GENETICS OF NORTHERN WOLF POPULATIONS

[1]L. E. Carmichael

[1]Department of Biological Sciences,
University of Alberta, Edmonton, AB, T6G 2E9

2007

Final Wildlife Report, No. 21

Carmichael, L. E. 2007. Genetics of Northern wolf populations. Government of Nunavut, Department of Environment, Final Wildlife Report: 21, Iqaluit, 45 pp.

Final Report

GENETICS OF NORTHERN WOLF POPULATIONS

Prepared by:

L. E. Carmichael, PhD
Department of Biological Sciences
University of Alberta
Edmonton AB
T6G 2E9
P: (780) 492-8368
F: (780) 492-9234
Email: lec@ualberta.ca

Submitted February 2007 to:

Mathieu Dumond, Kitikmeot Wildlife Biologist
Department of Environment
Nunavut Wildlife Management Division
Government of Nunavut
Kugluktuk NU

AND

Department of Environment and Natural Resources
Wildlife Division
Government of the Northwest Territories
Yellowknife NT

Executive Summary

Following the Pleistocene glaciation grey wolves (*Canis lupus*) were distributed throughout North America, but are now found primarily in Canada, Alaska, and some small regions of the United States. As many as five glacial refugia have been proposed for wolves, three south of the ice sheets, one in Pearyland (Northern Greenland), and one in Beringia; current recognition of five wolf subspecies, including *C. l. arctos* of the arctic islands, is based on this hypothesis.

Wolves prey primarily on large ungulates, and spatial and temporal variation in prey abundance may have direct impacts on wolf social structure, dispersal distances and territoriality. In North American tundra regions, where migratory barren ground caribou (*Rangifer tarandus groenlandicus*) are the dominant prey species, wolves are territorial only during the breeding season. Once pups are old enough to travel with the pack, wolves abandon their home ranges to follow caribou herds over distances which may total thousands of kilometers, and dispersal may occur during these journeys. In regions with non-migratory prey, young wolves may disperse farther than 800 km, although shorter dispersals are more common when suitable vacant territories are available near natal ranges.

Since genetic factors may influence persistence of species, particularly in island populations and in vulnerable ecosystems, an understanding of a species' population genetics can contribute to development of effective management strategies. North American wolves have been the focus of numerous genetic studies, but most work previously conducted has been devoted to historical, topographical or geological influences on genetic structuring, while only recently have authors begun to consider the influences of habitat and prey on canid population genetics. The goals of this study were: 1) to identify the influence of ecology on movement and gene flow in northern wolves and 2) to determine the genetic status of island wolves and their relationship to mainland populations.

Over 2000 wolf samples were collected from wolves on the arctic islands, barren ground tundra, and northern boreal forest. Samples originated from fur houses, museums, previous research projects, and were collected directly from hunters and trappers in Nunavut and the Northwest Territories. DNA was extracted and 14 bi-parentally inherited microsatellite loci PCR amplified to create a DNA fingerprint of each individual. After removal of duplicate genotypes, 1924 samples remained for analysis. A combination of classical population genetic methods and newer, Bayesian inference techniques were used to explore genetic variation, population genetic structure, and genetic exchange between wolves in different regions.

We found 10 genetically and spatially defined populations whose boundaries corresponded to transitions in habitat type. Clear genetic differentiation was observed between forest and tundra wolves, also corresponding to the shift between territorial and migratory behavior patterns. Gene flow was greater within habitat types than between them. Wolf populations may therefore be segregated by natal habitat-biased dispersal of individuals; chosen habitats are most often similar to birth habitats, with choices likely cued by familiar levels of vegetation cover (forest or tundra) and encounter of familiar prey types. In some areas, avoidance of humans, or assortative mating via pelt colour may reinforce these patterns.

Due to decreased population sizes and restricted gene flow, arctic island wolves possess significantly less variation than mainland populations. Lowest variation in Banks Island and especially High Arctic wolves is the legacy of population bottlenecks – on Banks due to wolf control in the 1950s, in the High Arctic following prey system collapse early this century. North Baffin Island is the corridor for gene flow between Eastern Island and mainland wolves. In the Western Arctic, high, asymmetric gene flow is occurring from Banks Island to Victoria Island. Island-mainland gene flow in the West occurs via Victoria Island and is likely mediated by annual over-ice migrations of the Dolphin-Union caribou herd.

Baffin Island wolves are currently classified as the mainland subspecies *C. l. occidentalis*, but this study shows they are more closely related to *C. l. arctos*. However, all molecular data currently available suggest that arctic island wolves, like mainland tundra populations, arose via post-glacial colonization by wolves from southern refugia, rather than representing a unique subspecies long isolated in a Pearyland refugium. Extinctions and recolonizations among arctic island wolf populations during the last century are consistent with metapopulation dynamics, and management decisions should therefore consider the status of Baffin and northern arctic island wolves as a whole. The Pleistocene history of island wolves likely included similar extinctions and recolonizations, such as those experienced by Beringian brown bears. In bears, spatial overlap of dispersal barriers throughout time resulted in consistent population structure; similar dynamics could have resulted in consistent isolation of arctic island from mainland barren-ground wolves following each colonization of this region. If so, contemporary arctic island wolf populations may reflect a repetitive long-term process that should be recognized as endemic and unique, regardless of their taxonomic status.

Arctic climate change has the potential to dramatically alter the genetics of both mainland and island wolves. As the treeline continues to shift northward, wolves may begin to den at higher latitudes, increasing their access to caribou calves during breeding season, and thus increasing survivorship of pups. However, shifts in the distribution of vegetation and associated prey species may also result in intermingling of forest and tundra wolf ecotypes, a loss of regional differentiation, and perhaps ultimately the loss of migratory wolves. There is also evidence that severe winter conditions associated with climate warming (e.g. deep snow and freezing rain) periodically reduce survival of caribou and muskoxen on the arctic islands, and loss of ungulate prey has led to decline of wolf populations in the past. Island populations already display reduced genetic variation that may restrict their ability to adapt to a changing environment. At present, inbreeding depression is not a significant risk, probably due to intermittent arrival of divergent migrant wolves from the large, continuous mainland population. However, as global warming continues, the number of ice-free weeks in the Northwest Passage will likely increase, especially in the Western Arctic. As winter ice cover becomes thinner, and ice is absent for longer periods, the international shipping community will call for increased traffic through the Passage. Facilitation of this traffic with icebreakers might further reduce the opportunity for mainland wolves to reach the arctic islands. We therefore suggest that human activity in this area be restricted to summer months when the Dolphin-Union caribou are not migrating, such that anthropogenic impacts on both this process, and on wolf gene flow into the Western Arctic Islands, will be minimized. Results of the present study should be used as a baseline for monitoring response of arctic wolf populations to climate change.

Introduction

Origins of Arctic Canids

Members of the family *Canidae* are found on all continents except Antarctica, thriving in habitats both unmodified and highly disturbed (Sillero-Zubiri & MacDonald 2004; Wandeler *et al.* 2003). Canids are at home in ecosystems as divergent as deserts and rain forests, but only two species are distributed throughout the arctic islands and tundra regions of North America. These are the grey wolf (*Canis lupus*) and the arctic fox (*Alopex lagopus*).

The antecedents of wolves (likely *Canis etruscus*) and arctic foxes (likely *Vulpes alopecoides*) evolved in the New World before invading Siberia via the Bering Land Bridge (Kurtén & Anderson 1980). Modern wolves and arctic foxes then arose in the Old World before recolonizing North America. Adaptation of these species to northern environments thus began with their earliest evolution, during repeated exposures to the Beringian Filter (Kurtén & Anderson 1980). Despite similar early origins, however, the later Pleistocene history of wolves and arctic foxes was quite different. This report will focus on grey wolves; for discussion of foxes, please see Carmichael (2006).

Morphological studies of modern wolf skulls indicate highest divergence at the periphery of the species' North American range; for example, in the Mexican wolf (*C. l. baileyi*) and the arctic island wolf (*C. l. arctos*). Such patterns have been termed "centrifugal evolution" and are thought to result from arrival of Old World colonists in waves, each subsequently isolated in a different glacial refugium (Nowak 2003). As many as five refugia have been proposed for wolves, three south of the Pleistocene ice sheets, one in Pearyland (Northern Greenland), and one in Beringia; current recognition of five wolf subspecies is based on this hypothesis, with original subspecies boundaries indicating the limits of post-glacial expansion for each previously isolated population (Brewster & Fritts 1995; Nowak 1995). However, recent surveys of mitochondrial DNA sequence diversity found little correspondence between haplotype distribution and geography (Vilà *et al.* 1999), and the contemporary northern wolf population possesses only a subset of the variation found in southern historical samples (Leonard *et al.* 2005). Current hypotheses may therefore be inconsistent with the true evolutionary history of this species.

The Grey Wolf

Grey wolves are the largest of the *Canidae*, with males weighing up to 62 kg and females slightly smaller (Mech & Boitani 2004); they are distinguished from red wolves (*Canis rufus*) by size, skull morphology, and distribution. Prior to European colonization of North America, grey wolves ranged from Mexico to the Canadian Arctic Archipelago – with red wolves found in the southeastern United States (USA) – but are currently restricted to Alaska, Canada, and a few small populations in the conterminous USA. Pelage colours in grey wolves are extremely variable and widely distributed; however, the frequency of pale wolves increases with increasing latitude and almost all individuals on the arctic islands (*C. l. arctos*) are white. This suggests pale colouration may be an adaptation for hunting in open tundra environments.

Wolves are opportunistic carnivores, and their diet is diverse and variable (e.g., Hayes *et al.* 2000; Kohira & Rexstad 1997; Kuyt 1972; Larter *et al.* 1994). However, stable wolf populations cannot be maintained in the absence of large ungulates (Mech 2005), and spatial and temporal variation in abundance of ungulate prey may have direct impacts on wolf social structure, breeding patterns, dispersal distances and territoriality.

A social species, wolves form packs as large as 42 individuals that center around a dominant breeding pair (Mech & Boitani 2003). Subordinate females occasionally breed, but additional adult family members most frequently act as non-breeding helpers, protecting and provisioning the offspring of the dominant pair (Mech & Boitani 2003). These helpers may be mature relatives of the breeders, their offspring from previous years, or unrelated (Lehman *et al.* 1992; Mech & Boitani 2003). Regardless of composition, the size of a wolf pack is determined by the amount of prey available; competition increases within the pack during food shortages, and may be a primary impetus behind wolf dispersal (Mech & Boitani 2003).

Wolf home range sizes also vary with availability of prey, and wolves generally defend larger territories when ungulate density declines (Mech & Boitani 2003). In North American tundra regions, where migratory barren ground caribou (*Rangifer tarandus groenlandicus*) are the dominant prey species, wolves are territorial only during the breeding season. Adults make long distance foraging movements while denning (Frame *et al.* 2004), and once pups are old enough to travel with the pack, wolves abandon their home ranges to follow caribou herds over distances which may total thousands of kilometers, and dispersal may occur during these journeys (Walton *et al.* 2001). Even in regions with non-migratory prey, young wolves may disperse farther than 800 km (Fritts 1983), although shorter dispersals are more common when suitable vacant territories are available near natal ranges (Mech & Boitani 2003).

Recent History and Current Status of Grey Wolves

The first wildlife legislation in North America was enacted in 1630 and offered a one-cent bounty for the killing of wolves (Kellert *et al.* 1996); their current restricted range is testament to the efficacy of this historical persecution. In Alaska and the Canadian North, wolf control (through poisoning or shooting) is also a contemporary phenomenon, enacted to reduce both predation pressure on ungulates used by humans and the loss of trapped arctic foxes to wolves (Boertje *et al.* 1996; Hayes & Harestad 2000; McEwen 1955; Usher 1965). While non-lethal methods of wolf control are in development (Boertje *et al.* 1995; Spence *et al.* 1999), wolves in Alaska and the Canadian Territories are also currently harvested for both private and commercial use. However, as this harvest represents a relatively small proportion of the estimated population, legal harvesting may not threaten northern wolf populations as a whole (Mech & Boitani 2004; Van Zyll de Jong & Carbyn 1999).

An external influence more likely to jeopardize wolf persistence, particularly in the Canadian Arctic Archipelago, is climate change. Severe winter weather producing deep or hard snow has been implicated in mortality of Peary caribou (*R. t. pearyi*) and muskoxen (*Ovibos moschatus*; Gunn *et al.* 1991; Larter & Nagy 2001a; Larter & Nagy 2001b). Since arctic foxes, arctic hares (*Lepus arcticus*), and small rodents are the only other mammalian prey in the

Archipelago, islands without ungulates will not support wolf populations (Mech 2005)., Documented changes in population size (McEwen 1955; Usher 1965; Gunn *et al.* 1991; Larter & Nagy 2000; Mech 2005) and skull morphology through the 20th century (Manning & Macpherson 1958; Clutton-Brock *et al.* 1994) suggest island wolf populations are particularly volatile, and contemporary *C. l. arctos* may therefore be at increased risk of extinction. However, the extent and current status of this subspecies are not well known (Miller 1995).

