An enigmatic group of arctic island caribou and the potential implications for conservation of biodiversity

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Abstract: We investigated the status of caribou classified as *Rangifer tarandus pearyi* by DNA analyses, with an emphasis on those large-bodied caribou identified as ultra *pearyi* that were collected in summer 1958 on Prince of Wales Island, south-central Canadian Arctic Archipelago. Our comparative assessment reveals that the ultra *pearyi* from Prince of Wales Island belong to a group of *pearyi* and are not hybrids of *pearyi x groenlandicus*, as we found for the caribou occurring on nearby Banks Island and northwest Victoria Island. The ultra *pearyi* from Prince of Wales Island cluster with high arctic *pearyi* and are separated genetically from the caribou populations that we sampled on the low Canadian Arctic Islands and the Canadian mainland. Our findings reveal biodiversity below the level of subspecies or regional designations. These results support the position that to retain the biodiversity present among caribou populations on the Canadian Arctic Islands, conservation efforts should be targeted at the smaller scale level of the geographic population, rather than on a wider regional or subspecific range-wide basis.

Key words: biodiversity; Canadian Arctic Islands; conservation; geographic population; microsatellite DNA; *Rangifer*; Peary caribou; ultra *pearyi*.

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Introduction

Caribou (*Rangifer tarandus*) exhibit tremendous ecological plasticity and genetic diversity across the species range. Much of the existing and extinct genetic variation of this culturally and ecologically important species has received attention (*e.g.*, Courtois *et al.*, 2003; McLoughlin *et al.*, 2004; Cronin *et al.*, 2005; Kuhn *et al.*, 2010; Petersen *et al.*, 2010; Klütsch *et al.*, 2012; Weckworth *et al.*, 2012). However, a fine-scale

analysis of population genetic status and structure, with a connection to observed phenotypic plasticity, is needed to recognize and protect the extent of cryptic biodiversity (*i.e.*, biodiversity hidden below the subspecific level) that could exist within a caribou population. This is particularly relevant across the northern portion of the North American caribou range where Peary caribou (*R. t. pearyi*) occur in the Canadian Arctic Archipelago, as environmental change is occurring rapidly and few previous studies on this topic have been performed. Understanding if hidden biodiversity exists within these caribou populations will better enable us to assess the consequences of climate change in the Canadian Arctic Archipelago. The preservation of heritable biodiversity is crucial to improve a population's ability to adapt to changing environmental conditions and respond to natural selection pressures (Franklin, 1980; Frankham *et al.*, 1999), as well as reduce the risk of inbreeding depression, population extirpation, or reduced population fitness (Lynch, 1997; Coulsen *et al.*, 1998; Saccheri *et al.*, 1998; McKay *et al.*, 2005).

Debate around the taxonomical classification of Peary caribou (*Rangifer tarandus pearyi*) is typical of the uncertain nature of the taxonomical nomenclature of Rangifer in general (Miller *et al.*, 2007b; Serrouya *et al.*, 2012; Weckworth *et al.*, 2012). Both Manning (1960) and Banfield (1961) recognized considerable phenotypic diversity in caribou from the Canadian Arctic Islands. They concluded that the purest stock of *pearyi* was on the Queen Elizabeth Islands (QEI: Fig. 1) (north of 74° N latitude) and that caribou from the low Arctic Islands (between approximately 70° N and 74° N latitude) were intergrades of *pearyi x groenlandicus*. Manning (1960) and Banfield (1961) also reported a north-south morphological cline within the range occupied by Peary caribou, from the QEI in the north, through the western low Arctic Islands and onto the Canadian mainland in the south. Both Manning (1960) and Banfield (1961) postulated that the north-south cline occurred due to intergradation between *pearyi* and *groenlandicus* that invaded the low Arctic Islands.

Thomas & Everson (1982) found a similar north-south morphological cline among those caribou, from western QEI in the north, across Prince of Wales and Somerset islands, and along the mainland Boothia Peninsula. To accommodate their described north-south morphological cline, they attributed three classifications for the caribou: typical *pearyi*, intergrades between *pearyi* and *groenlandicus* (referred to as *pearyi x groenlandicus*), and typical *groenlandicus* (Thomas & Everson, 1982).

Morphological variation among caribou would be expected given the numerous environmental and demographic factors that can impact caribou body size. Vors & Boyce (2009) found that landscape changes — both anthropogenic and climate-modulated — influence caribou demography. In turn, recent studies have shown that demographic factors can directly impact body condition. For example, among migratory caribou, major influences on body size include reproductive rates (Taillon *et al.*, 2012), as well as population density, intraspecific competition, and migration duration (Courturier *et al.*, 2010).

Despite such recognized morphological variation across the Canadian Arctic Islands, Banfield (1961) used an "umbrella" classification for Peary caribou in his revision of the genus *Rangifer*. He based the distribution of *R. t. pearyi* on a relatively small sample size of *pearyi* and *pearyi* > *groenlandicus* specimens (*i.e.*, intergrade specimens that were more *pearyi* than *groenlandicus* in morphology) that was not well represented from across the Canadian Arctic Archipelago. Typical *pearyi* specimens were from the QEI, and also included seven specimens from Prince of Wales Island, lying south of 74° N latitude (Banfield, 1961:64).

Table 1. The seven large-bodied adult male caribou shot on Prince of Wales Island in summer 1958 and used by Manning & Macpherson (1961) in their assignment of ultra *pearyi* from which microsatellite DNA was obtained and tested in this study (all samples were identified genetically as ultra *pearyi*).

NMC[a] specimen no.	Prince of Wales Is. Location	Date (1958)
22970	Inner Browne Bay	1 Jun
22968	Inner Browne Bay	1 Jun
22972	Inner Browne Bay	11 Jun
22975	Inner Browne Bay	4 Jul
22978	Crooked Lake	16 Jul
22979	Central west coast	10 Aug
22981	North of Scrap Brook	16 Aug

[a] Currently the Canadian Museum of Nature.

No specimens from north of 74° N latitude were identified as intergrades (*pearyi x groenlandicus*), and no specimens from south of 74° N latitude (Victoria Island, Somerset Island, or the mainland Boothia Peninsula) were identified as typical *pearyi* or even as *pearyi* > *groenlandicus* at that time.

The seven individuals from Prince of Wales Island (Banfield, 1961:63) were interesting and form the specific focus of our study. Unlike typical Peary caribou, they were large-bodied animals, but maintained other Peary caribou morphological characteristics (Table 1; Fig. 2). Banfield (1961:63) concluded that those seven large adult male caribou possessed the diagnostic characters of *pearyi*; *e.g.,* shortened rostrum, high cranium, and pale pelage. However, he considered them unique as they were much larger than typical *pearyi* and showed no significant signs of intergradation with *groenlandicus*. Manning & Macpherson (1961) labeled those large Prince of Wales caribou as 'ultra *pearyi*' and Banfield (1961) classified them as a 'super *pearyi* deme; thus, both labels reflect their *pearyi* characteristics and their very large body size. Not all caribou from Prince of Wales Island were large-bodied, but no detailed assessment of the normal-sized *pearyi*-type caribou that occurred on Prince of Wales Island was made at that time. Manning & Macpherson (1961) and then Banfield (1961) assumed, without verification, that the normal-sized *pearyi*-type caribou on Prince of Wales Island intergrades of *pearyi* x *groenlandicus*. Previously, there has been no genetic confirmation of any of these assumptions or descriptions.

