

Northwest passages: conservation genetics of Arctic Island wolves

Lindsey E. Carmichael · Julia Krizan ·
John A. Nagy · Mathieu Dumond · Deborah Johnson ·
Alasdair Veitch · Curtis Strobeck

Received: 23 April 2007 / Accepted: 9 August 2007 / Published online: 12 September 2007
© Springer Science+Business Media B.V. 2007

Abstract Wolves in the Canadian Arctic Archipelago face several challenges to persistence: a harsh habitat, an unstable prey base, and potentially significant anthropogenic influences. These external factors, if combined with genetic constraints common to island populations, could be particularly difficult to withstand. To determine the genetic status of Arctic Island wolves, we used 14 microsatellite loci to estimate population variation and the extent of inter-island and island-mainland gene flow. All island populations were significantly less variable than mainland wolves; although inbreeding is currently insignificant, the two least variable populations, Banks and the High Arctic (Ellesmere and Devon Islands), showed genetic signatures of recent population declines. Recovery after a bottleneck appears to result, in large part, via recolonization from other islands. These extinction-recolonization dynamics, and the degree of similarity among island wolves revealed by Bayesian clustering, suggest that Arctic Island wolves function as a

metapopulation. Persistence of the metapopulation may be supported by periodic migration from mainland populations, occurring primarily through two corridors: Baffin Island in the Eastern Arctic, and Victoria Island in the Western Arctic. This gene flow could be compromised or eliminated by loss—due to climatic warming or increased human activity—of sea ice in the Northwest Passage.

Keywords *Canis lupus* · Metapopulation · Gene flow · Bottleneck · Refugium

Introduction

The Canadian Arctic Islands may represent the most inimical habitat in the range of the gray wolf (*Canis lupus*). Average daily minimum temperature is below -20°C , and lows of less than -50°C have been documented (Environment Canada 2000). Climatic variation resulting in deep winter snow, or ice buildup following freezing rain, may have negative impacts on survival of caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*; Gunn et al. 1991; Larter and Nagy 2001a, b). Small prey species like Arctic hares (*Lepus arcticus*), Arctic foxes (*Alopex lagopus*), sea birds and microtine rodents (e.g. *Lemmus* sp.) are insufficient to meet the nutritional requirements of large carnivores in years of low ungulate density, so wolf populations decline with declining ungulate prey (Mech 2005). For example, wolves had continually inhabited the Fosheim Peninsula of Ellesmere Island for decades, were not observed during the 2001–2002 collapse of the local muskoxen population, and began to return to the area when their prey base recovered (Mech 2005).

In addition to climatic and energetic constraints, wolves on the Arctic Islands may face anthropogenic threats to

Electronic supplementary material The online version of this article (doi:10.1007/s10592-007-9413-0) contains supplementary material, which is available to authorized users.

L. E. Carmichael (✉) · C. Strobeck
Department of Biological Sciences, University of Alberta,
CW405 Biological Sciences Building, Edmonton, AB, Canada
e-mail: lec@ualberta.ca

J. Krizan
IMG-Golder Corporation, Inuvik, NT, Canada

J. A. Nagy · D. Johnson · A. Veitch
Department of Environment and Natural Resources, Government
of the Northwest Territories, Yellowknife, NT, Canada

M. Dumond
Department of Environment, Government of Nunavut,
Kugluktuk, NU, Canada

persistence. On Banks Island in the 1950s, wolf scavenging on trapped Arctic foxes prompted a poisoning program which severely reduced or extirpated this population (McEwen 1955; Usher 1965); wolves began to reappear in the late 1970s and 1980s, and have since increased to approximately 200 individuals (Gunn et al. 1991; Miller 1995; Miller and Reintjes 1995; Larter and Nagy 2000; Carmichael et al. 2001). Wolf control has been discontinued, and absence of infrastructure means contemporary island wolves do not suffer road or railway mortalities as those in southern populations do. However, *C. lupus* is currently considered a big game species throughout the Canadian Territories, and wolves are harvested for both commercial and subsistence use (Van Zyll de Jong and Carbyn 1999). On some islands, this harvest may be as high as 25% of the total population annually (Carmichael et al. 2001).

Considering these significant external impediments to continued lupine inhabitation of the Canadian Arctic Islands, genetic threats to persistence may be of particular concern. If island populations are demographically isolated, mating between close relatives may increase, and fitness may be lost through inbreeding depression (Frankham 2005). Since demographic isolation also results in genetic isolation, loss of genetic variation via accelerated drift may hamper the population's ability to adapt to a changing environment (Frankham 2005). From a conservation perspective, Arctic Island wolves may be of particular significance. *C. lupus* colonized the region as early as the Pleistocene (Kurtén and Anderson 1980), and contemporary island wolves are thought to have descended from a refugial population in Ellesmere Island and/or Pearyland (north Greenland) that expanded across the Arctic Archipelago after the last glacial maximum (Nowak 2003). Supporting this idea are the unusually large carnassial teeth characteristic of most island populations, which have prompted the subspecific designation *C. l. arctos*: only Baffin Island wolves are thought to belong to the mainland subspecies *C. l. nubilis* (Nowak 1995). Arctic Island wolf populations may therefore retain unique adaptations and genetic characteristics not found in mainland wolves, representing a disproportionate fraction of total wolf genetic variation (Leonard et al. 2005).

In 1999, *C. l. arctos* was considered for protected status by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), but was not listed due to insufficient data (Van Zyll de Jong and Carbyn 1999). An improved understanding of the nature and characteristics of wolves on the Arctic Islands may facilitate assignment of an appropriate conservation priority, permitting management decisions suited to wolf populations inhabiting the changing Arctic environment. In this paper, we explore island wolves' genetic health and potential for persistence via

analysis of nuclear microsatellites, estimating genetic variation and inbreeding within island wolf populations, and assessing levels of inter-island, and island-mainland, gene flow. We investigate whether recovery of island wolf populations has been entirely due to the impact of increased prey density on local survivors, or is prompted by over-ice recolonization from other wolf populations (Manning and MacPherson 1958; Usher 1965). Although microsatellites are not well suited to subspecies-level investigations (Paetkau et al. 1997), we also use these data to construct a preliminary molecular hypothesis regarding the evolutionary origin of *C. l. arctos*.

