledge by applying the assumption that ASD and Nei's genetic distance values are linear with sequence divergence, and can therefore be used as molecular clocks (Paetkau *et al.,* 1997; Sun *et al.,* 2009). The linearity of the microsatellite molecular clock persists for about 10 000 generations (Feldman *et al.*, 1997; Paetkau *et al.,* 1997), which is well-within the time frame of population expansion and divergence that we are examining in this study. Based on the evidence that Nei's genetic distance has been shown to be more applicable as a molecular clock (Paetkau *et al.,* 1997), our data suggest that Dolphin and Union diverged from each of the mainland subpopulations around the same time, about 1000 ybp. The more eastern-located Southampton Island caribou, which originated from Coats Island, diverged from mainland subpopulations much earlier, perhaps over 3000 ybp. This corresponds with assumptions that the Coats Island caribou likely originated from subpopulations in northern Quebec, on the other side of Hudson's Bay. Both ASD and $D_S$ values clearly show a more recent divergence among the mainland migratory barren-ground subpopulations than between mainland and island subpopulations.

*Conservation implications*

Our analyses provide insight into the patterns of gene flow, genetic diversity and genetic differentiation that may be common to large

populations that historically displayed a continuous distribution. The conservation implications of this study are apparent. First, efforts should be made to maintain high levels of genetic diversity. Second, while satellite telemetry supports functionally separate subpopulations, their large Ne and occasional dispersal have maintained genetic connectivity among subpopulations.

The large effective population sizes and dispersal patterns of barren-ground caribou may have implications for their response to future disturbances, including climate change. Pinsky *et al.* (2010) suggest several criteria that confer higher resilience against anthropogenic and climate-related stressors: 1) high gene flow; 2) stable genetic diversity; 3) a wide geographic distribution; 4) behavioural plasticity; and 5) a secure refuge during years of range limitations. Barren-ground caribou meet all these criteria, and will likely prove to be a highly resilient subspecies in the face of future environmental changes. It is important to note, however, that genetic studies do not predict the effects of anthrogenic and climate-related disturbances on local depletions and the hardships they would cause to local subsistence economies and cultures. Additionally, resilience of a population can only be substantiated within intact seasonal ranges. Anthropogenic disturbance of a scale that could render long-term distributional and/or behavioural shifts in seasonal range use is very real, and no amount of resilience within the species will mitigate the fundamental and large scale spatial shifts that could be realized as a result. Importantly, connectivity among subpopulations must be maintained to permit occasional dispersal. Indeed, our findings from this study are in accordance with those of Yannic *et al.* (2014a), who showed that caribou can demonstrate temporal variations in habitat selection. Similar connectivity was also likely present among bison and wapiti, prior to population declines in those species. Thus, the results from this study can then be used as a benchmark to compare the effects of habitat fragmentation and bottlenecks on other large terrestrial mammalian species.

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