We are particularly concerned with the origin of the ultra *pearyi*, the enigmatic large-bodied Peary caribou found only on Prince of Wales Island in the south-central Canadian Arctic Archipelago. The seven ultra *pearyi* specimens were never compared to normal-sized *pearyi* specimens obtained in the subsequent decades on Prince of Wales or neighbouring Somerset Island. Unfortunately, given the near extirpation of caribou on those islands at the end of the 20th century, it is now highly probable that the ultra *pearyi* line of caribou no longer exists, and further morphological comparisons are no longer possible.

We present three alternatives for the origin of the ultra *pearyi*. One possibility is that these large-bodied ultra *pearyi* represent a unique type of caribou, not previously described. If so, these caribou reflect cryptic biodiversity among the Canadian Arctic Archipelago. A second possibility is that the large-bodied ultra *pearyi* represent a hybrid form (intergrades between *pearyi x groenlandicus*), aligning with previously described morphological clines (Manning, 1960; Banfield, 1961; Thomas & Everson, 1982) and as assumed for all caribou occupying islands south of 74°N. A third possibility is that the ultra *pearyi* may belong to the typical *pearyi* group, along with caribou occurring on islands north of 74°N (*i.e.*, QEI).

In this study, we use microsatellite DNA analysis to assess the three origin alternatives, examine whether the north-south morphologi-

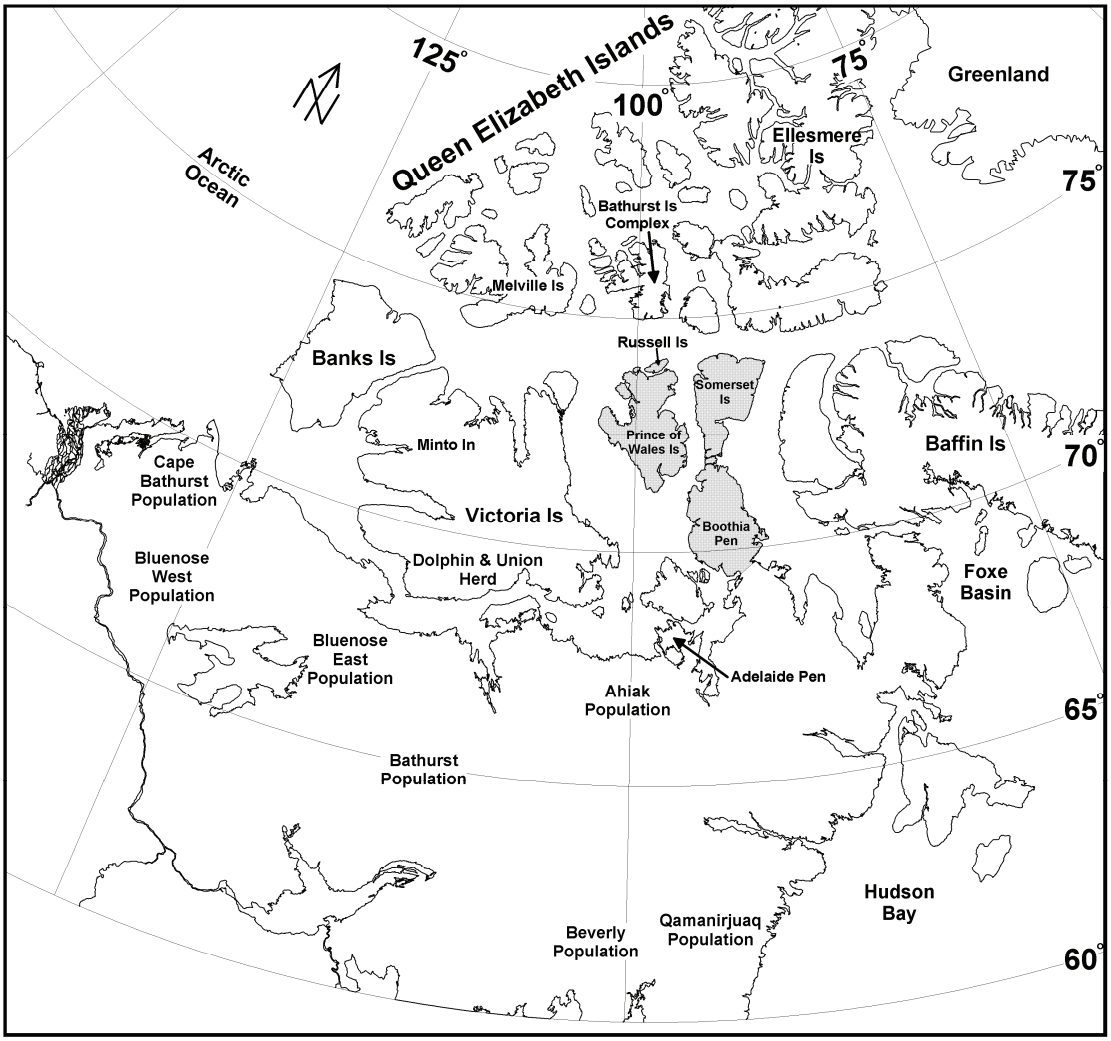

Fig. 1. Canadian Arctic Islands and north-central mainland Canada: shaded area indicates the Prince of Wales Island-Somerset Island-Boothia Peninsula Complex and its relative position among the islands and to the mainland.

cal cline has a genetic basis, and test the assumption by Banfield (1961) and Manning & Macpherson (1961) that normal-sized *pearyi*-type caribou on Prince of Wales Island were intergrades of *pearyi* x *groenlandicus* and similar to caribou from Banks Island.

Materials and Methods

Study population

The specimens assessed in this study include caribou from the western Canadian Arctic Archipelago — a group of populations designated as Endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2004); the barren-ground caribou from the Dolphin and Union Herd on Victoria Island, designated as Special Concern by COSEWIC (2004); and barren-ground caribou from Boothia Peninsula and the Canadian mainland (Cape Bathurst, Bluenose East, Bathurst, Ahiak and Adelaide Peninsula, Beverly, and Qamanirjuaq).

Caribou that occupy Prince of Wales Island (33 339 km^2) also seasonally occupy ranges on Somerset (24 786 km^2) and Russell (940 km^2) islands and their respective satellite islands (collectively, 1220 km^2), as well as the mainland Boothia Peninsula (32 715 km^2). Therefore, for the purposes of conservation and management we consider those caribou to constitute one geographic caribou population (Fig. 1: Miller *et al.*, 2005; Gunn *et al.*, 2006; Miller *et al.*, 2007b). This population will hereafter be referred to as the Prince of Wales Island-Somerset Island-Boothia Peninsula Complex (PSBC) caribou population. Many of these caribou annually make a complex web of seasonal inter-island or island-peninsula migrations within the PSBC, while some relatively few appear to remain year-round on a single island (Miller *et al.*, 1982, 2005). No consistent differences in body size or other traits between the inter-island migrants and the resident caribou have been detected. Boothia Peninsula also contains a resident population of barren-ground caribou, but their range does not appear to overlap temporally with that of the migrant island caribou (F. Miller, unpublished data; Miller *et al.*, 2005). We consider any caribou, other than barren-ground caribou, that occurs or was collected on Prince of Wales Island as a potential seasonal resident anywhere within the PSBC.