Materials and methods

Sample collection and laboratory analysis

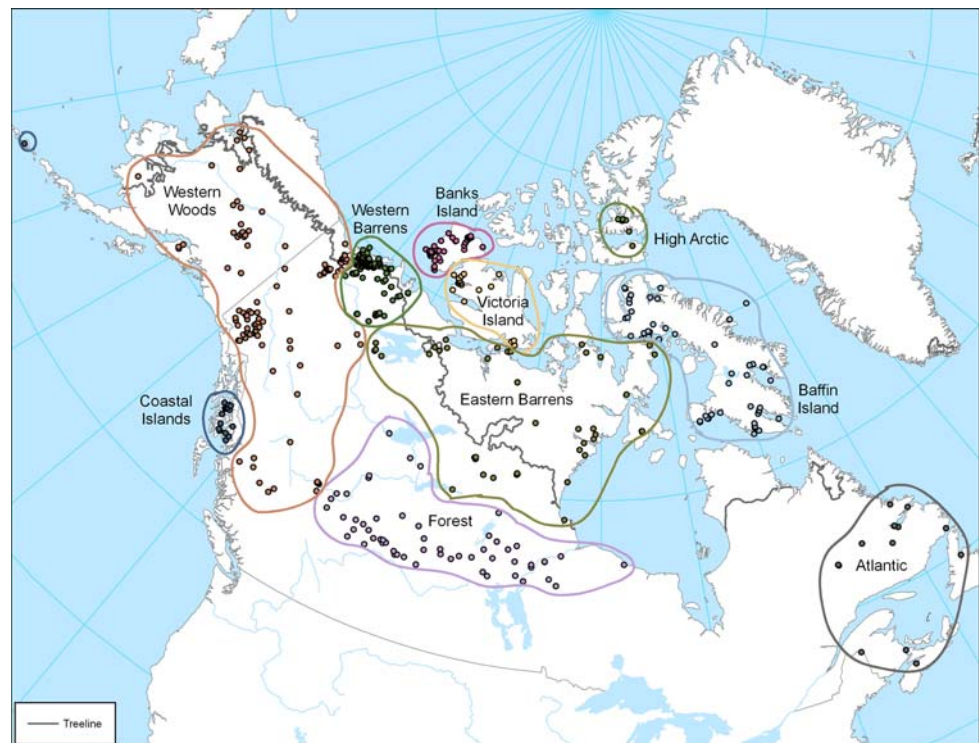
We analyzed contemporary samples of 1,924 wolves from across the North American Arctic (Fig. 1). Carmichael et al. included these individuals in their recent study (2007), which explored general dynamics structuring, primarily, mainland Arctic canid populations. Here, we devote our attention to conservation genetics of Canadian Arctic Island wolves, including those on: Banks Island ($n = 163$); Victoria Island ($n = 52$); the High Arctic (Ellesmere and Devon Island, $n = 11$); and Baffin Island ($n = 116$). Coastal Island wolves from southeastern Alaska were included for comparison to northern populations ($n = 35$). The remaining 1,546 samples were collected on the mainland.

We used DNeasy tissue kits (QIAGEN, Germany) to extract genomic DNA from all samples. Fourteen microsatellite loci were PCR-amplified using fluorescently-labeled primers from domestic dogs: CPH5 and CPH16 (Fredholm and Wintero 1995); CXX140, CXX173, CXX250, CXX251, and CXX377 (Ostrander et al. 1993); CXX618, CXX671, CXX733, CXX745, CXX758, CXX781, and CXX2079 (Mellersh et al. 1997). PCR and electrophoresis conditions are given in Carmichael et al. (2007).

Genetic delineation of wolf populations

Bayesian clustering of genotypes was conducted in STRUCTURE 2.1 (Pritchard et al. 2000) using 100,000 burn-in cycles followed by 1,000,000 iterations of the Markov Chain. We chose the admixture model due to prior genetic and ecological evidence for gene flow among wolf populations in our study area (Carmichael et al. 2001; Walton et al. 2001; Carmichael et al. 2007); clustering was conducted without reference to spatial data. To estimate

Fig. 1 Genetic clusters of grey wolf samples based on STRUCTURE and GENELAND analysis, with treeline shown for reference. Adapted from Carmichael et al. (2007)



appropriate priors, the number of clusters (K) was allowed to vary between 1 and 6, assuming a unique level of admixture (α) for each cluster, and inferring the shape of the allele frequency distribution of each locus (λ). Using parameters suggested by these initial tests, we performed three replicates each of $K = 1$ –13, setting λ to 0.4 and ALPHAPROPSD to 0.1. Maximization of $\ln\text{Prob}(D)$ (Pritchard et al. 2000), and minimization of admixture in each cluster, indicated the most appropriate value of K under this model.

GENELAND is a Bayesian clustering program that incorporates spatial coordinates of individuals via Voronoi tessellation; GENELAND therefore assigns greater probability to genetic clusters that are continuous within the spatial landscape (Guillot et al. 2005). For comparison to aspatial inference performed in STRUCTURE, we conducted GENELAND analysis using the following model: delta.coord 0.15; 1,000,000 iterations; burn-in 100,000 iterations; thinning 1000; and the Dirichlet allele frequency model (Guillot et al. 2005). Outputs of the two methods were combined to create wolf population clusters for further analysis (Carmichael et al. 2007).