Project Objectives

North American wolves have been the focus of numerous genetic studies undertaken at a range of scales and employing a variety of molecular markers (recently reviewed by Wayne & Vilà 2003), but most population-level studies previously conducted have been devoted to historical, topographical or geological influences on genetic structuring, while only recently have authors begun to consider the influences of habitat and prey on canid population genetics (Geffen *et al.* 2004; Sacks *et al.* 2004; Sacks *et al.* 2005). Since "organisms mostly form their own environments, and nearly all of the important context for organisms is other organisms," (p. 217, Pratchett *et al.* 2005) a major goal of this work is to identify the influence of ecology on the genetics of northern wolves.

From a genetic perspective, persistence of populations depends upon two factors: maintenance of adequate genetic variation and avoidance of inbreeding depression. Evolution cannot occur without pre-existing genetic variation, and genetically depauperate populations may therefore be unable to adapt to changing environmental conditions. Island populations, which are usually of smaller size, lose genetic variation quickly due to elevated rates of genetic drift (Frankham 2005). Drift may be countered by gene flow between populations, which may both increase genetic variation and reduce inbreeding (Vilà *et al.* 2003); however, island populations, by their very physical nature, are expected to experience less gene flow than contiguous mainland ones, and thus may also face higher risk of inbreeding depression.

The genetic variation and isolation of wolves in the Canadian Arctic Archipelago, which are capable of traversing annual sea ice, has not been thoroughly examined (but see Carmichael *et al.* 2001). However, given the potentially dramatic effects of climatic change on arctic ecosystems, and the inherent demographic stochasticity arctic island canid populations may already face, genetic threats to their persistence are of particular concern. A second goal of this work was thus to determine the genetic nature and status of arctic island wolf populations, relative to those on the mainland. Since wolf pelts are a valuable source of income for many northern residents, appropriate management of both island and mainland wolf populations may be of economic as well as ecological significance.

Methods

Sample Collection

Contemporary samples of over 2000 wolves were collected from throughout the northern boreal forest and tundra regions of North America (Fig. 1a). Hunters from communities across Nunavut (NU) and the Northwest Territories (NT) were asked to provide material from legally harvested wolves. Wolf skulls collected in Nunavut were used for genetic work and for complementary studies of wolf morphology (Krizan 2005); hunters were paid for each skull contributed, including information regarding harvest date, location, and sex of the animal if known. Sample collection for genetic work began in 1998, and continued through December 2004. Samples obtained directly from hunters were supplemented with those received from fur auction houses, museums, and other research projects.

All laboratory analysis described in this report was conducted at the University of Alberta.

Laboratory Methods and Dataset Validation

Tissue and blood samples were stored frozen while dry material such as pelt or hair was kept at room temperature. DNeasy tissue kits were used to extract genomic DNA from all samples (QIAGEN, Germany). Fourteen biparentally inherited microsatellite loci were PCR-amplified using fluorescently-labeled primers from domestic dogs (locus names and reaction conditions given in Carmichael *et al*., submitted A.). The pseudoautosomal loci DBX and DBY were also amplified from all samples as a molecular sex test (Seddon 2005). All genotypes were checked twice by eye and all ambiguous results repeated. The Microsatellite Excel Toolkit (Park 2001) was used to scan the dataset for typographical errors and for samples with identical genotypes. After elimination of matching individuals, 1924 wolves remained for analysis (genotypes given in Carmichael *et al.* submitted A.).

Delineation of Regions and Preliminary Analysis

Capture locations of all wolves were mapped using ARCGIS 9.1 (Environmental Systems Research Institute 1999-2004) and individuals were divided into geographic regions based on three hierarchical criteria: 1) gaps in the sampling distribution, 2) ranges of associated barren ground caribou herds (Carmichael *et al.* 2001; Hall 1989; Zittlau 2004), and 3) political boundaries of Canadian provinces (Fig. 1a). Regions considered to be occupied by migratory barren ground wolves, and regions considered to be occupied by sedentary forest wolves, are listed in Fig. 1a. This categorization was based on the distribution limit of migratory barren ground caribou (e.g. Musiani 2003).

Each region was tested for genic differentiation, linkage disequilibrium, and Hardy-Weinberg Equilibrium (HWE) using the Markov Chain method of GENEPOP 3.4 (Raymond & Rousset 1995) with dememorization of 10,000, 1000 batches, and 10,000 iterations per batch. Genic differentiation results were combined across loci using Fisher's method (Sokal & Rohlf 1995), and Bonferroni corrections used to obtain P values of 0.05 for all tests.

Delineation of Genetic Clusters

STRUCTURE 2.1 was used to perform Bayesian clustering of genotypes, including all loci and without any prior population information (Pritchard *et al.* 2000). Methods followed those for arctic foxes (Carmichael 2006), except that λ was set to 0.4 and three replicates each of K=1-13 were conducted. STRUCTURE results were confirmed using GENELAND, a Bayesian clustering program that incorporates spatial coordinates of individuals into the analysis via Voronoi tessellation, thus assigning greater probability to genetic clusters that are continuous within the spatial landscape (Guillot *et al.* 2005). The following settings were used in GENELAND: delta.coord 0.15 (to "de-noise" the spatial coordinates); 1,000,000 iterations; burn-in 100,000 iterations; thinning 1000; the Dirichlet allele frequency model; and 7 populations (based on STRUCTURE results, Fig. 2a-b). Delineation of mainland clusters was nearly identical between GENELAND and STRUCTURE but the methods differed with regards to island populations (Carmichael *et al.*, submitted A). Ten wolf clusters were therefore defined, with ecotype (migratory or territorial) of each cluster shown in Fig. 1b.

Most analyses of wolves used genetically defined clusters as the unit of comparison; however, finer scale investigations of island-mainland relationships were conducted using geographic regions (Fig. 1a). Throughout the paper, "region" refers to a geographically defined group of samples, "cluster" refers to a genetically defined group of samples, and "population" is used inclusively.

Determinants of Genetic Structure in Wolves

Nei's standard genetic distance (D_S) among all genetically defined clusters was calculated in PHYLIP 3.65 (Felsenstein 1995; Nei 1972). We then used distance based redundancy analysis (dbRDA, Geffen *et al.* 2004; McArdle & Anderson 2001) to identify factors influencing relationships among clusters. dbRDA allows the user to test up to N-1 predictor variables (N = number of populations) either individually, or fitted in sequence to produce a combined model.

Correlations between Nei's D_S among our wolf clusters and 8 potential determinants of genetic structure were tested. We first designed a predictor which indicated the dominant prey species within the range of each wolf cluster, based upon distribution of large ungulate species and available wolf diet studies (Hayes *et al.* 1997; Hayes *et al.* 2000; Kohira & Rexstad 1997; Larter *et al.* 1994; Mahoney & Virgl 2003; Olsen *et al.* 2001; R Popko, pers. comm.; Schaefer *et al.* 1999; Spaulding *et al.* 1998; Stenhouse *et al.* 1995; Urton & Hobson 2005). However, wolf diet is complex and variable over space and time, and we were forced to make a number of assumptions while constructing this predictor. To simplify and to focus on an aspect of prey behavior that influences movement patterns of associated wolves (Ballard *et al.* 1997; Walton *et al.* 2001), we next designed an indicator denoting the behavior, sedentary or migratory, of the dominant prey species in the range of each wolf cluster (migratory barren-ground caribou = 0, all other species = 1). These predictors were tested singly and as a set called "prey."

Water barriers between populations – the Mackenzie River, channels of the Arctic ocean and the straights between the Coastal Islands and the mainland (Fig. 1b) – were coded in a similar fashion. Annual minimum temperature and annual rainfall in each area were obtained from Environment Canada (2000) and the National Climatic Data Center's online databases (2000), and vegetation was categorized using the World Wildlife Fund's Terrestrial Ecosystems (ESRI 2006). These habitat descriptors were tested separately and as a set called "habitat." Finally, average latitude and longitude for each cluster were tested individually, as a set called "spatial", and in combination with other variable sets.

We used the program PCO to perform principle coordinate analysis (PCA) on our genetic distance matrix (Anderson 2003b), then conducted dbRDA on all variables using DISTLM *forward* (Anderson 2003a). Marginal tests of each predictor or set of predictors were made, followed by sequential tests using a forward selection procedure to produce a combined model of genetic differentiation in wolves.

Genetic Variation

Expected heterozygosity H_E (Nei & Roychoudhury 1974) of each cluster was calculated in the Microsatellite Excel Toolkit, and significant differences in H_E identified using Wilcoxon's signed-ranks tests (Sokal & Rohlf 1995). The rarefaction method implemented in CONTRIB 1.01 (Petit *et al.* 1998) was used to calculate allelic richness after correction for variation in sample size, with a rarefaction size of 22 allele copies.

BOTTLENECK 1.2.02 was used to test for recent bottlenecks in all island populations using a range of mutational models (Piry *et al.* 1999; Spencer *et al.* 2000; Carmichael *et al.*, submitted B). All tests were assessed for significance using a one-tailed Wilcoxon's test for excess heterozygosity. Consistent evidence of population declines was found for Banks Island and the High Arctic; the M-ratio test was therefore performed to confirm results for these populations (Garza & Williamson 2001), using a range of pre-bottleneck population sizes estimated from available literature (Carmichael *et al.*, submitted B).

Gene Flow Among Wolf Populations

Mainland wolf clusters derived in STRUCTURE encompassed broad geographical areas (Fig. 1b); to identify gene flow corridors between island and mainland wolves at a finer physical scale, we assessed genetic distance among geographic regions (Fig. 1a). PHYLIP was used to generate 1000 bootstrap pseudoreplicates, D_S was calculated for each replicate, and a neighbor-joining majority-rule consensus tree constructed (Felsenstein 1985; Saitou & Nei 1987). Fig. 3 shows the relationship between regions; for reference, membership of each geographic region in each STRUCTURE cluster is also indicated.

Paetkau *et al.*'s classical assignment test (1995) was conducted among clusters as in (Carmichael 2006). We performed further assignment using the Bayesian model implemented in BAYESASS, which also provides estimates of inbreeding within each population and the asymmetrical rates of migration between them (Wilson & Rannala 2003). Two replicates were conducted, each consisting of 3,000,000 iterations, with a burn-in of 999,999 cycles and a thinning interval of 2000 (Carmichael *et al.*, submitted B). Results of all four assignment methods (STRUCTURE, GENELAND, classical, and BAYESASS) were compared to identify island-mainland migrants (Carmichael *et al.*, submitted B).

Results

Genetic Structure of Northern Wolf Populations

North American arctic foxes formed a single genetic unit (Carmichael 2006); in contrast, K = 7 was the most appropriate choice for wolves (Fig. 2a-b). STRUCTURE recovered an Atlantic group, a western and eastern boreal forest group (Western Woods and Forest) and a western and eastern barren ground group (Western Barrens and Eastern Barrens), as shown in Fig. 1b. Assignment of mainland clusters was nearly identical in GENELAND as in STRUCTURE, however, the methods differed with regards to island populations. GENELAND separated Coastal Island wolves and grouped all arctic island wolves into a single cluster; STRUCTURE divided the arctic islands into a Western grouping (Banks and Victoria Island) and an Eastern grouping (North and South Baffin Island), and did not delineate Coastal Island wolves until K = 9 (data not shown). We suspect this difference is due to spatial concentration of the Coastal samples, which would receive high weighting in the GENELAND framework.

We combined results from STRUCTURE and GENELAND to devise genetic clusters of wolves in all regions (Carmichael *et al.*, submitted A). Because of inconsistency in partitioning island populations, and to retain the ability to explore the genetics of island wolves in detail, the Coastal Islands, Banks Island, Victoria Island, and Baffin Island (Northern and Southern samples combined, Carmichael *et al*. submitted A) were considered distinct populations. STRUCTURE described the High Arctic region as a mixture of Western Island wolves, Eastern Island wolves, and mainland types. However, these samples were analyzed as a discrete population due to their physical isolation.

Clustering analysis suggested genetic discontinuities between wolves occupying forested versus tundra habitats (sedentary vs. migratory wolves, Fig. 1b). In addition to observation of distinct wolf populations in distinct habitat types, classical assignment tests suggested higher gene flow within habitat types than between habitat types, regardless of intervening distances (Table 1, Carmichael *et al*., submitted A). These observations suggested habitat is critical to genetic structuring of wolves and influenced the suite of predictor variables chosen for dbRDA analysis (below).