Tissue samples and DNA extractions

We obtained bone and skin samples from 30 caribou from the Arctic Islands and the coastal mainland from the specimen collection at the Canadian Museum of Nature, Ottawa. These specimens were collected between 1914 and 1958. Excepting the ultra *pearyi* — which are the specific focus of this paper — , all other museum specimens were amalgamated with contemporary samples from within the same geographic populations. As subsequent analyses confirmed the museum specimens are not genetically differentiated from contemporary samples, the influence of past demographic trends is not considered here. We extracted DNA from these samples, which included the large-bodied caribou used by Manning & Macpherson (1961) in their description of ultra *pearyi* (collected in 1958, n = 7); as well as caribou from Banks Island (collected in 1914, n = 7); Dolphin and Union Herd (Victoria Island, collected in mid-1900s (specific date unknown), n = 10); and the mainland Adelaide Peninsula (collected in 1957, n = 6). We isolated DNA from ~25 mg tissue samples using spin columns (DNeasy Mini Kit, QIAGEN Inc., Mississauga, Ontario).

Because of the age of the samples, during DNA extraction and subsequent microsatellite analysis steps we took standard precautions to prevent contamination. Sample preparations and DNA extractions were performed in a fume hood, in a separate room that was free of amplified DNA. The work area and tools were cleaned with bleach before and after each use. During PCR analysis, we used negative controls to detect the presence of contamination. As no contamination was observed, we analyzed the 30 genotypes (16 complete eight-locus genotypes, and 14 partial genotypes of three to seven loci) obtained specifically for evaluating the status of ultra *pearyi* with an additional 682 microsatellite genotypes of caribou from the Canadian mainland (n = 395), Dolphin and Union Herd (n = 38), and the Canadian Arctic Islands (n = 249) that were examined by Zittlau (2004) (sample sizes for those populations are given in Table 2). Overall, the set of samples from Prince of Wales Island represents two separate time points (1958 ultra *pearyi* and 1970s *pearyi*).

Microsatellite genotyping

We used eight microsatellite primer pairs in this study: seven derived from caribou, RT1, RT5, RT6, RT7, RT9, RT24, and RT27 (Wilson *et al.*, 1997); and one from bovids, BM4513

(Bishop *et al*., 1994). To allow subsequent visualization and assessment, we amplified microsatellite alleles by polymerase chain reaction (PCR) in a final reaction volume of 15 µL with ~100 ng of DNA, 0.16 µM of each primer, 120 µM dNTP, 2 mM $MgCl_2$, 0.6 units of AmpliTaq Gold® DNA polymerase (ABI, Foster City, CA), and 1X PCR buffer (10 mM Tris buffer, pH 8.8, 0.1% Triton X100, 50 mM KCl, and 0.16 mg/mL BSA). We fluorescently labeled one primer from each pair. PCR thermal cycling conditions were as follows: 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, 1 s at 72°C, and a final extension of 30 min at 72°C. To visualize the amplified microsatellite alleles, we pooled and then loaded fragments from primer pairs producing alleles in non-overlapping size ranges, along with internal size standard on polyacrylamide gels on a 377 Automated Sequencer (Perkin-Elmer Biosystems). We then resolved allele sizes by using the Applied Biosystems software ABI Prism™ GENESCAN™ 2.0.2 and GENOTYPER® 2.0 (Applied Biosystems, Inc., Foster City, CA) software.

Statistical analyses

We examined the caribou populations for deviations from Hardy-Weinberg Equilibrium and for evidence of linkage disequilibrium among loci using GENEPOP Version 4.0 (Rousset, 2008). Error rates were adjusted using the Bonferroni correction to account for multiple tests. Populations that deviated from Hardy-Weinberg Equilibrium were further investigated for heterozygote deficits using MICRO-CHECKER (van Oosterhout *et al*., 2004).

Genetic variation within each caribou population was measured and compared across geographic locations. We used MS_{TOOL} kit (Park, 2001) to calculate unbiased expected heterozygosity (Nei & Roychoudhury, 1974) and observed heterozygosity. Allelic richness, which offers a standardized measure of alleles per locus based on sample size (in this case, based on a minimum sample size of five individuals), was calculated using FSTAT Version 2.9.3.2 (Goudet, 1995). We used GENALEX Version 6.5 (Peakall & Smouse, 2012) to calculate probability of identity as an estimate of the diversity across multilocus genotypes. To determine if a geographic cline exists among genetic diversity levels, we performed a linear regression to measure R^2 between median latitude and expected heterozygosity. For the regression analysis, heterozygosity values from Banks and northwest Victoria islands and PSBC caribou were grouped according to their median latitude of approximately 72° N. To assess the degree of relatedness within populations, and to confirm that the large-bodied ultra *pearyi* were not from a group of related bulls, we calculated F_{IS} (using FSTAT Version 2.9.3.2; Goudet, 1995).

To enhance our understanding of the amount of genetic variation within each population, we assessed whether individual populations might have experienced genetic bottlenecks by calculating the M-ratio (Garza & Williamson, 2001) and using BOTTLENECK Version 1.2.02 software (Cornuet & Luikart, 1996). The M-ratio compares the number of alleles per locus to the range in allele size; a low M-ratio reflects a significant decline in population size. We manually calculated M-ratios for each population of a minimum critical size (in this case, $n \geq 24$), according to recommendations by Garza & Williamson (2001) to maintain population size in excess of twice the number of alleles, and following adjustments recommended by Excoffier *et al*. (2010) to avoid zeroes. The populations of caribou from the mainland, QEI, Banks and northwest Victoria islands, Dolphin and Union, and Boothia Peninsula met these criteria. We compared calculated M-ratios to the generic critical value ($M_{crit} = 0.68$) suggested by Garza & Williamson (2001).

In contrast to the M-ratio, BOTTLENECK software compares observed heterozygosity to that expected based on the number of alleles, using a Wilcoxon signed-rank test (Piry *et al.*, 1999). An excess of observed heterozygosity compared to that expected under mutation-drift equilibrium is indicative of a significant genetic bottleneck. We assumed a two-phase model of mutation, which attributes 95% of mutations to the stepwise mutation model and 5% to the infinite alleles model, as recommended for microsatellite analyses (Piry *et al.*, 1999). We also report results from the infinite alleles model and the stepwise mutation model for comparison.