Variation within wolf clusters

Expected heterozygosity H_E (Nei and Roychoudhury 1974) of each genetic cluster was estimated in the Microsatellite Excel Toolkit (Park 2001). To identify significant

differences in H_E , we performed two-tailed Wilcoxon's signed-ranks tests (Sokal and Rohlf 1995) between pairs of populations within each species, using critical values of $P = 0.05$ for each test and 13 degrees of freedom (number of loci minus 1). We used the rarefaction method implemented in CONTRIB 1.01 (Petit et al. 1998) to calculate allelic richness after correction for variation in sample size (Table 1).

BOTTLENECK 1.2.02 was used to test for recent bottlenecks in all island populations (Piry et al. 1999; Spencer et al. 2000). Loci CPH16 and CXX781 possessed single-base-pair alleles suggesting complex mutational dynamics (data not shown); we therefore used the Infinite Allele Model (IAM, Kimura and Crow 1964) and the Two-Phase Mutation Model (TPM, di Rienzo et al. 1994) only. For the TPM, the following combinations of variance and probability were employed: 4 and 90%; 12 and 70%; 12 and 90%; and 12 and 95%. Significance was assessed using one-tailed Wilcoxon's tests 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, using a microsatellite mutation rate of 5×10^{-4} , a 90% chance of single-step mutations, an average multi-step mutation size of 3.5 repeats, and 10,000 permutations to assess significance (Garza and Williamson 2001). CPH16 and CXX781 were excluded from these tests. Since the change in M can be strongly dependent on the pre-bottleneck effective population size (N_e) assumed (Garza and

Table 1 Genetic variation in Arctic Island wolf populations

Island	N^a	H_E^b	H_E SD	A^{Rc}	F_{IS}^d
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
Average		0.60		3.88	
Mainland ^e		0.74		5.92	

^a Sample size

^b Expected heterozygosity, with standard deviation indicated by SD

^c Allelic richness, with rarefaction size set to 22 alleles

^d Estimated in BAYESASS

^e Average of all mainland populations

This table contains data from the present study and adapted from Carmichael et al. (2007)

Williamson 2001), we tested a range of values for this parameter. Our High Arctic population is located in the Queen Elizabeth Islands chain, for which a maximum theoretical carrying capacity of approximately 205 individuals (Miller 1995) has been estimated; we used N_e 's of 205, 100, 50, and 20 to account for dispersion of wolves across the island group, and for complexity in wolf social structure (i.e., variable pack size and number of breeders within each pack, Mech and Boitani 2003). On Banks Island, a total of 54 wolves were observed in 1955 prior to initiation of wolf control (McEwen 1955); 43 wolves were poisoned before the program was discontinued in 1959 due to apparent absence of wolves on the island (Usher 1965). We therefore used pre-bottleneck N_e 's of 54 and 43. Assuming that each of the 8 groups of 2 or more wolves observed prior to poisoning in 1955 (McEwen 1955) represented a different pack, each with 2 breeding adults, we repeated the test setting $N_e = 16$. Finally, we assumed a pre-bottleneck N_e of 200, the current estimated total population of wolves on Banks Island (Carmichael et al. 2001).

Migration and gene flow among populations

Paetkau et al.'s classical assignment test (1995) was conducted among clusters with allele frequencies adjusted to avoid zeros (Titterton et al. 1981), and 10,000 randomizations—creating new individuals from each population's allele frequencies—to discriminate between cross-assignments signaling true migration and those resulting from correlated allele frequencies (Carmichael et al. 2001). 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 and Rannala 2003). Each run consisted of 3,000,000 iterations, with a burn-in of 999,999 cycles and a thinning interval of 2000. After initial runs to determine appropriate update values for allele frequencies (0.05), rates of migration (0.025), and inbreeding in each population (0.08), two replicates were performed with unique random number seeds and convergence of the outcomes graphically assessed. Results of all four assignment methods (STRUCTURE, GENELAND, classical, and BAYESASS) were combined to identify island-mainland migrants (Supplementary Table S1).

Corridors for island-mainland migration

Mainland wolf clusters derived from STRUCTURE and GENELAND encompassed broad geographical areas (Fig. 1). Therefore, genetic similarities among islands and large mainland populations could not be used to identify specific, local regions where island-mainland migration most often occurs. To find such gene flow corridors, we divided our wolf samples into smaller geographic regions based on the following hierarchical criteria: (1) gaps in the sampling distribution, (2) ranges of associated barren ground caribou herds, and (3) political boundaries of Canadian provinces (British Columbia through Manitoba; Carmichael et al. 2007). The first criterion reflects physical discontinuities in sampling, the second ecology of barren ground wolves (Carmichael et al. 2001; Walton et al. 2001). The use of political boundaries in southern forested regions was intended to produce samples of comparable size and area throughout our study distribution, and does not imply any assumption of impact on the behavior or genetics of wolves in this region. Further, this choice is of little import in the

current analysis, as island wolves do not seem connected via migration with these boreal forest wolves (Carmichael et al. 2001; Carmichael et al. 2007; Supplementary Table S1).

We used PHYLIP 3.65 (Felsenstein 1995) to generate 1000 bootstrap pseudoreplicates of our geographic regions; Nei's standard genetic distance (D_S , Nei 1972) was calculated among populations for each replicate, and a neighbor-joining majority-rule consensus tree constructed (Felsenstein 1985; Saitou and Nei 1987). Island-mainland migration was assumed to occur most frequently between geographic regions separated by the smallest genetic distances. This analysis was used to confirm interpretations based on assignment methods.

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.