The matrix of D_S between wolf populations contained several vectors with large and negative Eigenvalues, suggesting genetic distance was highly non-metric (Laub & Muller 2004; Table 2a). Negative Eigenvectors have been shown to correspond to hidden aspects of data variation (Laub & Muller 2004), and their exclusion biases significance calculations in dbRDA (McArdle & Anderson 2001). These vectors were therefore included despite resultant oddities such as negative F statistics (with associated P values above 0.95) for some predictor variables, and sequential tests that explained more than 100% of the variation in D_S (Table 3). This complexity does not invalidate the dbRDA procedure (MJ Anderson, pers. comm.).

Minimum temperature explained 98% of the variation in D_S ($P = 0.0001$) when the 8 predictors were tested individually; addition of longitude to temperature in a sequential test explained 113%. Significant positive associations were also obtained between latitude or rainfall and D_S, while behavior of prey (migratory or non-migratory) was significantly negatively associated with genetic distance (Table 3). This negative association signified correlation to the "imaginary" dimensions of D_S identified by negative Eigenvalues in the PCA (MJ Anderson, pers. comm.). When we grouped variables into sets, the spatial coordinates displayed the strongest relationship to D_S, explaining 98.14% of the genetic distance ($P = 0.0005$, Table 3). However, tests for correlations between predictors indicated that each spatial variable was strongly correlated, positively or negatively, to most of the other predictors in our matrix (Table 2b), implying that the high explanatory power of the spatial variables is more complex than a simple causal increase in D_S with geographic distance.

Variation, Population Bottlenecks, and Inbreeding

On average, island wolves had 14% less H_E than mainland wolves, and all island populations were significantly less variable than those on the mainland (Table 4). In contrast to the relatively consistent H_E among islands, allelic richness (A^r) values suggested two general categories of island wolves: the Coastal Islands, Victoria Island, and Baffin Island had more than 4 alleles per locus, while Banks Island and the High Arctic had fewer than 4 alleles per locus (Table 4). These estimates were corrected for sample size, and thus suggest a genuine loss of allelic diversity in the latter two populations.

Similar contrasts between H_E and A^r were observed in the recently bottlenecked Phillip Island red fox population (Lade *et al.* 1996). Since Banks Island and the High Arctic are also known to have suffered demographic bottlenecks in the last 50 years (Mech 2005; Usher 1965), we tested for genetic signatures of population declines. Banks Island showed significant evidence of bottleneck under all but one mutational model, and the High Arctic population was always marginally significant (e.g., $P = 0.08$, two phase model). We calculated M ratios to confirm these results assuming a range of pre-bottleneck effective population sizes (*Ne)*. Average M was 0.64 for the High Arctic and 0.70 for Banks Island under all conditions, and all ratios were significantly different from equilibrium expectations ($P \leq 0.01$).

However, inbreeding does not appear to be significant in these populations (Table 4). Banks Island's inbreeding coefficient was 0.003; while F_{IS} was 0.63 in the High Arctic, the genetic complexity of this population (identified by STRUCTURE analysis) suggested a Wahlund effect rather than non-random mating. Similarly, an F_{IS} of 0.43 in Victoria Island likely reflects the presence of multiple migrants within the population (below). However, the F_{IS} of 0.18 in the Coastal Islands (Table 4) may represent true inbreeding.

Since our total Banks Island sample consisted of wolves hunted between 1991-93, 1997-99, and 2002-04, we were able to use changes in allele frequencies over time to estimate effective population size (Carmichael *et al*., submitted B). *Ne* ranged from 51 to 53 (depending on source of immigrants assumed), or 25% of the estimated total population (Carmichael *et al.* 2001).

Differentiation of Island and Mainland Wolves

Among the arctic islands, High Arctic was most distinct, perhaps reflecting the population's physical separation or its small sample size (Table 5). D_S between islands, and between islands and the mainland, was greater than between any pair of mainland populations with three exceptions: Victoria Island and Eastern Barrens (0.160); Baffin Island and Eastern Barrens (0.159); and Banks and Victoria Island (0.089).

Mainland wolf clusters derived in STRUCTURE spanned large geographical areas. To identify mainland wolves most similar to the island populations at a finer scale, and thus to identify specific locations where island-mainland gene flow might occur, this analysis was repeated using geographic regions (Fig. 1a). The Western Islands and the High Arctic plotted proximate to the Bathurst region within the Eastern Barrens cluster, while North and South Baffin Island were nearest the NE Mainland region of the Eastern Barrens (Fig. 3); these mainland groups are those physically proximate to each island set (Fig. 1a). It is also worth noting that D_S between North Baffin Island and the mainland was smaller than that between South Baffin Island and the mainland, with one exception: the genetic distances to the Atlantic population (0.398 vs. 0.078 respectively).

Migration and Gene Flow Among Island and Mainland Wolves

Self-assignment rates for mainland wolf populations averaged 75% (range 59-96%); the average for island wolves was 90%, ranging from 69% in Victoria Island to 100% in the High Arctic (Table 1). In contrast to the relatively low rate for Victoria, Banks Island – the other Western Island population – had a self-assignment rate of 94%. This difference resulted from lower genetic differentiation and thus higher cross assignment between Victoria Island and the mainland (Fig. 4a-b), and from apparent high gene flow from Banks Island to Victoria (below). In the Eastern Arctic, Baffin Island's relationship with mainland wolves was comparable to that of Victoria Island, rather than that of Banks (Fig. 4c).

Bayesian estimations of migration rates among populations are shown in Table 6. Total migration between Baffin Island and all mainland populations was low but approximately equal in each orientation, averaging 0.0157 ± 0.0020. In contrast, total migration between the Western Islands and all mainland populations was directionally biased: 0.0013 from mainland to Banks Island and 0.0161 from Banks Island to the mainland; 0.0523 from mainland to Victoria Island and 0.0065 from Victoria to the mainland. The difference in frequency of island-mainland movements for each Western Island was supported by agreement between all four assignment tests (STRUCTURE, GENELAND, classical, and BAYESASS): 4 of 52 individuals sampled in Victoria Island likely originated in barren ground populations; 4 of 941 barren ground wolves originated in Victoria Island; 3 of 941 barren ground wolves migrated from Banks Island; no wolf sampled on Banks Island had migrated from the mainland (Carmichael *et al*., submitted B).

BAYESASS also indicated highly asymmetric migration between the Western Islands: 26% of Victoria Island samples had migrated from Banks Island, with no movement in the opposite direction (Table 6). These estimates differ slightly from those obtained through classical assignment tests (Table 1) due to computational differences between methods, but regardless of the exact rate, migration between the Western Islands occurs primarily in an eastern orientation, from Banks Island into Victoria Island.

Discussion

Ecologically-Defined Genetic Structure of Grey Wolves

D_S between wolf populations was higher than among arctic foxes in almost all cases (Carmichael *et al.*, submitted A). Similarly, with the exception of Svalbard at 42%, self-assignment rates for arctic foxes were below 14%; the smallest self-assignment rate for wolves was 59% (Forest cluster, Table 1). Therefore, with the possible exception of migratory tundra animals, wolves likely disperse shorter distances, or disperse long-distances less often than foxes do. More interesting is the observation that the amount of wolf gene flow varies with habitat type, and gene flow occurs in non-random directions. Differentiation was lower among barren ground populations than territorial forest populations (Table 1, 5), consistent with the extensive annual migrations which facilitate long-distance dispersal of tundra wolves (Walton *et al.* 2001), and with the high potential for gene flow when wolves follow distinct caribou herds into common wintering grounds. Despite separation by half the distance, differentiation between Western Barrens (migratory tundra) and Western Woods (territorial forest) wolves was equivalent to that among forest wolves, suggesting the transition between wooded and tundra habitats discourages gene flow between wolf populations (Table 1, 5). Indeed, boundaries of Bayesian-derived genetic clusters correspond to boundaries of habitat types (Fig. 1b).

The single greatest predictor of wolf genetic differentiation in our study was climate (minimum annual temperature, Table 3). It is not clear that this result represents a causal link between climate and gene flow; indeed, it is difficult to imagine how temperature could directly influence the amount or direction of genetic exchange between wolf populations. However, two correlates of temperature (Table 2b), vegetation type (0.7332) and prey species (-0.4712) could direct the dispersal choices of individual wolves (Geffen *et al.* 2004). Description of these complex factors required simplifying assumptions that may have hampered our ability to directly detect correlations, but it is interesting to note that the behavior of the dominant prey species in each area (resident or migratory) is significantly correlated to the imaginary vectors within wolf Ds (Table 3). Distance was not significantly correlated with wolf D_S (Mantel test, data not shown), but when combined, latitude and longitude explained more variation in D_S than minimum temperature alone (Table 3). As with climate, we suggest that the high explanatory power of this predictor set also reflects a more complex, underlying causal process. This idea is supported by correlations between these variables and all other factors in our predictor set. In other words, these spatial descriptors provide a strong summary of all variables describing the habitat and ecology of wolves in each region (Table 2b).

Considered together, the outcomes of our Bayesian clustering, classical assignment, and dbRDA analysis support the hypothesis that natal habitat-biased dispersal drives genetic differentiation in wolves (Davis & Stamps 2004; Geffen *et al.* 2004; Sacks *et al.* 2004). In canids, natal habitat-biased dispersal was first suggested for coyotes (Sacks *et al.* 2004), but likely also occurs between urban and rural populations of red foxes (Wandeler *et al.* 2003). For northern wolves, a familiar level of vegetation cover – forest or tundra – could signify a suitable habitat, encouraging dispersing wolves to remain within their natal habitat type. Dispersers that settle in familiar areas may also increase their reproductive success via cultural mechanisms, as hunting strategies specific to local prey would be learned during tenure with their natal pack

(Sacks *et al.* 2005). In our study area, learned behavior is most likely to isolate forest from tundra wolves, which have adapted their denning and territorial behavior to cope with the large scale seasonal movements of barren ground caribou (Heard & Williams 1992; Walton *et al.* 2001). Prey specialization as a barrier to gene flow has been suggested by other authors (Carmichael *et al.* 2001; Geffen *et al.* 2004; Musiani 2003), and has been used to explain differences in skull morphology between wolf populations in other regions (Brewster & Fritts 1995).

Assortative mating via pelage colour could also contribute to differentiation along the north-south axis (between the Eastern Barrens and the southern Forest population), as a significant increase in frequency of pale and white wolves is observed with increasing latitude (Musiani 2003). However, wolves from the Eastern Barrens invade the range of Forest wolves following the southern winter migration of barren ground caribou, and since this period includes wolf breeding season (Mech 2002), a high potential for admixture exists. While dominant wolves are most likely to mate with dominant partners within their own pack, gene flow between forest and tundra wolves may occur via interbreeding of subordinate individuals, as in other canids (e.g. Baker *et al.* 2004). The frequency of such events in wolves is not well known, but gene flow may be overestimated by our assignment data for two reasons (Table 1). Samples contributed by hunters and trappers are most often collected during winter, and may thus represent admixture of Eastern Barrens and Forest individuals without admixture of tundra and forest genes (mingling of individuals without gene flow). Furthermore, hunters from Northern Saskatchewan often harvest wolves in the Northwest Territories, but return home before selling the resultant pelts (D Bewick, pers. comm.). Samples identified by fur houses as originating in Saskatchewan (Forest cluster) might therefore truly originate in the Eastern Barrens. Significant cross-assignment from the Forest into the Eastern Barrens cluster (Table 1) supports, however, some level of genetic exchange between forest and tundra wolves in this area.

Genetics of Island Wolves

Coastal Island Wolves

The genetics of Coastal Island wolves have been discussed in detail by Weckworth *et al.* (2005); we included them here for comparison to Arctic Island wolves. In our study, the Coastal Island population had the only positive F_{IS} value likely attributable to inbreeding, consistent with isolation of these wolves from mainland populations via intervening mountain ranges (Weckworth *et al.* 2005), which may also have contributed to D_S values between the Coastal Islands and all other populations greater than any other we observed. However, STRUCTURE partitioned the arctic island populations as early as K = 3, while Coastal samples were not segregated until K = 9. Such conflicts between assignment tests and genetic distances likely reflect respective sensitivities of each method to events at different time scales (Castric & Bernatchez 2004). One possible interpretation of our results under this assumption is that Coastal Island wolves have been isolated for a longer period of time, while recent drift in arctic island populations – resulting from isolation, demographic bottlenecks, or a combination thereof – has been rapid and severe.