To explore the degree of genetic separation (differentiation) of caribou across the Canadian Arctic Islands, and to ascertain the validity of Manning & Macpherson's (1961) and Banfield's (1961) assumption about Prince of Wales caribou, we performed a broad scale analysis of population differentiation, including a comparison to caribou from the Canadian mainland. We used a Bayesian clustering method (STRUCTURE version 2.2; Falush *et al.*, 2003; Pritchard *et al.*, 2000) to examine population substructure among those caribou. STRUCTURE estimates the number of genetic clusters that occur within the set of sampled individuals. For an ancestry model, we assumed that some proportion of each individual's genome could be derived from each of the populations examined. We also assumed that allele frequencies are correlated within populations. We did not assign prior population information to the individuals in the overall dataset. We used an iterative approach to select the best STRUCTURE run. Each chain was run for 330 000 iterations with the first 30 000 discarded. We estimated the number of existing genetic clusters by performing three independent runs for K = 1 to 10 to account for at least the eight regional locations where samples were obtained (across the Canadian Arctic Islands (n = 5), Boothia Peninsula (n = 1), Dolphin and Union Herd (n = 1), and Canadian mainland (n = 1)). The number of genetic clusters was estimated in two ways: first, using the model that resulted in the highest Ln likelihood (Pritchard *et al.*, 2000); and second, by plotting the change in Ln likelihood (ΔK) against estimated number of populations (Evanno *et al.*, 2005).

To assess finer-scale subpopulation structure, we performed nested analyses on all identified genetic clusters and on any group of individuals that did not assign to a cluster. For each nested analysis, we used STRUCTURE to perform three independent runs for K = 1 to K = 6. Each chain was run for 550 000 iterations with the first 50 000 discarded. We estimated the most likely number of genetic clusters according to Pritchard *et al.* (2000) and Evanno *et al.* (2005), as described above.

We used a Bayesian MCMC analysis (BAYESASS 1.3; Wilson & Rannala, 2003) to estimate recent dispersal rates (within the last several generations) among the eight regional locations where samples were obtained. Each chain was run for 5 000 000 iterations, with the first 1 000 000 discarded, and a sampling frequency of 2000. To test that the program converged during separate runs, the analysis was run three times with different seed numbers for each run.

As additional measures of the genetic separation among caribou populations, we calculated F_{ST} (using FSTAT Version 2.9.3.2; Goudet, 1995) and Nei's standard genetic distance (Nei, 1972) between pairs of populations across the study region. Significance of F_{ST} values was determined by performing 1000 permutations and using the Bonferroni correction to account for multiple tests.

Results

Genetic data and tests of disequilibrium

Heterozygote deficiency was significant in three of the 64 locus-population comparisons after

Fig. 2. Large ultra *pearyi*-like adult male caribou that occurred on northern Prince of Wales Island during at least the late 1970s and early 1980s (summer 1980: courtesy of H.P.L. Kiliaan, Canadian Wildlife Service, retired).

sequential Bonferroni adjustment for multiple tests ($P < 0.00078$): in the mainland (at loci RT1, RT9), and Banks and northwest Victoria islands (at locus BM4513) populations. MICRO-CHECKER also detected heterozygote deficiency in four populations: in the mainland (at all loci except RT1 and RT7), in QEI (at loci RT9, BM4513), in Banks and northwest Victoria islands (at BM4513), and in Dolphin and Union (at RT5). Heterozygote deficiencies are not unexpected in the mainland, QEI, and Banks and northwest Victoria islands populations because these geographic populations include pooled samples from two or more locations or time points that were not deemed to be statistically genetically differentiated according to Zittlau (2004). As analyses focus on regional (*i.e.*, high arctic, low arctic, and mainland) comparisons among arctic island caribou and to ultra *pearyi*, all loci were retained for subsequent analyses.

When sample locations were considered separately, three of the 224 locus-locus comparisons exhibited evidence of significant linkage disequilibrium (RT1/RT24, RT6/RT24, and RT24/BM4513 in the mainland, and RT1/RT5 in the Dolphin and Union Herd). No evidence of genotypic disequilibrium was detected in Peary caribou, regardless of location. None of the locus pairs showed linkage in all populations. As there is no consistent evidence for null alleles, allelic dropout, or deviations from random mating, all loci were included in the analyses.

Genetic variation

Our results show that caribou populations from Prince of Wales Island, Somerset Island,

Table 2. Genetic variation among the ultra *pearyi* caribou and other populations from the Canadian Arctic Islands and Canadian mainland.[a]

Location where samples were obtained	H_E	H_O	N_{ar}	PI	F_{IS}	N
Canadian Arctic Islands and mainland Boothia Peninsula (*pearyi* and *pearyi*-type)						
ultra *pearyi*, Prince of Wales Is.	0.67	0.64	4.1	6.6E-7	0.04	7
1970s Prince of Wales Is.	0.69	0.71	3.9	4.2E-7	-0.03	9
1970s Somerset Is.	0.65	0.65	4.0	3.8E-6	-0.01	5
Queen Elizabeth Is.[b]	0.70	0.66	4.0	5.7E-8	0.05	159
Banks Is./NW Victoria Is.[c]	0.81	0.80	5.3	1.0E-10	0.02	83
Boothia Peninsula	0.79	0.80	5.1	6.8E-10	-0.01	25
Dolphin and Union Herd, plus Canadian mainland (*groenlandicus*)						
Dolphin & Union Herd, Victoria Is.	0.85	0.79	5.8	6.7E-12	0.06	48
7 mainland populations[d]	0.87	0.83	6.2	3.7E-13	0.05	376

[a] Based on measures of H_O, observed heterozygosity; H_E, unbiased expected heterozygosity based on allele frequencies; N_{ar}, allelic richness (alleles per locus, standardized for a sample size of five individuals); PI, probability of identity; and F_{IS}, inbreeding coefficient.

[b] Queen Elizabeth Islands equal Melville Island (n = 30) and the Bathurst Island Complex (n = 129).

[c] Banks Island (n = 71) and northwest Victoria Island (n = 12).

[d] Mainland caribou populations include Cape Bathurst (n = 45), Bluenose West (n = 80), Bluenose East (n = 79), Bathurst (n = 55), Ahiak (n = 46, includes six samples from Adelaide Peninsula), Beverly (n = 25), and Qamanirjuaq (n = 46).

and QEI are much less genetically variable than caribou on other Canadian Arctic Islands or the Canadian mainland (Table 2). Expected heterozygosities of these caribou range from 65–70% (on average, 20% lower than mainland caribou) and standardized allelic diversities show an average of 4.0 alleles per locus, which is only 2/3 the value for mainland caribou. Probabilities of identity reveal a five- to six-fold decrease in variation between caribou from these populations and the Canadian mainland, and a two- to three-fold decrease compared to the caribou on other Canadian Arctic Islands (Table 2). Overall, the caribou from the Canadian Arctic Islands did not possess any unique alleles that were not also present in the mainland populations.

A decreasing trend in genetic variation occurs from south to north (R^2 = 0.87, P = 0.01, Fig. 3), although this relationship is based on only five points. The most genetically diverse caribou are from the seven mainland populations and Dolphin and Union Herd in the southern portion of the study area (Table 2). The caribou from Banks and northwest Victoria islands and Boothia Peninsula are considerably more diverse than the caribou from QEI, Prince of Wales Island, and Somerset Island (mean H_E = 0.80, mean N_{ar} = 5.2; Table 2).