Results

Genetic delineation of wolf populations

On the mainland, both STRUCTURE and GENELAND recovered an Atlantic group, a western and eastern boreal forest group (Western Woods and Forest) and western and eastern barren ground groups (Western Barrens and Eastern Barrens). Under the optimal model $K = 7$ (Carmichael et al. 2007), STRUCTURE pooled the Coastal Islands with the Western Woods and split the Arctic Islands into a Western cluster (Banks and Victoria Island) and an Eastern cluster (North and South Baffin Island). GENELAND, in contrast, grouped all Arctic Islands into one population and segregated the Coastal Islands, likely because of the high spatial concentration of these samples (Guillot et al. 2005). While STRUCTURE recognized the Western Islands at $K = 3$, and the Eastern Islands at $K = 4$, the Coastal Islands were not segregated until $K = 9$ (data not shown).

Outcomes of both analyses suggest a certain genetic homogeneity among Canadian Arctic Island wolves. Similarity does not necessarily imply panmixia, however, and treating these samples as one or two large populations would prohibit the detailed analysis of variation and gene flow patterns, specific to individual islands, that is the purpose of this study. Therefore, the Coastal Islands, Banks Island, Victoria Island, and Baffin Island (North plus South Baffin) were considered distinct populations. Samples from the High Arctic Islands (Ellesmere and Devon Island) were pooled due to low sample size and analyzed as a discrete population because of their physical isolation from the remaining groups. The 10 wolf clusters used as the basis of further analysis are shown in Fig. 1.

Variation, population bottlenecks, and inbreeding

On average, island wolves had 14% less H_E than mainland wolves (Table 1); all island populations were significantly less variable than those on the mainland (Wilcoxon's signed-ranks tests, $P = 0.05$). Among islands, Victoria Island was most variable, and significantly more diverse than the population with lowest variation, the High Arctic. In contrast to the relatively consistent levels of H_E among islands (Table 1), allelic richness (A') 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 1). These estimates were corrected for sample size, and thus suggest a genuine loss of allelic diversity in the latter populations.

Since Banks Island and the High Arctic are known to have suffered demographic bottlenecks in the last 50 years (Usher 1965; Mech 2005), we tested for additional genetic consequences of population declines. When we used BOTTLENECK and the IMM, all 10 populations (including historically abundant mainland wolves) showed significant ($P < 0.05$) or nearly significant ($P < 0.1$) evidence of bottlenecks, suggesting this mutational model may be inappropriate for our loci. Under all parameter sets used for the TPM, mainland populations showed no bottlenecks, while Banks Island showed consistent significant evidence of decline (e.g., $P = 0.01$, TPM with variance = 12% and probability = 70%), and the High Arctic population was always marginally significant (e.g., $P = 0.08$, TPM 12% and 70%). We calculated M ratios to confirm these results assuming a range of pre-bottleneck N_e . 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 ($P \leq 0.01$).

As Table 1 indicates, three island populations possessed large, positive F_{IS} : the High Arctic (0.63); Victoria Island (0.43); and the Coastal Islands (0.18). No indication of inbreeding was found for Banks Island (Table 1).

Differentiation and migration among island and mainland wolves

In classical assignment tests (Paetkau et al. 1995), self-assignment rates for mainland wolf clusters averaged 75% (range 59–96%); the average for island wolves was 90%, ranging from 69% in Victoria Island to 100% in the High Arctic. 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. 2A,

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. 2C).

We performed two independent Bayesian estimations of migration rates among our wolf clusters; since both runs reached stationarity and appeared well converged (data not shown), we present results from the replicate with the highest likelihood (Table 2). Total migration between Baffin Island and all mainland clusters 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 (Table S1).

BAYESASS also indicated highly asymmetric migration between the Western Islands: 26% of Victoria Island samples were identified as migrants from Banks Island, with no movement inferred in the opposite direction (Table 2). If all cross-assigned wolves in classical tests are assumed to represent migrants (as suggested by significance of these counts, Carmichael et al. 2007), 23% of individuals on Victoria Island originated in Banks Island, while 6% of the Banks Island samples had migrated from Victoria. The conflict between methods arises from BAYESASS's lower bound of 0.67 on self-migration rates, which could affect estimates involving the Victoria Island sample, where non-migration is near this limit (G. A. Wilson, pers. comm.; Wilson and Rannala 2003). Regardless of the exact rate, we can conclude that migration between the Western Islands occurs primarily in an eastern orientation, from Banks Island into Victoria Island.

Corridors for island-mainland migration

Largest D_S was found between the Coastal Islands and all other populations (Table 3), suggesting lowest levels of gene flow. Among the Arctic Islands, High Arctic was most distinct, perhaps reflecting the population's physical separation or its small sample size. D_S between islands, and between islands and the mainland, was greater than between any pair of mainland clusters with three

exceptions: Victoria Island and Eastern Barrens (0.16); Baffin Island and Eastern Barrens (0.16); and Banks and Victoria Island (0.09, Carmichael et al. 2007).