Banks Island Wolves

Poisoning of the Banks Island wolf population began in the mid 1950s and concluded when residents no longer observed wolves on the island. However, it is not clear whether the contemporary population descended from individuals persisting in the remote, uninhabited north-east corner of the island, or from wolves immigrating from other arctic islands (Usher 1965), and our data can not distinguish between these hypotheses. However, significant changes in skull morphology between Banks Island wolves collected in 1914-16 and in 1953-55 (prior to wolf control) suggest extinction and recolonization occurred early in the century (Manning & Macpherson 1958), and such events may thus have produced the contemporary population as well. D_S between Banks and Victoria Island is less than half the next smallest island-to-island distance (Table 5); therefore, of populations surveyed here, Victoria Island is the most likely origin of post-poisoning Banks Island wolves.

Since 1974, the Banks Island muskoxen population increased from 3800 to 65,000 individuals, and is currently estimated at 45,000 (Gunn *et al.* 1991; Larter & Nagy 2001a). Peary caribou (*R. t. pearyi*) populations declined during the same period (Larter & Nagy 2000), but there is no doubt island wolves have access to ample prey. Therefore, resource competition is not a likely explanation for the high rate of wolf migration from Banks to Victoria Island (Table 3). However, with an estimated 200 individuals, the Banks Island wolf population is larger than at any time in the past 50 years, and wolves may be leaving the island in search of unoccupied territories (Mech & Boitani 2003). It is interesting to speculate that the current direction of migration arises from a reversal of events which led to colonization of Banks Island by wolves from Victoria Island earlier this century.

If, on average, 2 wolves breed in a pack of 6-8 individuals (Mech & Boitani 2003), the calculated effective population size of 51-53 is higher than expected for a total estimated population size of 200 wolves. This result may indicate that the total wolf population is larger than previously thought, or could reflect a perturbation of wolf social structure resulting from annual harvesting of approximately 25% (Hayes & Harestad 2000). Wolf harvesting as a key influence is supported by our observation of small changes in allele composition and frequencies over time (data not shown). In addition to the impact of a relatively high *rate* of harvest, genetic drift in this population may be accelerated by hunters' tendency to harvest several individuals from the same pack (Carmichael *et al.* 2001); however, it should be noted that this practice may also have inflated estimations of drift from our samples. Continued monitoring of drift and variation in this population may be warranted, especially if ingress is reduced or the ungulate prey base begins to decline.

Victoria Island

Relative to Banks Island, Victoria Island wolves are less genetically differentiated from mainland populations (Table 1, Fig. 4), and the rate of migration between Victoria and the mainland is substantially higher (Table 6). D_S between the islands is consistent with separation by linear distance only, and wolf tracks have been observed on the sea ice between the islands, suggesting no barrier to gene flow exists (Carmichael *et al.* 2001). Therefore, Victoria Island likely acts as the prime contact point between the Western Arctic Islands and the mainland, with gene flow occurring between Banks Island and Victoria, and between Victoria Island and the mainland. It is worth noting that, historically, Banks Island Inuit would not travel directly south to the mainland, as sea ice conditions in the Amundsen Gulf were considered unstable and treacherous; as we suggest for wolves, the Inuit traveled first from Banks Island to Victoria Island, despite the increased distance involved (Usher 1965).

While sea ice conditions may influence the success of wolf migration, we support the hypothesis that annual over-ice migrations of the Dolphin-Union caribou herd – which calve on Victoria Island, but winter on the mainland (Fig. 5) – facilitate island-mainland wolf gene flow, and that wolves migrate incidentally while in pursuit of their prey (Carmichael *et al.* 2001). It is less clear, however, why migration occurs primarily from the mainland to the island, instead of equally in both directions (Table 6). One possibility is that Western Island wolves have dense muskoxen populations as an alternative to migrating Dolphin-Union caribou, while mainland wolves are largely dependent on caribou (Kuyt 1972), and must either follow the Dolphin-Union herd or switch to an alternate barren-ground population until their return (Walton *et al.* 2001). Timing of wolf denning relative to the position of their prey may also be relevant, as mainland wolves following caribou would reach the island in spring, and might thus need to establish local territories for whelping. Regardless of the underlying mechanism, it seems clear that mainland wolves arrive in the Western Islands via Victoria Island: in addition to identifiable migrants (Fig. 4b) and a high Wahlund-induced F_{IS} (Table 4), Victoria Island contains the highest genetic diversity of any island surveyed here (Table 4).

High Arctic Island Wolves

Samples were collected from Ellesmere and Devon Islands between 1999-2002. Since this period corresponded to the collapse of the High Arctic prey system (Mech 2005), we could obtain only 11 individuals, and results presented here should be considered preliminary. Despite this limitation, our data suggests several interesting genetic features of the High Arctic island wolf population.

STRUCTURE identified this sample as a mixture of Western Island, Eastern Island, and mainland wolves. However, when the results of all four assignment tests were combined, the High Arctic population consisted of two resident wolves, five migrants from the Western Islands, two likely hybrids of residents and Western Island migrants, and a Baffin Island immigrant (Carmichael *et al.*, submitted B). It is interesting to note that the only two resident wolves, GF44 and GF45, were harvested in November of 1999, prior to the population decline. The putative hybrids were sampled in 2002, after the first migrants had been harvested on the island. While these results are tentative, our sample appears to contain pre-bottleneck residents and post-bottleneck colonists of the High Arctic Islands. This hypothesis suggests that observed high F_{IS} reflects a Wahlund effect – although inbreeding could also have occurred in such a small population – and explains why significant evidence of genetic bottlenecks was detected in M-ratio tests, but not tests for relative excess heterozygosity conducted in BOTTLENECK (Piry *et al.* 1999): the decline in heterozygosity produced by a Wahlund effect would have reduced the power of this test.

Baffin Island Wolves

Morphological subspecies investigations suggest Baffin Island wolves are more closely related to the mainland that to other arctic island populations (Nowak 1995). While the magnitude of D_S between Baffin and other clusters supports this idea, clustering analysis using STRUCTURE and GENELAND, and levels of differentiation within classical assignment tests (data not shown), suggest a greater current affinity to island wolves over mainland ones. These observations may be analogous to those for Coastal Island wolves, reflecting on the one hand post-glacial colonization of Baffin Island, and on the other, divergent behaviors with opposing influences on the genetics of island and mainland wolves (island wolves, with a more spatially stable prey base, are likely more territorial than mainland barren-ground wolves in general).

Functionally, Baffin is most similar to Victoria Island: it is the contact point for migration between Eastern Island wolves and those on the mainland (Fig. 4). Lower migration relative to Victoria (Table 6) may be due to estimation using the Bayesian cluster composed of the total Baffin Island population; fine-scale analysis with Baffin Island divided into two geographically defined subpopulations (Carmichael *et al*. submitted A) revealed greater differentiation between South Baffin and the mainland than North Baffin and the mainland, and migration rates between regions within the Eastern Barrens cluster and the Baffin Island subpopulations reflected this result (data not shown). Baffin caribou herds use distinct calving grounds in the northern and southern parts of the island (Ferguson 1989), and the differentiation of Baffin wolf subpopulations from each other and from the mainland may result from prey specialization on distinct groups of caribou (Clark 1971).

D_S between the South Baffin region and the NE Mainland region (Eastern Barrens cluster) was almost twice the distance between South Baffin and the Atlantic population (0.149 vs. 0.078). It is interesting to speculate that wolf migration through the South Baffin region connects the arctic islands to southern tundra populations in Quebec and Labrador, while North Baffin connects the Eastern Islands to mainland arctic tundra wolves. This hypothesis is supported by recent morphological studies suggesting reduction in size of South Baffin wolves relative to North Baffin wolves, but especially relative to large-skulled mainland populations in Nunavut (Krizan 2005).

Implications of the Present Work

Mainland Wolf Populations

Unlike panmictic arctic foxes, wolves exhibit natal habitat-biased dispersal – likely resulting from both physical aspects of their environment and learned hunting behaviors – which may in some areas be reinforced by assortative mating or anthropogenic influences (Mackenzie River region, Carmichael *et al.* 2001). Whatever the underlying mechanisms, dispersal of wolves is decidedly non-random, and genetic discontinuities correspond closely to changes in prey behavior and habitat type.

Arctic climate change has the potential to dramatically alter wolf population boundaries. As the treeline continues to shift northward (Grace *et al.* 2002), wolves may begin to den at higher latitudes (Heard & Williams 1992), increasing their access to caribou calves during breeding season (Frame *et al.* 2004), and thus increasing survivorship of pups (Fuller *et al.* 2003). However, shifts in the distribution of vegetation and associated prey species (Brotton & Wall 1997; Mech 2005) may also result in intermingling of forest and tundra wolf ecotypes, a loss of regional differentiation, and perhaps ultimately the demise of migratory wolves. Results of the present study could therefore be used as a baseline for monitoring future changes in these populations.

Origin and Conservation of Arctic Island Wolves

Morphological data has been used to suggest Baffin Island was colonized – along with mainland tundra populations – by wolves from southern glacial refugia, while northern arctic island populations arose from wolves previously isolated in Pearyland (North Greenland, Nowak 1995). Distinct subspecies, *C. l. occidentalis* (mainland and Baffin) and *C. l. arctos* (northern arctic island) have thus been proposed. However, mtDNA sequence analysis showed low correlation between haplotype distribution and geography, a result that is generally unsupportive of subspecies in wolves (Vilà *et al.* 1999), and suggests most or all mainland North American populations may have expanded from glacial refugia in the southern United States (Leonard *et al.* 2005). Similarly, results presented here do not support the existence of a Pearyland refugium for arctic wolves.

Baffin and northern arctic island wolves are genetically similar, and genetically distinct from mainland populations, but D_S values were greatest for the southern Coastal Islands (Table 5). This supports the hypothesis that Coastal wolves have a long history distinct from those on the mainland (Weckworth *et al.* 2005), and may also suggest that arctic island populations were more recently isolated. Although Banks and Victoria Island shared an allele found in no other population (total frequency 1%, data not shown), private alleles were not found within any island sample. Major Histocompatability Complex genes sequenced from Alaskan and Canadian wolves showed greatest diversity with unique haplotypes in boreal forest populations, moderate diversity with no unique haplotypes in mainland barren-ground populations, and lowest diversity in Banks Island wolves (Kennedy *et al.* submitted). Our own preliminary mtDNA sequencing revealed lower haplotype diversity in, and no haplotypes unique to the arctic islands (unpublished data). All molecular data currently available thus suggest that arctic island wolves, like mainland tundra populations, arose via post-glacial colonization by wolves from southern refugia, rather than representing a unique subspecies long isolated in a Pearyland refugium. Indeed, the pattern of declining variation observed here is typical of repeated founding effects during initial colonization of previously glaciated areas (Hewitt 1996). Furthermore, mitochondrial sequence data suggests similar histories for bison (*Bison bison*, Shapiro *et al.* 2004) and mainland barren-ground caribou populations (Dueck 1998).

Extinctions and recolonizations among arctic island wolf populations during the last century are consistent with metapopulation dynamics (Elmhagen & Angerbjorn 2001), and management decisions should therefore consider the status of Baffin and northern arctic island wolves as a whole. We can also speculate that the Pleistocene history of island wolves included similar extinctions and recolonizations, such as those experienced by Beringian brown bears (*Ursus arctos*), whose range expanded and contracted with each glacial cycle (Barnes *et al.*

2002). In the latter case, population genetic structure following each recolonization was similar, implying spatial overlap of dispersal barriers throughout time. Similar overlap of barriers has been observed in Italian wolves (Lucchini *et al.* 2004), and could have resulted in consistent isolation of arctic island from mainland barren-ground wolves following each colonization of this region. If so, contemporary arctic island wolf populations may reflect a repetitive long-term process that should be recognized as endemic and unique, regardless of their taxonomic status.

Two threats to persistence of these unique wolves exist. While prey population dynamics are influenced by a number of factors, there is some evidence that severe winter conditions associated with climate warming (e.g. deep snow and freezing rain) periodically reduce survival of caribou and muskoxen on the arctic islands (Larter & Nagy 2001b; Mech 2005). Loss of ungulate prey has led to decline of wolf populations (Gunn 2006; Mech 2005), while presence of wolves may be contributing to the decline of endangered Peary caribou (COSEWIC 2004). Development of complimentary management plans for these species may therefore be challenging.

Extinction risk for wolves will doubtless be greatest on smaller high arctic islands, where demographic stochasticity may have a more immediate effect, but the metapopulation should persist so long as adequate food resources exist in at least some regions. However, our results suggest arctic island wolves may soon face genetic, as well as ecological threats. Island populations already display reduced genetic variation (Table 4) that may restrict their ability to adapt to a changing environment. At present, inbreeding depression is not a significant risk, probably due to intermittent arrival of divergent migrant wolves from the large, continuous mainland population. However, as global warming continues, the number of ice-free weeks in the Northwest Passage will likely increase, especially in the Western Arctic (Johnston 2002). As winter ice cover becomes thinner, and ice is absent for longer periods, the international shipping community will call for increased traffic through the Passage (Charron 2005; Johnston 2002). Facilitation of this traffic with icebreakers might further reduce the opportunity for mainland wolves to reach the arctic islands. We therefore suggest that human activity in this area be restricted to summer months when the Dolphin-Union caribou are not migrating, such that anthropogenic impacts on both this process, and on wolf gene flow into the Western Arctic Islands, will be minimized.