A past genetic bottleneck may have occurred among caribou on Boothia Peninsula, according to M-ratios when compared to the generic M_{crit} = 0.68 (Garza & Williamson, 2001) (Table 3). Significant bottlenecks were not detected among any of the island or Canadian mainland populations that were examined by the M-ratio, nor according to the BOTTLENECK two-phase model or stepwise mutation

Table 3. Bottleneck results for the ultra *pearyi* caribou and other populations from the Canadian Arctic Islands and Canadian mainland. M-ratios represent the mean value across loci (interlocus variance indicated in parentheses). BOTTLENECK values represent the one-tailed probability of obtaining the observed heterozygosity excess under the three mutation models, based on Wilcoxon's signed-rank test. Significant values ($P < 0.05$) are indicated with an asterisk.

Location where samples were obtained	*n*	M-ratio	Bottleneck p-value for heterozygosity excess[a]		
			IAM	TPM	SMM
ultra *pearyi*, Prince of Wales Is.	7	*n*/a[b]	0.578	0.963	0.980
1970s Prince of Wales Is.	9	*n*/a[b]	0.098	0.371	0.371
1970s Somerset Is.	5	*n*/a[b]	0.844	0.998	0.998
Queen Elizabeth Is.	159	0.76 (0.024)	0.004*	0.980	0.994
Banks Is./NW Victoria Is.	83	0.86 (0.006)	0.002*	0.980	0.998
Dolphin & Union Herd	48	0.82 (0.016)	0.002*	0.422	0.875
Boothia Peninsula	25	0.66 (0.027)	0.098	0.963	0.994
Mainland populations	376	0.94 (0.011)	0.002*	0.973	0.998

a According to three mutation models: infinite alleles model (IAM), two-phase model with 95% stepwise mutations (TPM), and the stepwise mutation model (SMM).

b M-ratios were not calculated for populations with $n < 24$, according to Garza & Williamson (2001).

models, which are the recommended models for microsatellite markers (Table 3). According to the BOTTLENECK software IAM model, neither the ultra *pearyi* nor caribou from PSBC experienced a bottleneck. All other populations show a signature of a genetic bottleneck according to the IAM model.

The inbreeding coefficient, F_{IS}, ranges from -0.01 to 0.05 for the caribou on the Canadian Arctic Islands and Boothia Peninsula (Table 2). None of these values is significantly different from zero, indicating that the populations are not inbred or more related than expected based on Hardy-Weinberg Equilibrium.

Genetic heterogeneity

The clustering analysis of STRUCTURE supports two distinct genetic clusters among caribou on the Canadian Arctic Islands and Canadian mainland (Fig. 4). Individual proportional memberships (*q*) were highest among individuals belonging to Cluster-1. Cluster-1 corresponds to caribou from Prince of Wales Island (89% at $q > 0.90$), Somerset Island (80% at $q > 0.90$), and QEI (87% at $q > 0.90$); Cluster-2 corresponds to specimens from Boothia Peninsula (8% at $q > 0.90$), the Dolphin and Union

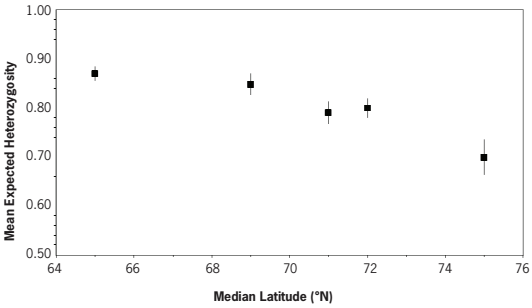

Fig. 3. Mean expected heterozygosity as a function of median latitude of caribou population. Population heterozygosity of Banks and northwestern Victoria islands and PSBC have been grouped according to their median latitude of approximately 72° N. $R^2 = 0.87$, $P = 0.01$.

Table 4. Pairwise F_{ST} values (below diagonal) and genetic distances (above diagonal) between ultra *pearyi* and caribou from 1970s Prince of Wales Island, Queen Elizabeth Islands (QEI), low Arctic Islands, and mainland populations. Significant F_{ST} values are indicated with an asterisk.

	F_{ST} and genetic distance (D_S)							
Location where samples were obtained	ultra *pearyi*	1970s Prince of Wales	1970s Somerset	QEI	Banks/ NW Victoria	Dolphin & Union	Boothia Peninsula	mainland populations
ultra *pearyi*, Prince of Wales Is.	-	0.16	0.31	**0.11**	0.20	**0.47**	0.21	0.37
1970s Prince of Wales Is.	0.016*	-	0.25	0.12	0.24	0.61	0.34	0.47
1970s Somerset Is.	0.069	0.051	-	0.17	0.23	0.42	0.32	0.49
Queen Elizabeth Is. (QEI)	**0.014**[a]	0.023	0.032	-	0.10	0.33	0.21	0.29
Banks/NW Victoria Is.	0.040	0.050*	0.044	0.034*	-	0.18	0.12	0.11
Dolphin & Union Herd[b]	0.088*	**0.106**	0.078*	0.084*	0.026*	-	0.30	0.13
Boothia Peninsula	0.037	0.073*	0.065	0.057*	0.017*	0.044*	-	0.18
Mainland populations	0.073*	0.086*	0.089*	0.075*	0.019*	0.014*	0.028*	-

[a] Boldface font indicates the smallest or largest genetic distances (D_S and F_{ST}) from the ultra *pearyi* caribou.
[b] On southwest and east Victoria Island.

Table 5. Gene flow estimates (m) between ultra *pearyi* and caribou from 1970s Prince of Wales Island, Queen Elizabeth Islands, low Arctic Islands, and mainland populations. "–" indicates values that are not significantly different from zero, based on 95% confidence intervals.

	Sink population for gene flow							
Source population for gene flow	ultra *pearyi*	1970s Prince of Wales	1970s Somerset	QEI	Banks/ NW Victoria	Dolphin & Union	Boothia Peninsula	mainland populations
ultra *pearyi*, Prince of Wales Is.	0.71	–	–	–	0.08	–	0.14	0.29
1970s Prince of Wales Is.	–	0.70	–	–	–	–	–	–
1970s Somerset Is.	–	–	0.71	–	–	–	–	–
Queen Elizabeth Is. (QEI)	0.20	0.22	0.16	1.00	0.17	–	0.08	–
Banks Is./NW Victoria Is.	–	–	–	–	0.68	–	–	0.03
Dolphin & Union Herd[a]	–	–	–	–	–	0.67	–	–
Boothia Peninsula	–	–	–	–	–	–	0.68	–
Mainland populations	–	–	–	–	0.05	0.26	0.08	0.68

[a] On southwest and east Victoria Island

Herd on Victoria Island (46% at $q > 0.90$), and caribou from seven mainland populations (52% at $q > 0.90$) (Fig. 4B). All of the ultra *pearyi* specimens assigned to Cluster-1, with 71% at $q > 0.90$. The specimens collected on Banks Island and northwest Victoria Island appear admixed and did not strongly assign to a single cluster, with 5% of individuals assigning at $q > 0.90$ to Cluster-1 and 8% assigning at $q > 0.90$ to Cluster-2. When each cluster and the admixed caribou from Banks and northwest