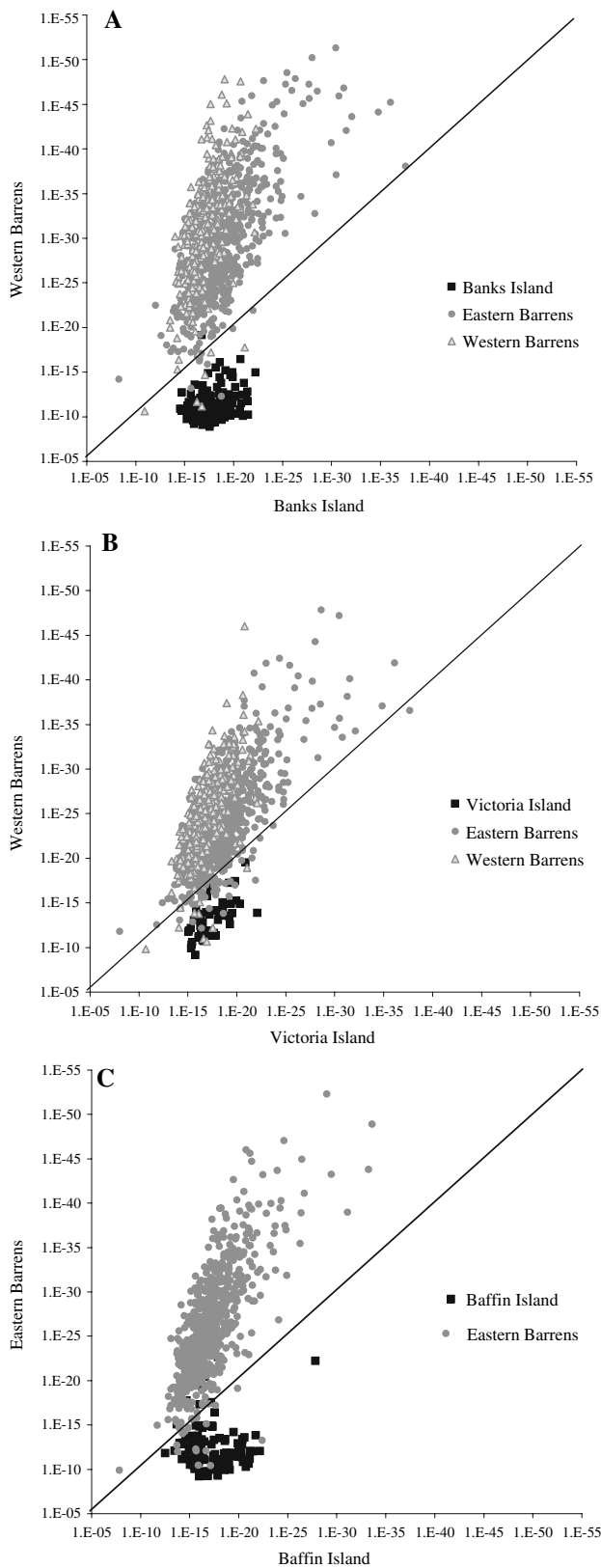
To identify mainland wolves most similar to the island populations at a finer scale, and thus to identify specific locations where island-mainland gene flow might occur, we calculated D_S among smaller geographic regions (Fig. 3A). Raw distances are shown in Table 3. In the majority-rule consensus tree (Fig. 3B), 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; these mainland groups are those separated by the smallest distances over sea ice (Fig. 3A). 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 (0.40 vs. 0.08 respectively, Table 3).

Discussion

Glacial refugia in the Canadian Arctic archipelago

Morphological data suggests Baffin Island was colonized—along with eastern mainland tundra regions—by wolves from southern glacial refugia, while Arctic Island populations are thought descended from those previously isolated in Ellesmere Island or neighboring Pearyland (Nowak 1995). Distinct subspecies, *C. l. nubilis* (mainland and Baffin) and *C. l. arctos* (northern Arctic Island) have thus been proposed. However, mtDNA sequence analyses showed low correlation between haplotype distribution and geography (a result that is generally unresponsive of subspecies in wolves; Vilà et al. 1999), and suggested most or all mainland North American wolf populations expanded from refugia in the southern United States (Leonard et al. 2005).

Previous genetic studies did not include Arctic Island wolves, but the existence of a refugium in the Canadian Arctic Archipelago is further unsupported by results presented here. If island wolves represent an ancient Arctic lineage, they should possess a relatively high proportion of unique alleles, despite recent bottlenecks. Banks and Victoria Island shared one allele found in no other population (total frequency 1%, data not shown), but private alleles were not observed within any island sample. Major Histocompatibility Complex genes 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. 2007). Our own preliminary mtDNA



◀ **Fig. 2** Results of the classical assignment test for wolf genetic clusters. 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). **(A)** Assignment between Banks Island and mainland barren ground wolves. The absence of overlap in assignment indices is suggestive of high genetic differentiation, despite low-level migration between populations. **(B)** Assignment between Victoria Island and barren ground wolves. Increased overlap in assignment indices relative to Banks Island indicates higher gene flow between populations, and is supported by a higher number of cross-assigned individuals (potential migrants). **(C)** Assignment between Baffin Island and Eastern Barrens wolves. Differentiation and migration are similar to that observed for Victoria Island

founding effects during initial colonization of previously glaciated areas (Hewitt 1996). Therefore, all molecular data currently available suggests Arctic Island wolves, like mainland tundra populations, arose via post-glacial colonization by wolves from southern (or perhaps Beringian) refugia.

This hypothesis does not eliminate the possibility that wolves which persisted in Arctic Island refugia have since been entirely replaced by expanding southern populations. The latter scenario would require existence, during the Pleistocene, of unglaciated habitat appropriate for mammalian species. Muskoxen populations are genetically depauperate, a finding more consistent with a severe bottleneck than survival in a glacial refugium (MacPhee et al. 2005). Furthermore, the oldest muskoxen remains found in northern Greenland date to only 2000 BP (Bennike and Andreasen 2005). Caribou antler from northeast Ellesmere Island was ~8500 years old, but its three potential origins—in a local refugium, by post-glacial colonization, or through sea-ice rafting—could not be distinguished (Stewart and England 1986). Furthermore, mtDNA suggests populations of small-bodied high Arctic caribou found throughout the Arctic are polyphyletic, supporting parallel evolution during independent post-glacial colonizations rather than expansion from a single high Arctic glacial refugium (Gravlund et al. 1998).

mtDNA phylogenies for collared lemmings (*Dicrostonyx groenlandicus*) and Arctic hares (*Lepus* sp.) are consistent with refugia in the more southerly Western Islands, along the former boundaries of the Innuitian and Laurentide Ice Sheets (Fedorov and Stenseth 2002; Waltari et al. 2004). However, the Innuitian Ice Sheet is now believed to have covered the remainder of the Canadian Arctic Archipelago, in addition to Pearyland in North Greenland (England 1999; Lamoureaux and England 2000; England et al. 2006). Some islands or parts thereof may have been unglaciated (Wolfe and King 1999), but absence of ice does not automatically imply habitat suitable for large mammals, especially carnivores, despite possible persistence of small mammals in these regions.