Recommendations for Future Research

Data presented here and elsewhere suggests that arctic island wolves, while unique, may not warrant a subspecific designation. However, final judgments as to the validity of *C. l. arctos* should not be made until further mtDNA and perhaps Y chromosome sequencing has been performed on these populations. Morphological or genetic studies of wolves from northern Quebec would also clarify the relationship between North and South Baffin populations and those on the mainland.

Results of this work and that of Musiani (2003) support genetic distinction of migratory tundra and territorial boreal forest wolves. We would expect a genetic contribution to the phenotypic and perhaps behavioral differences which result in this differentiation. Genome-wide screening of wolves representing each ecotype, using SNP technology developed by the Canine

Genome Project, has the potential to identify markers and genes association with each ecotype, and might thus illuminate the molecular process by which wolves adapt to their environments. A research project devoted to these questions is in development and will be undertaken as a collaboration between researchers at the University of Alberta, University of Calgary, and the University of Los Angeles (Davis).

Acknowledgements

Thanks to all those who contributed samples or facilitated their collection: J Nagy, A Veitch, and D Johnson with the DoENR (NWT); J Krizan and M Dumond with the DoE (NT); J Mattie of Alaska Raw Fur; D Bewick and North American Fur Auctions; G Jarrell and the University of Alaska Museum; P Merchant; R Mulders; P Clarkson; R Otto; D Berezanski; I Stirling; R Brenneman; and numerous Hunters and Trapper's Associations and wildlife officers across the Northwest Territories, Manitoba, and Nunavut.. Special thanks to MJ Anderson and G Guillot for assistance with DISTLM *forward* and GENELAND; to B Dust for sample collection assistance, computational support and memory allocation adjustments in STRUCTURE; to J Bonneville for assistance with DNA extraction and molecular sex testing; to G Carmichael for preparation of tissue samples for extraction; and to A Carmichael for verification of wolf harvest dates. R Popko offered information of dietary habits of wolves in the Sahtu. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada, the Alberta Ingenuity Fund, the Killam Foundation, the Government of Nunavut, and the Northern Scientific Training Program.

References

Anderson MJ (2003a) DISTLM forward: a FORTRAN computer program to calculate a distance-based multivariate analysis for a linear model using forward selection. , Auckland, New Zealand.

Anderson MJ (2003b) PCO: a FORTRAN computer program for principal coordinate analysis. , Auckland, New Zealand.

Baker PJ, Funk SM, Bruford MW, Harris S (2004) Polygynandry in a red fox population: implications for the evolution of group living in canids? *Behavioral Ecology*, 15, 766-778.

Ballard WB, Ayres LA, Krausman PR, Reed DJ, Fancy SG (1997) Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. *Wildlife Monographs*, 135, 1-47.

Barnes I, Matheus P, Shapiro B, Jensen D, Cooper A (2002) Dynamics of Pleistocene population extinctions in Beringian brown bears. *Science*, 295, 2267-2270.

Boertje RD, Kelleyhouse DG, Hayes RD (1995) Methods for reducing natural predation on moose in Alaska and Yukon: an evaluation. In: *Ecology and Conservation of Wolves in a*

Changing World (eds. Carbyn LN, Fritts SH, Seip DR). Canadian Circumpolar Institute, Edmonton.

Boertje RD, Valkenburg P, McNay ME (1996) Increases in moose, caribou, and wolves following wolf control in Alaska. *Journal of Wildlife Management*, 60, 474-489.Brewster WG, Fritts SH (1995) Taxonomy and genetics of the gray wolf in Western North America: a review. In: *Ecology and Conservation of Wolves in a Changing World* (eds. Carbyn LN, Fritts SH, Seip DR), pp. 353-374. Canadian Circumpolar Institute, Edmonton.

Brewster WG, Fritts SH (1995) Taxonomy and genetics of the gray wolf in Western North America: a review. In: *Ecology and Conservation of Wolves in a Changing World* (eds. Carbyn LN, Fritts SH, Seip DR), pp. 353-374. Canadian Circumpolar Institute, Edmonton.

Brotton J, Wall G (1997) Climate change and the Bathurst caribou herd in the Northwest Territories, Canada. *Climatic Change*, 35, 35-52.

Carmichael LE (2006) *Genetics of North American Arctic Fox Populations.* Report to DENR (NT) and DOE (NU).

Carmichael LE, Krizan J, Nagy JA, Fuglei E, Dumond M, Johnson D, Veitch A, Berteaux D, Strobeck C. (Submitted A) Historical and ecological determinants of genetic structure in arctic canids. Submitted to Molecular Ecology December 2006.

Carmichael LE, Krizan J, Nagy JA, Dumond M, Johnson D, Veitch A, Strobeck C. (Submitted B) Northwest passages: genetics of arctic island wolves over space and time. Submitted to Molecular Ecology December 2006.

Carmichael LE, Nagy JA, Larter NC, Strobeck C (2001) Prey specialization may influence patterns of gene flow in wolves of the Canadian Northwest. *Molecular Ecology*, 10, 2787-2798.

Castric V, Bernatchez L (2004) Individual assignment test reveals differential restriction to dispersal between two salmonids despite no increase of genetic differences with distance. *Molecular Ecology*, 13, 1299-1312.

Charron A (2005) The Northwest Passage - Is Canada's sovereignty floating away? *International Journal*, 60, 831-848.

Clark KRF (1971) *Food habits and behavior of the tundra wolf on central Baffin Island*, Ph.D. thesis, University of Toronto.

Clutton-Brock J, Kitchener AC, Lynch JM (1994) Changes in the skull morphology of the Arctic wolf, *Canis lupus arctos*, during the 20th century. *Journal of Zoology*, 233, 19-36.

COSEWIC (2004) COSWEIC assessment and update status report on the Peary caribou *Rangifer tarandus pearyi* and the barren-ground caribou *Rangifer tarandus groenlandicus* (Dolphin and Union population) in Canada., p. 91. Committee on the Status of Endangered Wildlife in Canada, Ottawa, ON.

Davis JM, Stamps JA (2004) The effect of natal experience on habitat preferences. *Trends in Ecology & Evolution*, 19, 411-416.

Dueck GS (1998) *Genetic relations and phylogeography of woodland and barrenground caribou*, Master's Thesis, University of Alberta.

Elmhagen B, Angerbjorn A (2001) The applicability of metapopulation theory to large mammals. *Oikos*, 94, 89-100.

Environment Canada (2000) Canadian Climate Normal Data. Government of Canada.

Environmental Systems Research Institute (1999-2004) ArcGIS 9.0 software, Redlands, California.

ESRI (2006).

Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution*, 39, 783-791.

Felsenstein J (1995) PHYLIP (Phylogeny Inference Package), Seattle.

Ferguson M (1989) Baffin Island. In: *People and Caribou in the Northwest Territories* (ed. Hall E), pp. 141-149. Department of Renewable Resources, Government of the Northwest Territories, Yellowknife.

Frame PF, Hik DS, Cluff HD, Paquet PC (2004) Long foraging movement of a denning tundra wolf. *Arctic*, 57, 196-203.

Frankham R (2005) Genetics and extinction. *Biological Conservation*, 126, 131-140.

Fritts SH (1983) Record dispersal by a wolf from Minnesota. *Journal of Mammalogy*, 64, 166-167.

Fuller TK, Mech LD, Cochrane JF (2003) Wolf population dynamics. In: *Wolves: behavior, ecology, and conservation* (eds. Mech LD, Boitani L), pp. 161-191. University of Chicago Press, Chicago.

Garza JC, Williamson EG (2001) Detection of reduction in population size using data from microsatellite loci. *Molecular Ecology*, 10, 305-318.

Geffen E, Anderson MJ, Wayne RK (2004) Climate and habitat barriers to dispersal in the highly mobile grey wolf. *Molecular Ecology*, 13, 2481-2490.

Grace J, Berninger F, Nagy L (2002) Impact of climate change on the tree line. *Annals of Botany*, 90, 537-544.

Guillot G, Estoup A, Mortier F, Cosso JF (2005) A spatial statistical model for landscape genetics. *Genetics*, 170, 1261-1280.

Gunn A, Miller FL, Barry SJ, Buchan A (2006) A near-total decline in caribou on Prince of Wales, Somerset, and Russell Islands, Canadian Arctic. *Arctic*, 59, 1-13.

Gunn A, Shank C, McLean B (1991) The history, status and management of muskoxen on Banks Island. *Arctic*, 44, 188-195.

Hall E (1989) People & Caribou in the Northwest Territories, p. 190. Department of Renewable Resources, Government of the Northwest Territories, Yellowknife.

Hayes B, Baer A, Clarkson P (1997) The Ecology and Management of Wolves in the Porcupine Caribou Range, Canada. Government of Yukon.

Hayes RD, Baer AM, Wotschikowsky U, Harestad AS (2000) Kill rate by wolves on moose in the Yukon. *Canadian Journal of Zoology*, 78, 49-59.

Hayes RD, Harestad AS (2000) Demography of a recovering wolf population in the Yukon. *Canadian Journal of Zoology*, 78, 36-48.

Heard DC, Williams TM (1992) Distribution of wolf dens on migratory caribou ranges in the Northwest Territories, Canada. *Canadian Journal of Zoology*, 70, 1504-1510.

Hewitt GM (1996) Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, 58, 247-276.

Johnston DM (2002) The Northwest Passage revisited. *Ocean Development and International Law*, 33, 145-164.

Kellert SR, Black M, Rush CR, Bath AJ (1996) Human culture and large carnivore conservation in North America. *Conservation Biology*, 10, 977-990.

Kennedy LJ, Angles JM, Barnes A, Carmichael L, Ollier WER, Happ GM (Submitted) DLA-DRB1, DQA1, and DQB1 alleles and haplotypes in North American grey wolves. Submitted November 2006.

Kohira M, Rexstad EA (1997) Diets of wolves, *Canis lupus*, in logged and unlogged forests of southeastern Alaska. *Canadian Field-Naturalist*, 111, 429-435.

Krizan J (2005) Nunavut Wolf Morphology and Diet Study, p. 59. Department of Environment, Nunavut Wildlife Management Division, Government of Nunavut, Iqualuit.

Kurtén B, Anderson E (1980) *Pleistocene mammals of North America* Columbia University Press, New York.

Kuyt E (1972) Food habits and ecology of wolves on barren-ground caribou range in the Northwest Territories. *Canadian Wildlife Service Report Series, Number 21*. Information Canada, Ottawa.

Lade JA, Murray ND, Marks CA, Robinson NA (1996) Microsatellite differentiation between Phillip Island and mainland Australian populations of the red fox *Vulpes vulpes*. *Molecular Ecology*, 5, 81-87.

Larter NC, Nagy JA (2000) Calf production and overwinter survival estimates for Peary caribou, *Rangifer tarandus pearyi*, on Banks Island, Northwest Territories. *Canadian Field Naturalist*, 114, 661-670.

Larter NC, Nagy JA (2001a) Calf production, calf survival, and recruitment of muskoxen on Banks Island during a period of changing population density from 1986-99. *Arctic*, 54, 394-406.

Larter NC, Nagy JA (2001b) Variation between snow conditions at Peary caribou and muskox feeding sites and elsewhere in foraging habitats on Banks Island in the Canadian High Arctic. *Arctic Antarctic and Alpine Research*, 33, 123-130.

Larter NC, Sinclair ARE, Gates CC (1994) The response of predators to an erupting bison, *Bison bison athabascae*, population. *Canadian Field-Naturalist*, 108, 318-327.

Laub J, Muller KR (2004) Feature discovery in non-metric pairwise data. *Journal of Machine Learning Research*, 5, 801-818.

Leonard JA, Vila C, Wayne RK (2005) Legacy lost: genetic variability and population size of extirpated US grey wolves (*Canis lupus*). *Molecular Ecology*, 14, 9-17.

Lucchini V, Galov A, Randi E (2004) Evidence of genetic distinction and long-term population decline in wolves (Canis lupus) in the Italian Apennines. *Molecular Ecology*, 13, 523-536.

Mahoney SP, Virgl JA (2003) Habitat selection and demography of a nonmigratory woodland caribou population in Newfoundland. *Canadian Journal of Zoology*, 81, 321-334.

Manning TH, Macpherson AH (1958) The Mammals of Banks Island. Arctic Institute of North America, Montreal.

McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*, 82, 290-297.

McEwen EH (1955) *A biological survey of the west coast of Banks Island*. Canadian Wildlife Service, Ottawa ON.Mech LD (2005) Decline and recovery of a high arctic wolf-prey system. *Arctic*, 58, 305-307.

Mech LD (2002) Breeding season of wolves, *Canis lupus*, in relation to latitude. *Canadian Field Naturalist*, 116, 139-140.

Mech LD (2005) Decline and recovery of a high Arctic wolf-prey system. *Arctic*, 58, 305-307.

Mech LD, Boitani L (2003) Wolf social ecology. In: *Wolves: behavior, ecology, and conservation* (eds. Mech LD, Boitani L), pp. 1-34. University of Chicago Press, Chicago.

Mech LD, Boitani L (2004) Grey Wolf. In: *Canids: foxes, wolves, jackals and dogs. Status survey and conservation action plan.* eds. Sillero-Zubiri C, Hoffman M, MacDonald DW), pp. 124-129. IUCN/SSC Canid Specialist Group, Gland, Switzerland.

Miller FL (1995) Status of wolves on the Canadian Arctic Islands. In: *Ecology and Conservation of Wolves in a Changing World* (eds. Carbyn LN, Fritts SH, Seip DR). Canadian Circumpolar Institute, Edmonton.

Musiani M (2003) *Conservation biology and management of wolves and wolf-human conflicts in western North America*, Ph.D. Thesis, University of Calgary.

National Climatic Data Center (2000) Alaska climate normals. U. S. Deparment of Commerce.

Nei M (1972) Genetic distance between populations. *The American Naturalist*, 106, 283-292.

Nei M, Roychoudhury AK (1974) Sampling variances of heterozygosity and genetic distance. *Genetics*, 76, 379-390.

Nowak RM (1995) Another look at wolf taxonomy. In: *Ecology and Conservation of Wolves in a Changing World* (eds. Carbyn LN, Fritts SH, Seip DR), pp. 375-398. Canadian Circumpolar Institute, Edmonton.

Nowak RM (2003) Wolf evolution and taxonomy. In: *Wolves: behavior, ecology, and conservation* (eds. Mech LD, Boitani L), pp. 239-258. University of Chicago Press, Chicago.

Olsen B, MacDonald M, Zimmer A (2001) Co-management of woodland caribou in the Sahtu Settlement area: workshop on research, traditional knowledge, conservation and cummulative impacts., p. 22. Sahtu Renewable Resources Board, Tulita.

Paetkau D, Calvert W, Stirling I, Strobeck C (1995) Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology*, 4, 347-354.

Park SDE (2001) *Trypanotolerance in West African cattle and the population genetic effect of selection*, Ph.D. Thesis, University of Dublin.

Petit RJ, El Mousadik A, Pons O (1998) Identifying populations for conservation on the basis of genetic markers. *Conservation Biology*, 12, 844-855.

Piry S, Luikart G, Cornuet JM (1999) BOTTLENECK: A computer program for detecting recent reductions in the effective population size using allele frequency data. *Journal of Heredity*, 90, 502-503.

Pratchett T, Stewart I, Cohen J (2005) *The Science of Discworld.* Ebury Press, London.

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics*, 155, 945-959.

Raymond M, Rousset F (1995) Genepop (Version-1.2) - Population-genetics software for exact tests and ecumenicism. *Journal of Heredity*, 86, 248-249.

Sacks BN, Brown SK, Ernest HB (2004) Population structure of California coyotes corresponds to habitat-specific breaks and illuminates species history. *Molecular Ecology*, 13, 1265-1275.

Sacks BN, Mitchell BR, Williams CL, Ernest HB (2005) Coyote movements and social structure along a cryptic population genetic subdivision. *Molecular Ecology*, 14, 1241-1249.

Saitou N, Nei M (1987) The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution*, 4, 406-425.

Schaefer JA, Veitch AM, Harrington FH*, et al.* (1999) Demography of decline of the Red Wine Mountains caribou herd. *Journal of Wildlife Management*, 63, 580-587.

Seddon JM (2005) Canid-specific primers for molecular sexing using tissue or non-invasive samples. *Conservation Genetics*, 6, 147-149.

Shapiro B, Drummond AJ, Rambaut A*, et al.* (2004) Rise and fall of the Beringian steppe bison. *Science*, 306, 1561-1565.

Sillero-Zubiri C, MacDonald DW (2004) Introduction. In: *MacDonald, D. W.Canids: foxes, wolves, jackals and dogs. Status survey and conservation action plan.* (eds. Sillero-Zubiri C, Hoffman M), pp. 2-7. IUCN/SSC Canid Specialist Group, Gland, Switzerland.

Sokal RR, Rohlf FJ (1995) *Biometry: The Principles and Practice of Statistics in Biological Research*, 3rd edn. W. H. Freeman and Company, New York.

Spaulding RL, Krausman PR, Ballard WB (1998) Summer diet of Gray Wolves, Canis lupus, in northwestern Alaska. *Canadian Field-Naturalist*, 112, 262-266.

Spence CE, Kenyon JE, Smith DR, Hayes RD, Baer AM (1999) Surgical sterilization of free-ranging wolves. *Canadian Veterinary Journal*, 40, 118-121.

Spencer CC, Neigel JE, Leberg PL (2000) Experimental evaluation of the usefulness of microsatellite DNA for detecting demographic bottlenecks. *Molecular Ecology*, 9, 1517-1528.

Stenhouse GB, Latour PB, Kutny L, Maclean N, Glover G (1995) Productivity, Survival, and Movements of Female Moose in a Low-Density Population, Northwest-Territories, Canada. *Arctic*, 48, 57-62.

Urton EJM, Hobson KA (2005) Intrapopulation variation in gray wolf isotope (delta N-15 and delta C-13) profiles: implications for the ecology of individuals. *Oecologia*, 145, 317-326.

Usher PJ (1965) *Banks Island: an area economic survey*. Industrial Division, Department of Northern Affairs and National Resources, Ottawa.

Van Zyll de Jong CG, Carbyn LN (1999) COSEWIC Status Report on the Grey Wolf (*Canis lupus*) in Canada. COSEWIC, Ottawa.

Vilà C, Amorim R, Leonard JA, *et al.* (1999) Mitochondrial DNA phylogeography and population history of the grey wolf *Canis lupus*. *Molecular Ecology*, 8, 2089-2103.

Vilà C, Sundqvist A-K, Flagstad Ø, *et al.* (2003) Rescue of a severely bottlenecked wolf (*Canis lupus*) population by a single immigrant. *Proceedings of the Royal Society of London Series B Biology*, 270, 91-97.

Wandeler P, Funk M, Largiadèr CR, Gloor S, Breitenmoser U (2003) The city-fox phenomenon: genetic consequences of a recent colonization of urban habitat. *Molecular Ecology*, 12, 647-656.

Walton LR, Cluff HD, Paquet PC, Ramsay MA (2001) Movement patterns of barren-ground wolves in the central Canadian Arctic. *Journal of Mammalogy*, 82, 867-876.

Wayne RK, Vilà C (2003) Molecular genetic studies of wolves. In: *Wolves: behavior, ecology, and conservation* (eds. Mech LD, Boitani L), pp. 218-238. University of Chicago Press, Chicago.

Weckworth BV, Talbot S, Sage GK, Person DK, Cook J (2005) A signal for independent coastal and continental histories among North American wolves. *Molecular Ecology*, 14, 917-931.

Wilson GA, Rannala B (2003) Bayesian inference of recent migration rates using multilocus genotypes. *Genetics*, 163, 1177-1191.

Zittlau KA (2004) *Population genetic analyses of North American caribou (Rangifer tarandus)*, Ph.D. Thesis, University of Alberta.

Table 1 Assignment among wolf clusters. The proportion of individuals sampled in each cluster, which assign to each cluster, is indicated by each row. Self-assignment proportions are outlined, and bold values represent significantly more cross-assignment than predicted given each sample's allele frequencies.

Sampling Cluster	**Assigned Cluster**									
	WW	FO	WB	EB	AT	CI	BI	VI	HA	BAF
Western Woods (WW)	0.904	**0.047**	0.037	0.012	0.000	0.000	0.000	0.000	0.000	0.000
Forest (FO)	0.050	0.589	0.074	**0.275**	0.000	0.000	0.000	0.004	0.000	**0.008**
Western Barrens (WB)	**0.084**	**0.110**	0.679	0.089	0.004	0.000	**0.008**	**0.025**	0.000	0.000
Eastern Barrens (EB)	**0.024**	**0.192**	0.080	0.635	**0.036**	0.000	0.001	0.013	0.000	**0.020**
Atlantic (AT)	0.000	0.040	0.000	0.000	0.960	0.000	0.000	0.000	0.000	0.000
Coastal Islands (CI)	**0.056**	0.000	**0.028**	0.000	0.000	0.917	0.000	0.000	0.000	0.000
Banks Island (BI)	0.000	0.000	0.000	0.000	0.000	0.000	0.939	**0.061**	0.000	0.000
Victoria Island (VI)	0.000	0.000	**0.038**	0.038	0.000	0.000	**0.231**	0.692	0.000	0.000
High Arctic (HA)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000
Baffin Island (BAF)	0.000	0.000	0.000	0.060	0.000	0.000	0.000	**0.009**	0.000	0.931

	% Variation Explained	
Axis	Individual	Cumulative
1	112.99	112.99
2	14.18	127.18
3	9.21	136.39
4	2.35	138.74
5	0.01	138.75
6	0.00	138.75
7	-0.29	138.45
8	-1.43	137.02
9	-2.42	134.60
10	-34.60	100.00

Table 2a Principle coordinate analysis of Nei's D_S among wolf clusters. The large negative Eigenvalue of axis 10 indicates non-metricity and implies complexity within the genetic distance.

Table 2b Correlation among predictor variables used in distance-based redundancy analysis of Nei's D_S among wolf clusters. Variable sets are indicated in bold.

		Spatial		**Prey**		**Habitat**		
	Barrier	Latitude	Longitude	Behavior	Species	Temperature	Rain	Vegetation
Barrier	1							
Latitude	0.5156	1						
Longitude	-0.2068	-0.097	1					
Behavior	0.6124	-0.0544	0.2056	1				
Species	0.5278	0.7424	-0.1747	0.068	1			
Temperature	-0.2059	-0.8524	-0.2934	0.1393	-0.4712	1		
Rain	0.1137	-0.5771	-0.2625	0.214	-0.0516	0.8482	1	
Vegetation	0.7013	0.531	0.2656	0.6247	0.7332	-0.3735	-0.0262	1

Table 3 Distance-based redundancy analysis of Nei's D_S among wolf clusters. We analyzed individual variables (single predictors) alone, then sequentially to obtain a combined model. Analysis was then repeated while treating variables as predictor sets (grouped as in Table 2b). Significant *P* values in marginal tests are shown in bold. The column headed % Var indicates the amount of variation in D_S explained by a particular variable, with Cumulative indicating the total variation explained by all fitted variables in sequential tests. Explanatory power of greater than 100% results from non-metricity in the D_S matrix.

Test		**Single Predictors**				
Marginal		Variable	F	P	% Var	
		Barrier	-0.65	0.9273	-8.80	
		Latitude	11.42	**0.0115**	58.80	
		Longitude	3.83	0.1188	32.37	
	Prey <	Behavior	-0.56	**0.9779**	-7.49	
		Species	0.24	0.6685	2.97	
		Temperature	392.34	**0.0001**	98.00	
		Rain	23.09	**0.0017**	74.27	
		Vegetation	0.21	0.6477	2.54	
Sequential		Variable	F	P	% Var	Cumulative
		Temperature	392.34	0.0001	98.00	98.00
		Longitude	-8.06	0.7760	15.17	113.18
		Predictor Sets				
Marginal		Variable	F	P	% Var	
		Barrier	-0.65	0.9287	-8.80	
		Spatial	185.06	**0.0005**	98.14	
		Prey	-0.12	0.8796	-3.46	
		Habitat	5.15	0.0623	72.03	
Sequential		Variable	F	P	% Var	Cumulative
		Spatial	185.06	0.0005	98.14	98.14

Table 4 Genetic variation in island and mainland wolves.