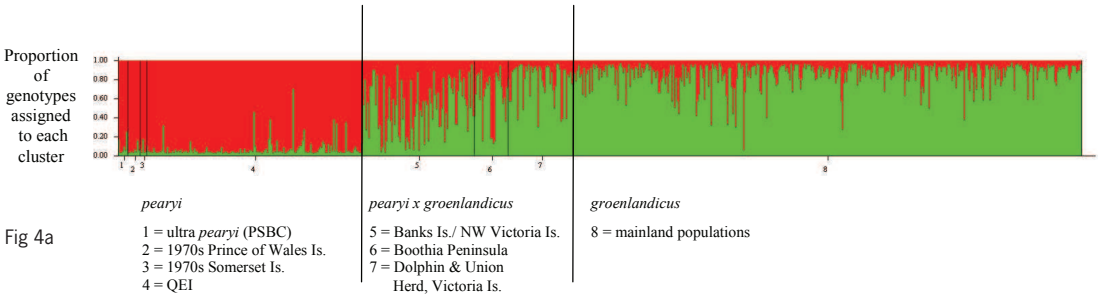

Fig 4a

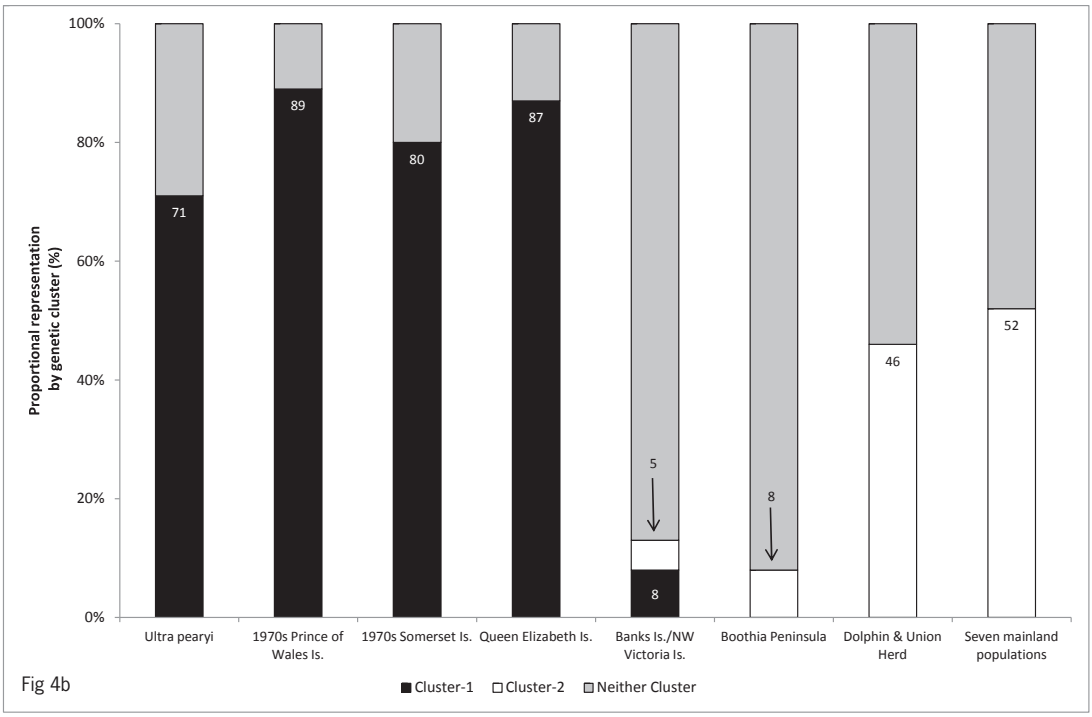

Fig 4b

Fig. 4. a) Proportions of individual genotypes assigned to K = 2 genetic clusters. Each bar represents an individual. Populations are numbered. Red represents Cluster-1 and green represents Cluster-2. Vertical lines show the distinction between genetic clusters and how they relate to traditional taxonomic names and the morphological cline identified by Manning (1960), Banfield (1961), and Thomas & Everson (1982), b) Percentage of individuals from each sample location that assign to Cluster-1, Cluster-2, or neither cluster at $q > 0.90$. Cluster-1 represents predominantly *R. t. pearyi* and Cluster-2 represents predominantly *R. t. groenlandicus*. Numbers indicate the percentage of individuals assigned to Cluster-1 and Cluster-2; percentage of individuals assigned to neither cluster is not shown.

Victoria islands were analyzed separately, K = 1 was the most likely number of genetic clusters.

We obtained significant F_{ST} values between sample collection locations for 64% of the 28 paired-comparisons (Table 4). All non-significant F_{ST} values are for caribou within the PSBC and the QEI, and between caribou from PSBC and Boothia Peninsula and Banks and northwest Victoria islands (Table 4). The greatest genetic distance from the ultra *pearyi* is to the Dolphin and Union Herd, followed by that to the mainland caribou (Table 4).