sequencing revealed lower haplotype diversity in, and no haplotypes unique to the Arctic Islands (unpublished data). These patterns of declining variation are typical of repeated

Table 2 Bayesian estimates of migration rates among wolf genetic clusters. Migrants originate in the clusters shown in the left column

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

“Self-migration” rates (analogous to self-assignment rates) are given in italics, and rates greater than 2% shown in bold. Standard deviation of migration rates averaged 0.005 and did not exceed 0.0382 (HA–HA)

Given the genetic and geological data currently available, we suggest that refugia for large mammals did not exist in the Canadian Arctic Archipelago during the last glacial maximum. Further, perhaps interdisciplinary research will be necessary to test this hypothesis. In addition, we believe firm conclusions regarding the taxonomic validity of *C. l. arctos* should be deferred until further mitochondrial or Y chromosome sequencing has been conducted.

Genetics of contemporary island wolves

Coastal Islands

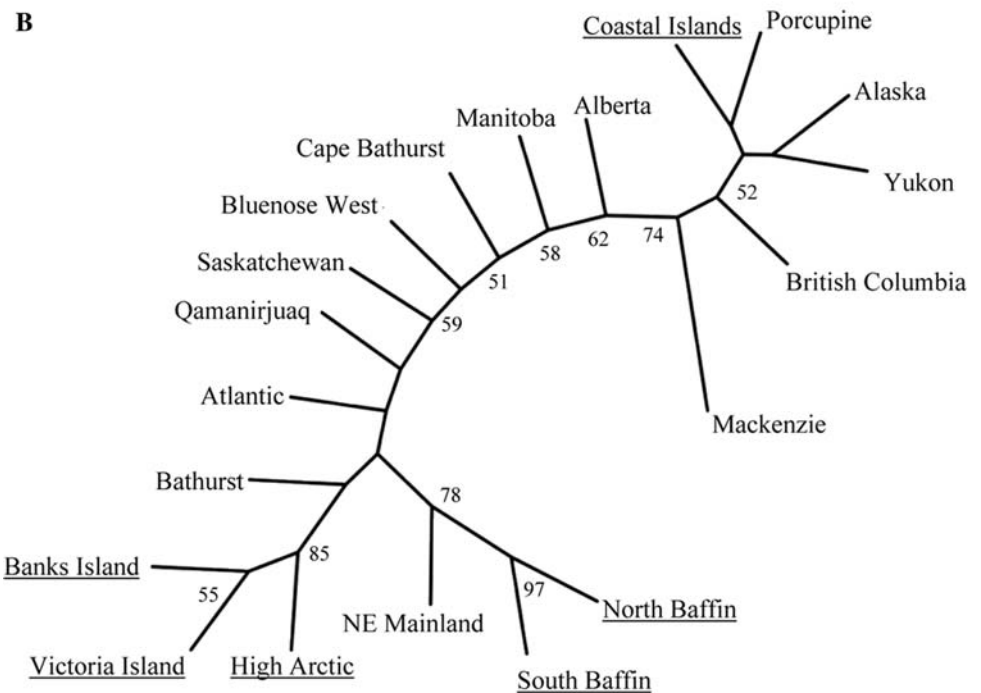
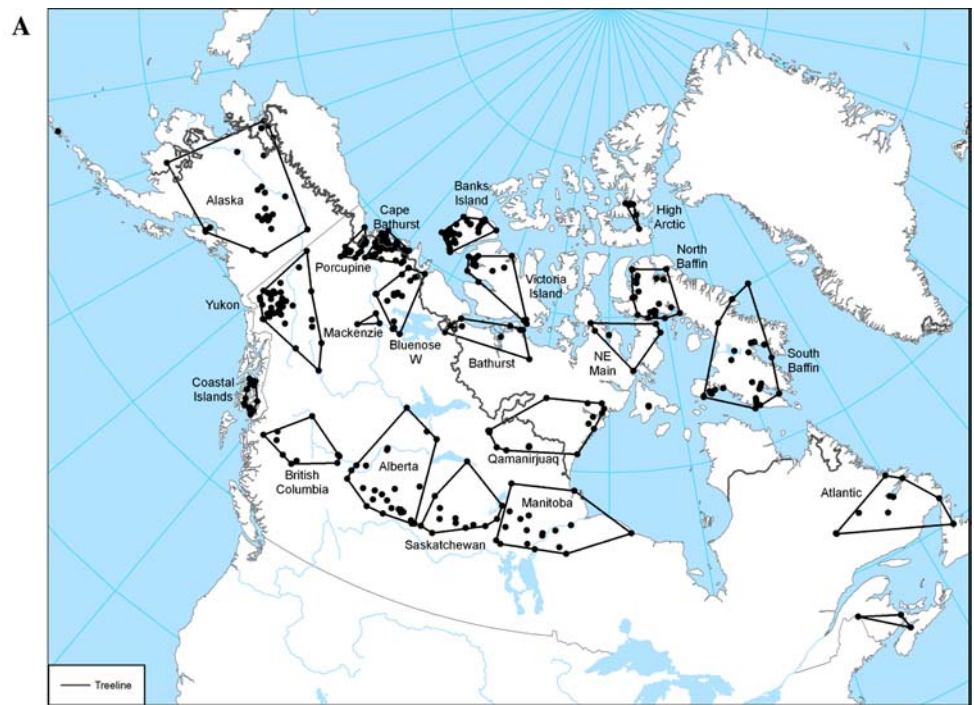
The genetics of Coastal Island wolves have been examined previously (Weckworth et al. 2005); we included them primarily for comparison to Arctic populations. In our study, Coastal Islands had the only positive F_{IS} potentially arising from inbreeding (see