	Variation					**Significant**[£]				
Cluster[*]	**N**[†]	**H_E**[§]	**H_E SD**	**A^R (22)**[¥]	**F_{IS}**[¶]	**CI**	**BI**	**VI**	**HA**	**BAF**
Western Woods	322	0.73	0.02	5.67	0.009	*	*	*	*	*
Forest	258	0.74	0.03	5.92	0.033	*	*	*	*	*
Western Barrens	237	0.74	0.02	5.92	0.024	*	*	*	*	*
Eastern Barrens	704	0.74	0.03	6.04	0.017	*	*	*	*	*
Atlantic	25	0.75	0.03	6.06	0.070	*	*	*	*	*
Mainland		**0.74**		**5.92**						
Coastal Islands (CI)	36	0.61	0.05	4.19	0.181					
Banks Island (BI)	163	0.63	0.03	3.65	0.003					
Victoria Island (VI)	52	0.65	0.03	4.30	0.427				*	
High Arctic (HA)	11	0.49	0.06	3.07	0.629					
Baffin Island (BAF)	116	0.60	0.04	4.20	0.031					
Island		**0.60**		**3.88**						

[*] Genetically defined clusters of wolves (Fig. 1b). Averages for population type are given in bold.

[†] sample size

[§] expected heterozygosity, with standard deviation indicated by SD

[¥] allelic richness, with rarefaction size (in alleles) given in brackets

[¶] population inbreeding estimated in BayesAss

[£] stars indicate significant differences in heterozygosity between pairs of populations

Table 5 Nei's standard genetic distance (D_S) between clusters. Mainland-mainland comparisons appear in the upper left triangle, island-island comparisons in the lower right triangle, with island-mainland comparisons in the square. Largest and smallest genetic distances are shown in bold.

	WW	FO	WB	EB	AT	CI	BI	VI	HA	BAF
Western Woods (WW)	0									
Forest (FO)	0.112	0								
Western Barrens (WB)	0.105	0.045	0							
Eastern Barrens (EB)	0.165	**0.039**	**0.039**	0						
Atlantic (AT)	0.351	0.262	0.267	0.218	0					
Coastal Islands (CI)	0.363	0.438	0.454	0.509	0.662	0				
Banks Island (BI)	0.302	0.270	0.240	0.225	0.381	0.887	0			
Victoria Island (VI)	0.325	0.216	0.185	0.160	0.424	0.871	0.089	0		
High Arctic (HA)	0.493	0.442	0.355	0.332	0.500	**1.229**	0.260	0.245	0	
Baffin Island (BAF)	0.360	0.255	0.222	0.159	0.345	0.729	0.424	0.343	0.344	0

Table 6 Bayesian estimates of migration rates among wolf populations. Direction of migration is from populations in the left column to those right of the vertical line. "Self-migration" rates (analogous to self-assignment rates) are outlined, rates greater than 2% shown in bold, and populations are abbreviated as in Table 2. Standard deviation of migration rates averaged 0.005 and did not exceed 0.0382 (HA-HA).

	To									
From	WW	FO	WB	EB	AT	CI	BI	VI	HA	BAF
Western Woods	0.9865	0.0040	**0.0541**	0.0013	0.0028	0.0020	0.0003	0.0049	0.0158	0.0009
Forest	0.0076	0.8405	0.0086	**0.0805**	0.0030	0.0018	0.0003	0.0050	0.0162	0.0009
Western Barrens	0.0021	0.0021	0.8987	0.0026	0.0033	0.0016	0.0003	**0.0204**	0.0163	0.0015
Eastern Barrens	0.0015	**0.1478**	**0.0237**	0.8901	0.0038	0.0019	0.0003	0.0172	**0.0238**	0.0130
Atlantic	0.0003	0.0006	0.0016	0.0145	0.9690	0.0015	0.0003	0.0049	0.0156	0.0009
Coastal	0.0003	0.0007	0.0010	0.0004	0.0029	0.9855	0.0003	0.0045	0.0155	0.0009
Banks Island	0.0004	0.0011	0.0087	0.0022	0.0037	0.0015	0.9975	**0.2590**	**0.0997**	0.0010
Victoria Island	0.0006	0.0006	0.0015	0.0007	0.0025	0.0014	0.0003	0.6746	0.0159	0.0009
High Arctic	0.0003	0.0005	0.0009	0.0009	0.0051	0.0014	0.0003	0.0047	0.7439	0.0009
Baffin Island	0.0004	0.0021	0.0012	0.0068	0.0038	0.0015	0.0003	0.0048	**0.0373**	0.9791

Figure 1a Sampling range of grey wolves, with treeline indicated by a black line. Wolf samples are shown grouped into geographic regions. Cape Bathurst, Bluenose W, Bathurst, NE Main and Qaminurjuaq are composed primarily of migratory wolves; all other populations are non-migratory.

Figure 1b Grey wolf samples grouped into genetic clusters based on results of analyses in STRUCTURE and GENELAND. Western Barrens and Eastern Barrens represent migratory wolves, with all other populations considered sedentary.

Figure 2A

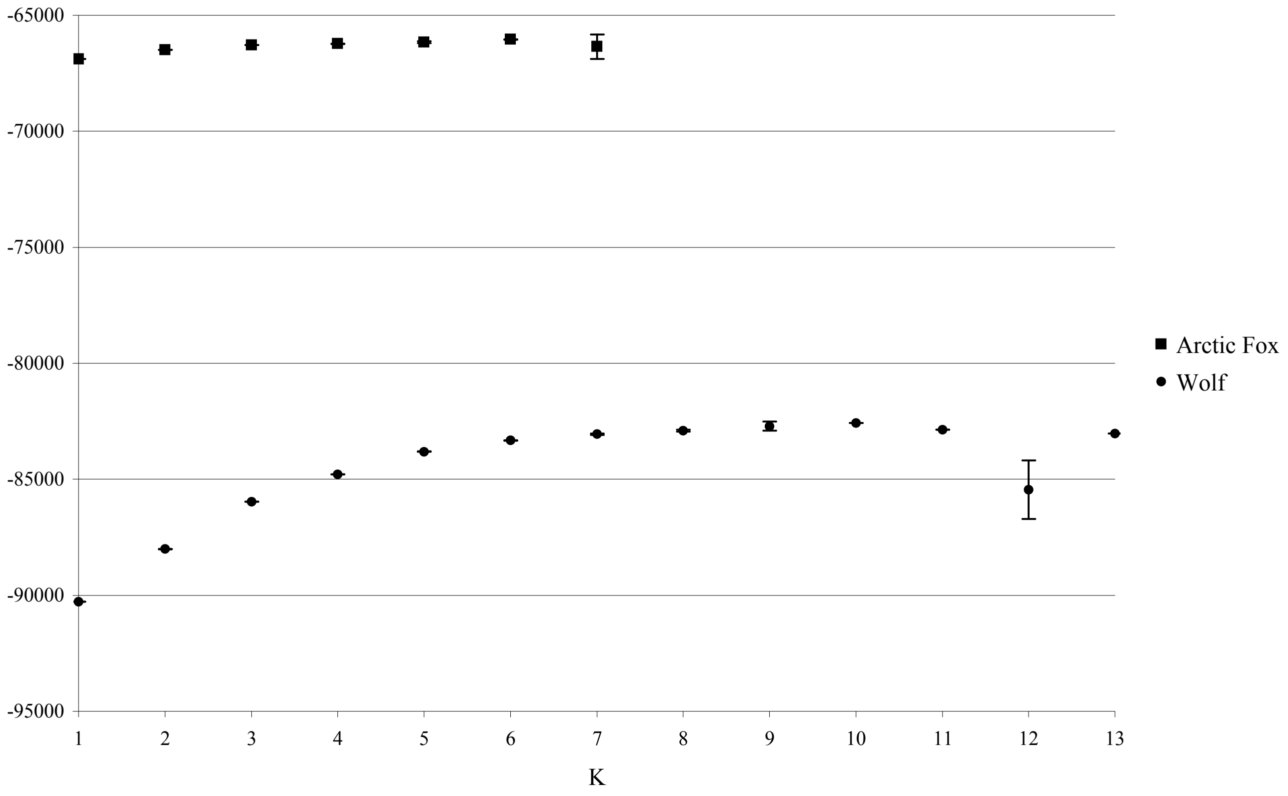

Figure 2a Average lnProb(D) as number of clusters is increased during STRUCTURE analysis of arctic foxes and grey wolves. Probability of wolf data began to peak around K=7. All values of K were similarly likely for arctic foxes.

Figure 2B

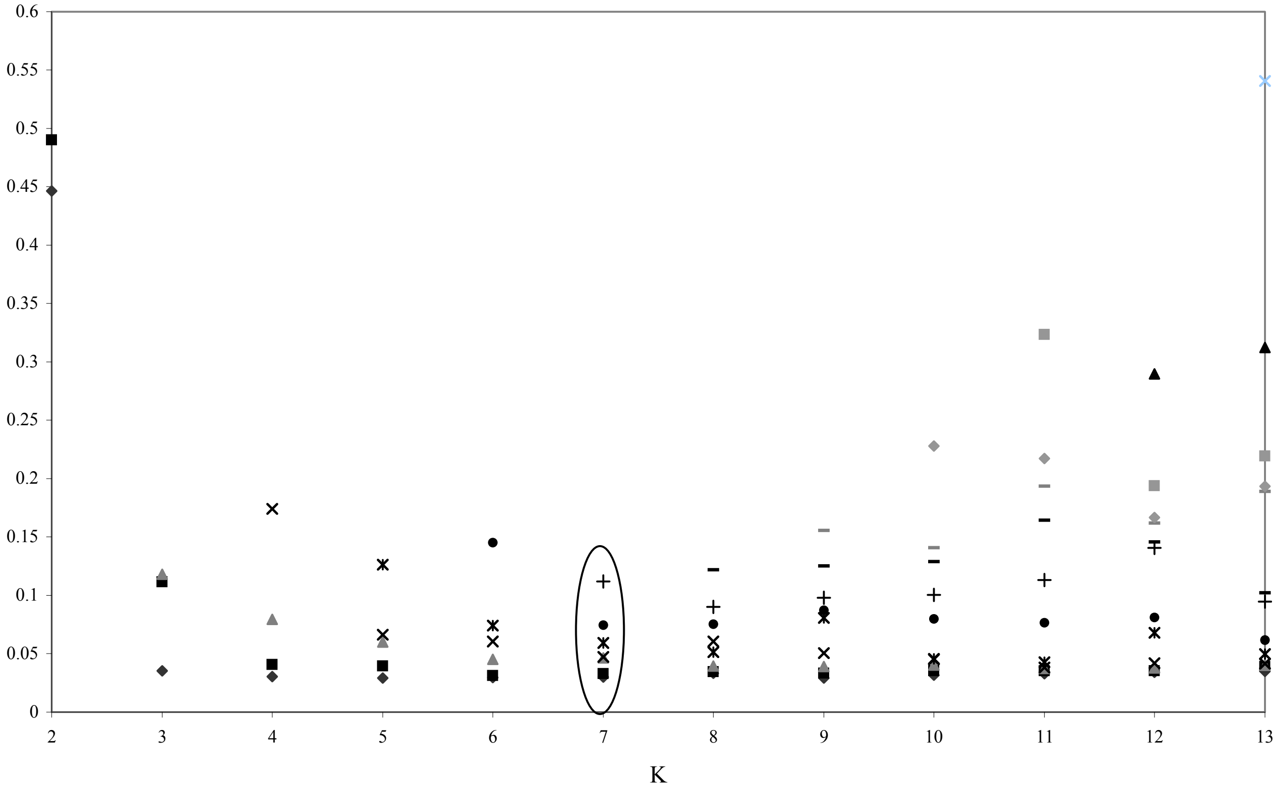

Figure 2b Average admixture of each wolf cluster as K is increased. Data from equivalent clusters at each value of K was pooled across three replicates. Lowest levels of admixture were obtained with K=7, suggesting highest group cohesion under this model.