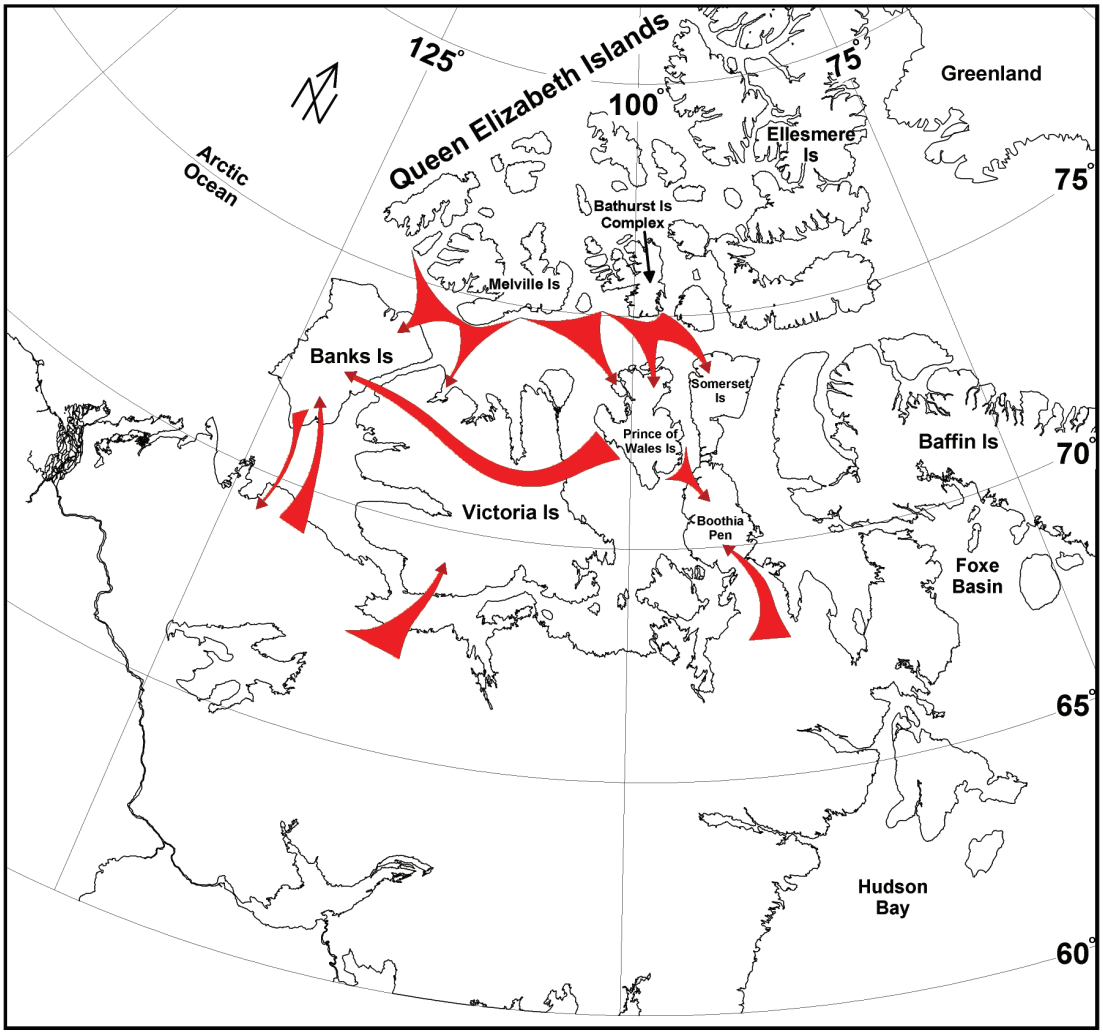

Fig. 5. Direction of gene flow *(m)* between or among Queen Elizabeth Islands, low Arctic Islands, PSBC and mainland populations. Arrow thickness reflects relative gene flow rate. Magnitude of gene flow estimates *(m)* are indicated in Table 5.

Estimates of recent dispersal (*i.e.*, within the last several generations) showed migration rates from QEI into PSBC ranges from 16–22% (Table 5; Fig. 5). Migration rates from QEI into Banks and northwest Victoria islands are also within this range (17%). Significant dispersal was also detected from the ultra *pearyi* gene pool into Boothia Peninsula and Banks and northwest Victoria islands.

Discussion

Characterization of ultra pearyi

Knowledge of the existence of ultra *pearyi* previously rested solely on the seven noticeably large adult male caribou obtained by Manning & Macpherson (1961) on Prince of Wales Island in summer 1958. Banfield (1961) reiterated Manning & Macpherson's (1961) findings, but labeled those caribou a *pearyi* super deme. There was no genetic characterization for the

ultra *pearyi* caribou until this microsatellite DNA study.

Of the three origin possibilities for the ultra *pearyi*, our results support their membership within the typical *pearyi* group. We determined that all seven of the adult male caribou used for the designation of ultra *pearyi* assigned to the *pearyi* genetic cluster (Cluster-1; Fig. 4). That is, their large body size was not a result of hybrid vigor (heterosis), nor additive genetic variation between *pearyi* and *groenlandicus*. In comparison, the caribou from Banks and northwest Victoria islands are admixed, with each individual assigned equally to both the *pearyi* (Cluster-1) and *groenlandicus* (Cluster-2) genetic clusters, indicating that those caribou are the result of intergradation between Peary and barren-ground caribou.

Manning & Macpherson (1961:225) proposed a 'nutrition plus selection or drift' hypothesis for the large body size of the ultra *pearyi*. They stated that the comparatively large size of the seven adult male caribou with complete skulls collected on Prince of Wales Island in summer 1958 could have resulted from feeding on high-quality forage. They also suggested — but did not have the tools for testing at the time — a genetic difference, resulting either from selection for larger size or genetic drift. They noted that the increase in skull size was not accompanied by modification of skull shape towards that of mainland barren-ground caribou (*groenlandicus*).

Our findings contrast with Manning & Macpherson's (1961) 'nutrition plus selection or drift' hypothesis, but do support their observation that the increased skull size and large body size of the ultra *pearyi* is not a result of intergradation between *pearyi* and *groenlandicus*. If the ultra *pearyi* represent a unique type of caribou, we would expect to detect a distinct genetic cluster within the *pearyi* genetic cluster (Cluster 1; Fig. 4). The ultra *pearyi* also would have displayed significant genetic differentiation from the other Peary caribou populations (on QEI and PSBC). Rather, the ultra *pearyi* definitively group with the Peary caribou.

Banfield (1961:63) argued against the nutrition hypothesis because no similarly noticeably large-bodied caribou were ever collected on other islands at similar latitude (nor have any been reported or collected since then). However, contrary to the assumption by Banfield (1961) that the smaller (normal-sized) caribou on Prince of Wales Island were genetically similar to the caribou from Banks Island (Manning, 1960), our results show that the caribou from Prince of Wales Island, at both the 1958 and 1970 time point, are significantly different genetically from the caribou on Banks and northwest Victoria islands (Table 4; Fig. 4). If Banfield's (1961) assumption about normal-sized caribou on Prince of Wales Island was correct, the PSBC or the ultra *pearyi* would have grouped with admixed caribou from Banks and northwest Victoria islands. We would also expect genetic distances to be smallest between the ultra *pearyi* and Banks and northwest Victoria islands. This, however, was not observed (Table 4).

Of relevance for this group of large-bodied ultra *pearyi* is the low F_{IS} values, which suggests those caribou were not a group of related individuals (Table 2). Inbreeding coefficients, such as F_{IS}, can range from -1 to 1, with values significantly greater than zero indicating inbreeding within the population, and values significantly lower than zero reflecting possible hybridization, outbreeding, or selection (Wright, 1965). The F_{IS} values measured for the caribou on the Canadian Arctic Islands, Boothia Peninsula, and mainland populations were not significantly different from zero, and the populations are neither inbred nor more related than expected by chance alone.

The ultra *pearyi* have low genetic variation compared to the other caribou populations that we sampled (Table 2), and especially com-

pared to Canadian caribou populations examined in many other studies (Zittlau *et al.*, 2000; Courtois *et al.*, 2003; McLoughlin *et al.*, 2004; McDevitt *et al.*, 2009; Roffler *et al.*, 2012; Mager *et al.*, 2013). In other small populations, Courtois *et al.* (2003) report allelic richness values of greater than 5.1 for all but one mountain population and one isolated population of forest-dwelling caribou. Comparatively, Peary caribou on northern Ellesmere Island, which had not experienced a genetic bottleneck but occur at small population sizes, show similarly low levels of genetic diversity to what we report here for ultra *pearyi* (Petersen *et al.*, 2010). Significant bottlenecks were not detected among the large-bodied ultra *pearyi* (Table 3), suggesting that low genetic variation may have persisted in this population for several generations. However, bottleneck data should always be viewed with caution because both the M-ratio and excess heterozygosity tests can be unreliable when fewer than 16 loci are used (Peery *et al.*, 2012). Furthermore, population subdivision and small sample size can inaccurately lead to Type I errors (Garza & Williamson, 2001; Peery *et al.*, 2012).

The two caribou sample collections examined from different time points (1958 ultra *pearyi* and 1970s *pearyi*) on Prince of Wales Island exhibit distinct morphological traits from each other. However, assignment tests and genetic distance measures do not support genetic distinction between the 1958 ultra *pearyi* and 1970s *pearyi* (Table 4; Fig. 4). Possibly, these two sample collections represent different morphological demes of caribou that have occurred within the PSBC. It is unfortunate that the ultra *pearyi* apparently are gone, and that this analysis cannot be extended.