Table 3 Nei's standard genetic distance (D_S) between wolf geographic regions

	AK	YK	PO	MA	BC	AB	SK	MB	CB	BW	BA	QA	NE	AT	CI	BI	VI	HA	NB	SB
Alaska (AK)	0																			
Yukon (YK)	0.07	0																		
Porcupine (PO)	0.07	0.08	0																	
Mackenzie (MA)	0.10	0.08	0.10	0																
British Columbia (BC)	0.12	0.09	0.12	0.08	0															
Alberta (AB)	0.16	0.14	0.14	0.11	0.08	0														
Saskatchewan (SK)	0.18	0.19	0.16	0.14	0.15	0.09	0													
Manitoba (MB)	0.21	0.18	0.18	0.16	0.14	0.06	0.05	0												
Cape Bathurst (CB)	0.12	0.13	0.11	0.10	0.13	0.09	0.04	0.08	0											
Bluenose W (BW)	0.19	0.20	0.18	0.15	0.19	0.11	0.04	0.09	0.03	0										
Bathurst (BA)	0.28	0.30	0.26	0.24	0.29	0.22	0.06	0.14	0.10	0.08	0									
Qamanirjuaq (QA)	0.20	0.22	0.18	0.15	0.18	0.12	0.01	0.07	0.05	0.04	0.04	0								
NE Mainland (NE)	0.26	0.30	0.26	0.23	0.30	0.26	0.09	0.18	0.10	0.08	0.08	0.06	0							
Atlantic (AT)	0.44	0.41	0.40	0.34	0.40	0.36	0.27	0.29	0.28	0.32	0.27	0.24	0.32	0						
Coastal Islands (CI)	0.40	0.40	0.38	0.50	0.39	0.44	0.47	0.46	0.45	0.48	0.63	0.50	0.59	0.70	0					
Banks Island (BI)	0.35	0.34	0.34	0.27	0.33	0.36	0.23	0.34	0.24	0.27	0.22	0.23	0.30	0.43	0.88	0				
Victoria Island (VI)	0.37	0.37	0.33	0.28	0.37	0.30	0.17	0.29	0.19	0.19	0.16	0.16	0.24	0.47	0.87	0.09	0			
High Arctic (HA)	0.59	0.52	0.49	0.45	0.58	0.55	0.39	0.48	0.36	0.35	0.30	0.34	0.35	0.52	1.22	0.26	0.25	0		
North Baffin (NB)	0.30	0.35	0.28	0.23	0.32	0.27	0.15	0.22	0.16	0.14	0.13	0.11	0.08	0.40	0.67	0.33	0.26	0.27	0	
South Baffin (SB)	0.44	0.52	0.41	0.36	0.48	0.44	0.28	0.36	0.31	0.26	0.24	0.23	0.15	0.08	0.79	0.51	0.42	0.42	0.31	0

Largest and smallest genetic distances are shown in bold

Fig. 3 (A) Wolf samples divided into geographic regions for finer-scale analysis. (B) Neighbor-joining consensus tree of Nei's standard genetic distance between wolves in geographic regions. Bootstrap support values are indicated for nodes appearing in more than 50% of the pseudoreplicates



below), consistent with isolation of these wolves from mainland populations via intervening mountain ranges (Weckworth et al. 2005). These mountains also likely contributed to D_S values for this population greater than any others we observed. However, STRUCTURE partitioned the Arctic Island populations beginning at $K = 3$, while Coastal samples were not segregated until $K = 9$. Apparent conflict between assignment and genetic

distances likely reflects respective sensitivities of each analysis to events at different time scales (Castric and Bernatchez 2004). One interpretation of our results under this assumption is that Coastal Island wolves have been longer isolated, while recent drift in Arctic Island populations—resulting from isolation, demographic bottlenecks, or a combination thereof—has been rapid and severe.

Banks Island

Poisoning of the Banks Island wolf population began in the mid 1950s and concluded when island residents no longer observed wolves. While relatively high H_E suggests rapid post-bottleneck expansion, we cannot distinguish recovery by overlooked resident wolves (Usher 1965) from founder effects during establishment of a novel population. However, significant changes in skull morphology between Banks Island wolves collected in 1914–1916 and in 1953–1955 (prior to wolf control) suggest extinction and recolonization occurred early this century (Manning and Macpherson 1958), and might therefore have produced the current population as well. D_S between Banks and Victoria Island is less than half the next smallest inter-island distance (Table 3), and so of populations surveyed here, Victoria Island is the most likely origin of post-poisoning Banks Island wolves.

The Banks Island muskoxen population has increased to 45,000 over the last two decades (Gunn et al. 1991; Larter and Nagy 2001a). Despite concurrent declines in Peary caribou (*R. t. pearyi*) density (Larter and Nagy 2000), there is no doubt wolves have access to ample prey. Therefore, resource competition is not a likely explanation for their high rate of migration from Banks to Victoria Island (Table 2). However, the Banks Island wolf population is larger now than at any time in the past 50 years, and wolves may be leaving the island in search of unoccupied territories (Mech and Boitani 2003). We can speculate that the current direction of migration reflects a reversal of dynamics which led to colonization of Banks Island by Victoria Island wolves earlier this century.

Victoria Island

Wolf tracks have been observed on the sea ice separating Banks and Victoria Island, and D_S between them is consistent with separation by linear distance only, suggesting no barrier to gene flow exists (Carmichael et al. 2001). Relative to Banks, Victoria Island wolves are less genetically differentiated from mainland populations (Table 3, Fig. 3), and the rate of migration between Victoria and the mainland is substantially higher (Table 2). Therefore, Victoria Island may be the primary contact point between the Western Islands and the mainland, with gene flow occurring between Banks Island and Victoria, and between Victoria Island and the mainland. Banks Island Inuit historically considered sea ice conditions in the Amundsen Gulf unstable and treacherous; as we suggest for wolves, the Inuit traveled from Banks Island to Victoria Island rather than directly to the mainland, despite the increased distance involved (Usher 1965).