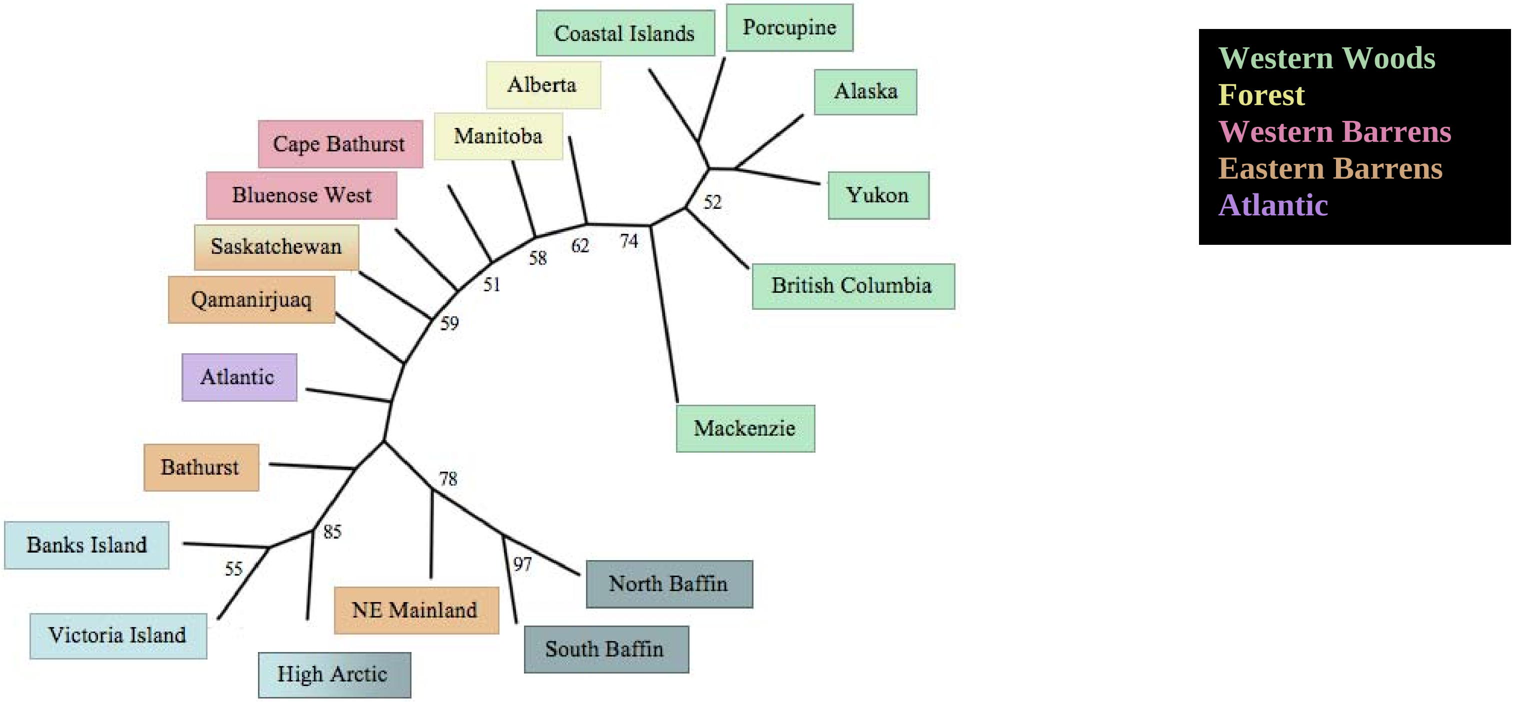

Figure 3 Neighbor-joining consensus tree of Nei's standard genetic distance between wolves in physical regions (Fig. 1a). Bootstrap support values are indicated for nodes appearing in more than 50% of the pseudoreplicates. Coloured boxes indicate membership of each region in its corresponding STRUCTURE cluster (K = 7); colour gradients represent regions that were split between two clusters. While STRUCTURE grouped the Coastal Islands with the Western Woods, and created a Western (light blue) and Eastern (dark blue) Island group, all island populations were considered distinct in our analyses (Fig. 1b).

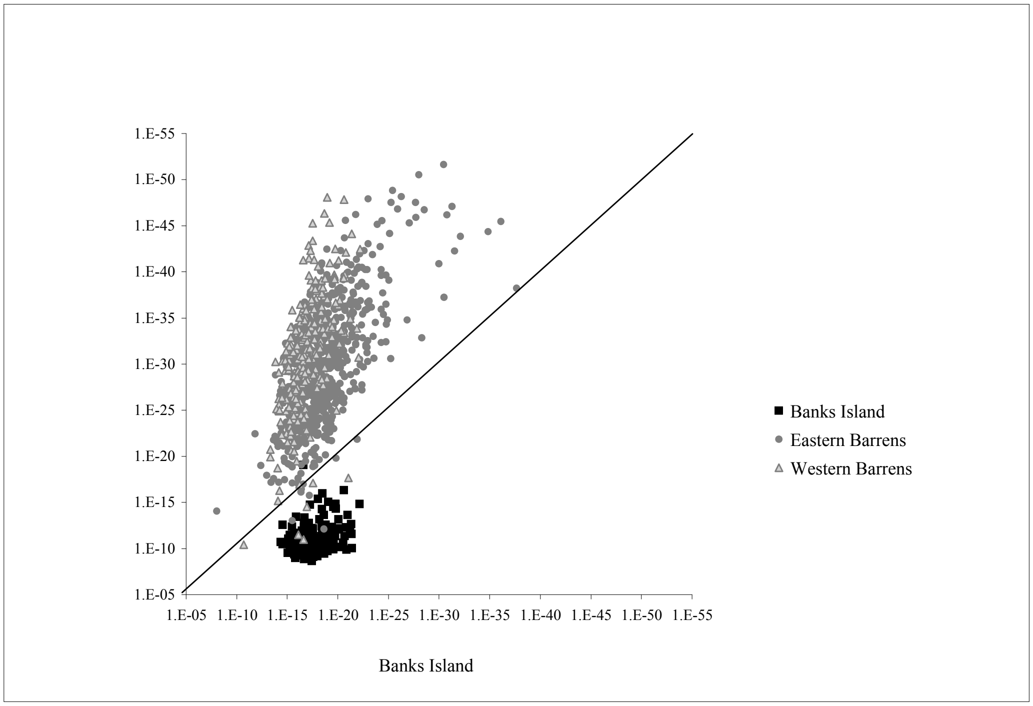

Figure 4a Classical assignment between Banks Island and mainland barren ground wolves. Symbols indicate the sampling cluster of each wolf. Individuals are plotted according to the probability that their genotype would arise in each cluster; the diagonal line represents genotypes equally likely in both (for example, hybrid offspring of mainland and island wolves). Here, the absence of overlap in assignment indices is suggestive of high genetic differentiation, despite low level migration between populations.

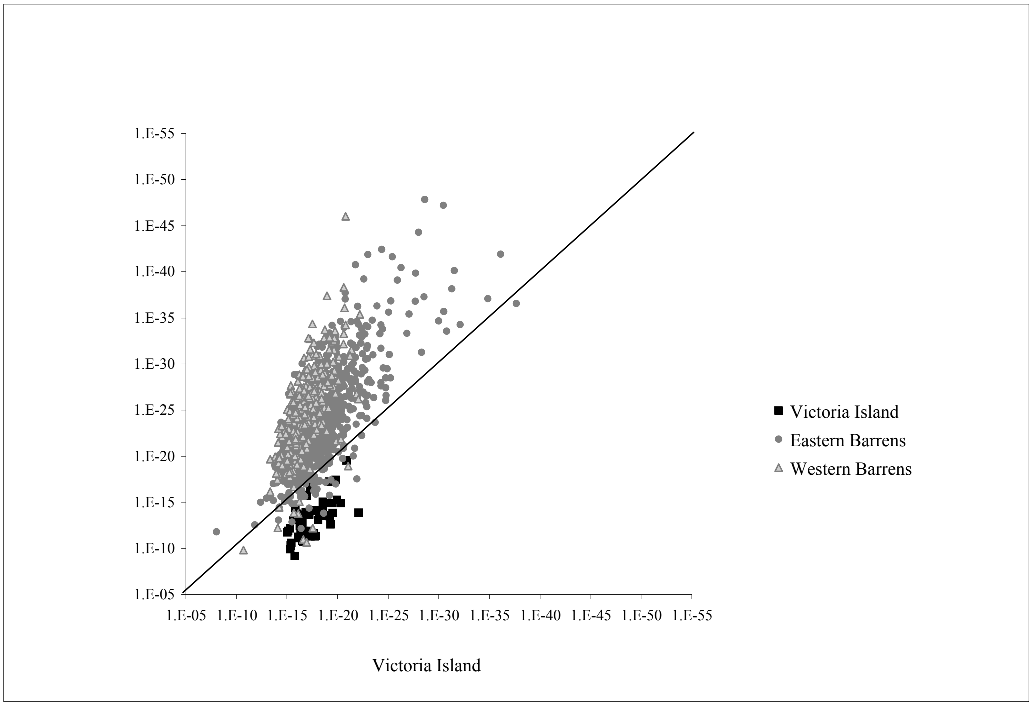

Figure 4b Assignment between Victoria Island and mainland barren ground wolves. Increased overlap in assignment indices relative to Banks Island (Fig. 4a) indicates higher gene flow between populations, and is supported by a higher number of cross-assigned individuals (potential migrants).

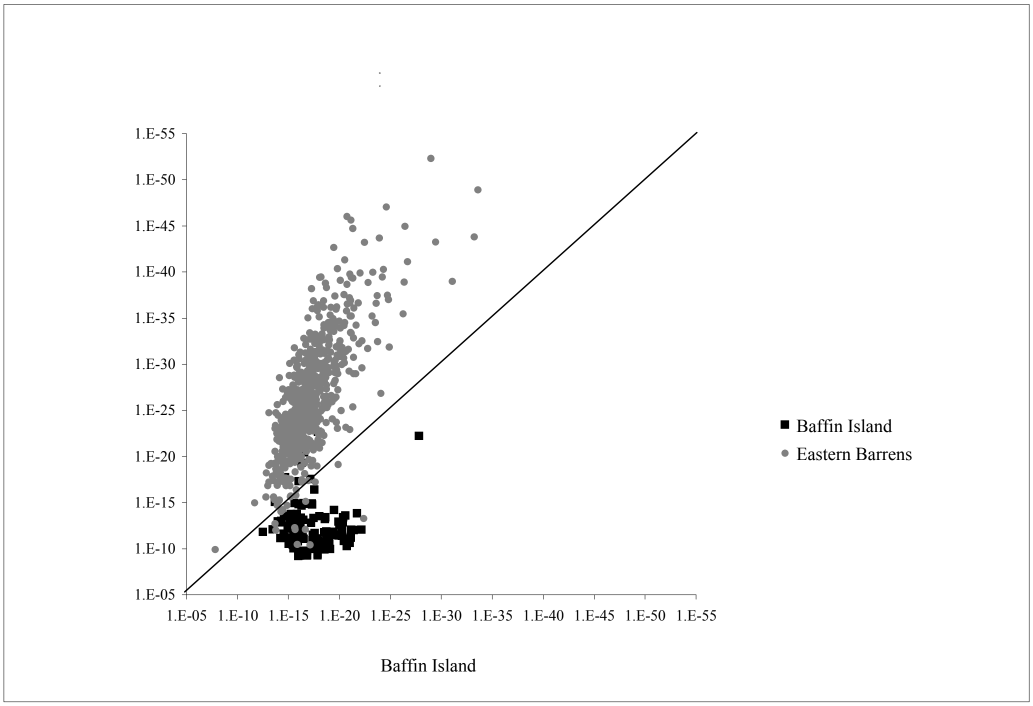

Figure 4c Assignment between Baffin Island and Eastern Barrens wolves. Differentiation and migration are similar to that observed for Victoria Island.

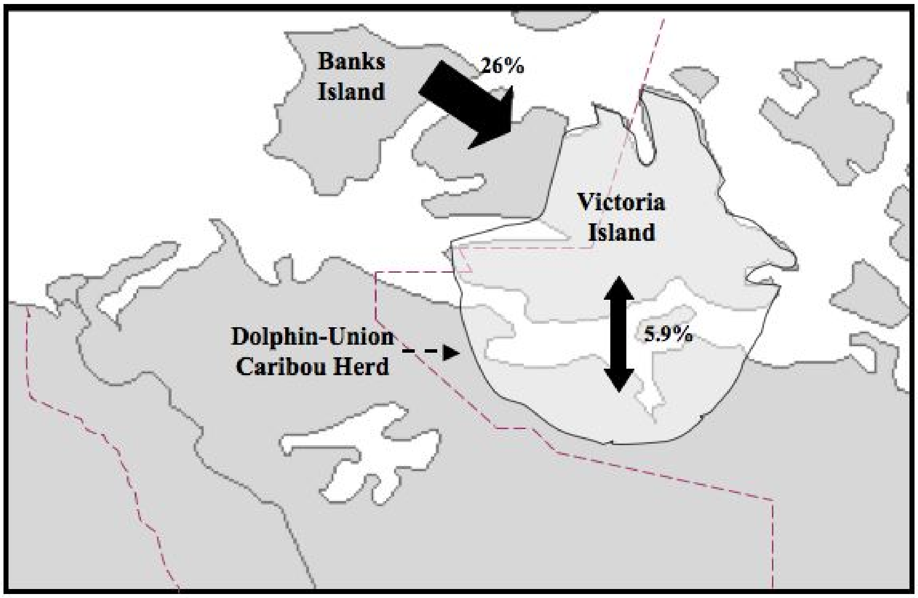

Figure 5 Total migration rate between Banks Island, Victoria Island, and mainland barren ground wolf populations as estimated in BAYESASS (comparable data from classical assignment tests is given in the text). The white region overlapping Victoria Island and the mainland is the home range of the Dolphin Union caribou herd, which migrates across the sea ice twice each year.