Gene flow estimates suggest unidirectional dispersal of caribou from QEI into the population of ultra *pearyi* (Table 5; Fig. 5). This further supports the origin of ultra *pearyi* from a group of typical *pearyi*. Similar gene flow rates are estimated from QEI into Prince of Wales and Somerset islands (Table 5; Fig. 5). The reverse direction of gene flow is not detected. Caribou movement during at least the early- to mid-1900s must have occurred in a northwest to southeast cline across the Canadian Arctic Islands. Given historical climate fluctuations in the Arctic and their influence on caribou diversity (Yannic *et al.*, 2013), these movements were likely driven by unstable climates during the past century.

While our results do not support a genetic basis for the ultra *pearyi*, they still represent an important example of hidden biodiversity within caribou. Certainly, not all variation in caribou body size has a purely genetic basis. Other demographic and environmental factors may have contributed to the large body size of this unique group of Peary caribou. For example, Courturier *et al.* (2010) have shown that migratory behaviour, population density, and intraspecific competition may influence body size of caribou. Regardless, the ultra *pearyi* remain an enigma because no other noticeably large-bodied caribou have ever been reported on any other island at similar latitude.

North-south cline

Our study suggests a genetic basis for the north-south morphological cline reported by Manning (1960) and Banfield (1961). Specifically, we have described a north-south distribution of three genetic groupings of caribou (*pearyi*, *pearyi* x *groenlandicus*, *groenlandicus*). These three groupings exhibit — both morphologically and genetically — decreasingly *pearyi*-like characteristics in a southward pattern (note that our data cannot reveal whether the morphological characteristics are genetically based, because the data are based on neutral markers). Assignment tests reveal a group of caribou from the low Arctic Islands that are hybrids of *pearyi* x *groenlandicus*, and which do not assign strongly to either of the two clusters (Fig. 4, Cluster-2).

Genetic distances suggest that caribou from Banks and northwest Victoria islands in the low arctic are just as genetically distant from caribou located north of 74ºN in the high arctic (*e.g.,* QEI) as they are to mainland populations (Table 4). Recent migration rates show a unidirectional southeastward movement from caribou populations north of 74ºN (QEI) into the populations on the Arctic Islands south of 74ºN (PSBC, Banks and northwest Victoria islands) (Table 5; Fig. 5). The direction and rate of gene flow between the mainland and Dolphin and Union populations are consistent with reports from observations and satellite telemetry (Wright *et al.*, 2002). These data empirically illustrate how latitude is correlated positively with genetic differentiation and inversely with genetic diversity (Eckert *et al.*, 2008; Hampe & Petit, 2005).

Conservation implications

The caribou from QEI represent the northwest extent of the Canadian caribou range. No evidence of north- or west-ward caribou movement was detected in our study (Table 5; Fig. 5). Gene flow estimates suggest a southward trend in caribou movement. It may, therefore, be unlikely that caribou would ever disperse north- or west-ward to occupy the QEI. Therefore, any genetic variation that is lost is unlikely to be naturally replenished. Until this is further investigated, caribou on the QEI should be protected independently of conservation programs designed for other populations of caribou on the Canadian Arctic Islands.

Arctic island biodiversity is intricate, subtle, and warrants protection. Our characterization of ultra *pearyi* reveals extensive complexity in the morphological plasticity of arctic caribou. Furthermore, allelic diversity, probabilities of identity and heterozygosities in the QEI and PSBC populations are low compared to other caribou populations (Table 2; Zittlau *et al.*, 2000; Côté *et al.*, 2002; Courtois *et al.*, 2003; McLoughlin *et al.*, 2004; McDevitt *et al.*, 2009; Petersen *et al.*, 2010; Kuhn *et al.*, 2011; Roffler *et al.*, 2012; Mager *et al.*, 2013). This, along with the lack of a strong signature of a genetic bottleneck among the ultra *pearyi* and PSBC caribou (Table 3) suggest that these populations have persisted for generations with low population sizes. Although each geographic arctic island population does not represent an evolutionarily significant unit on its own, the complexity of the biodiversity across the Canadian Arctic Islands merits conservation attention.

The PSBC caribou population declined from about an estimated 6000 in 1980 (Gunn & Miller, 1983) to no more than several dozen caribou in the mid 1990s (Miller, 1997; Gunn & Dragon, 1998; Gunn *et al.*, 2006; Miller *et al.*, 2007a). A remnant population remains, but there is no evidence of a documented major recovery since then. Based on the precautionary principle, there should be no augmentation of the remnant PSBC caribou population by the translocation of donor caribou from anywhere outside of the PSBC, unless as a last resort. Although the PSBC caribou are genetically clustered with caribou from QEI, the Boothia Peninsula caribou, which occur on the same geographic range, are not. Therefore, awareness of the biodiversity within each range is essential prior to translocation decisions. Such translocations would not be sound conservation actions, as the end goal should be to retain the existing biodiversity and distinctiveness in an endangered caribou population. Furthermore, the distinctive large-bodied morphology of the ultra *pearyi*, and the genetic differentiation between PSBC caribou and neighbouring populations from the lower Canadian Arctic Islands, suggest that each geographic caribou population may harbour cryptic biological diversity. There may be local adaptations and coadapted gene complexes that could be lost or disrupted if new caribou are introduced, thereby reducing

the fitness of these animals (Lynch, 1997; McKay *et al*., 2005; Muhlfield *et al*., 2009). An assessment of functional genetic diversity of caribou across the Canadian Arctic Islands would prove useful for revealing how genetic diversity is distributed across the range, and according to climate fluctuations. Further studies on population recovery mechanisms would shed light on these issues. To retain the naturally occurring diversity and differentiation present among the declining populations of caribou on the Canadian Arctic Islands, conservation efforts should always be targeted well-below the subspecific level at the level of the geographic population. Genetic profiles of each geographic population (*e.g.,* Prince Patrick, Eglinton, Vanier, Cameron, King William, Cornwallis, among many others) would yield a much better foundation for understanding the complexity of existing biodiversity in those populations. In turn, it would provide the most complete and feasible basis for better assessing and maintaining the biodiversity that exists among caribou populations on the Canadian Arctic Archipelago and the mainland Boothia Peninsula.

Conclusions

We have shown that those noticeably large adult male caribou collected by Manning & Macpherson (1961) on Prince of Wales Island in summer 1958 were a morphologically distinct phenotype within the *pearyi* genetic cluster, which were genetically different from other caribou sampled within other low Arctic Islands. Our data do not support the hypothesis that these large-bodied caribou were *pearyi* x *groenlandicus* intergrades. Our analyses also confirm a genetic basis for the north-south morphological cline along the Canadian Arctic Islands. We demonstrate that caribou from the Canadian mainland and caribou from the QEI are genetically distinct from each other and from those caribou found on the low Arctic Islands of Banks and Victoria. Overall, conservation efforts should be directed toward the Peary caribou due to their relatively restricted occurrence on the northern portion of Canadian caribou range where barren-ground caribou have failed to establish themselves, their distinctness from other island caribou, their potential for harbouring hidden biodiversity, and their low census size.

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