While ice conditions may influence wolf movement, annual over-ice migrations of the Dolphin-Union caribou herd (Fig. 4) may be the primary instigator of island-mainland wolf gene flow. Dolphin-Union caribou calve on Victoria Island, but winter on the mainland, and wolves may be migrating incidentally while in pursuit of their prey (Carmichael et al. 2001). The timing of caribou movements relative to denning season may also explain why wolves are more likely to migrate to the island, than to the mainland: mainland wolves following caribou would reach the island in spring, and might thus need to establish local territories for whelping. Regardless of the underlying mechanisms, it seems clear that mainland wolves arrive in the Western Islands via Victoria Island: in addition to identifiable migrants (Fig. 2B) and a high, likely Wahlund-induced F_{IS} (Table 1), Victoria Island contains the highest genetic diversity of any island surveyed here (Table 1).

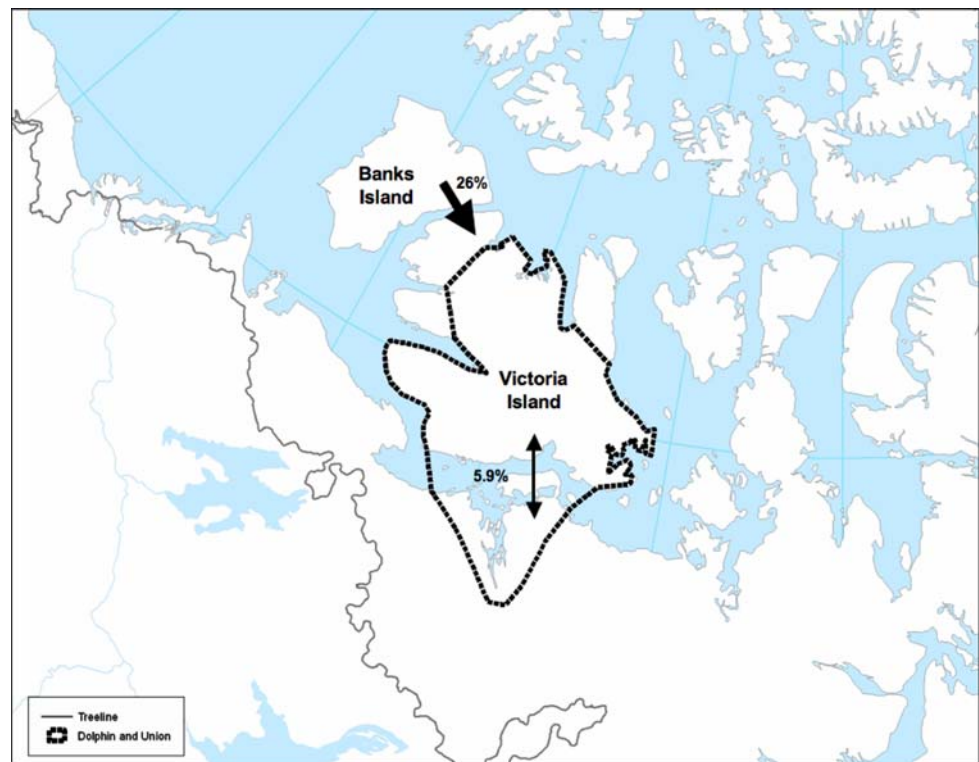
High Arctic Islands

STRUCTURE identified our High Arctic 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 (Table S1). The only two wolves considered resident, GF44 and GF45, were harvested in November of 1999, prior to the muskoxen population decline, while the putative hybrids were sampled in 2002, after the first migrants had been sampled. Therefore, our sample appears to contain pre-bottleneck residents and post-bottleneck colonists of the High Arctic Islands, suggesting observed high F_{IS} primarily reflects a Wahlund effect (although inbreeding could also have occurred in this small wolf population). Complex population composition also 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 resulting from a Wahlund effect would have reduced the power of this test.

Baffin Island

Morphological subspecies investigations suggest Baffin Island wolves to be more closely related to the mainland than to other Arctic island populations (Nowak 1995). The magnitude of D_S between Baffin and other populations supports this idea (Table 3), but Bayesian clustering analysis, and levels of differentiation within classical assignment tests (data not shown), suggest a greater current

Fig. 4 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 outlined 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



affinity to island wolves over mainland ones. As with Coastal Island wolves, these results suggest an earlier post-glacial colonization: Baffin may have been the first Arctic Island reached by southern refugial wolves. Since that time, ice conditions and divergent behaviors with opposing influences on the genetics of island and mainland wolves could have worked to align Baffin Island's characteristics with those of other island populations (island wolves, with a more spatially stable prey base, are likely more territorial than mainland barren-ground wolves in general, e.g. Walton et al. 2001).

Baffin Island may have been separated from the Western Islands in STRUCTURE analysis due to its receipt of migrants from different mainland populations. Migration between the NE Mainland region (Eastern Barrens) and North Baffin is relatively high (Tables 2 and 3, Fig. 2C). However, D_S between the South Baffin region and the NE Mainland was almost twice that between South Baffin and the Atlantic population (0.149 vs. 0.078), suggesting latitudinal, rather than longitudinal gene flow (Fig. 3A). Eastern Island wolves thus appear to be connected to both mainland tundra populations and those in more southern regions. 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). Specialization of North and South Baffin wolves on caribou herds with distinct calving grounds may

also contribute to their differentiation (Table 3; Ferguson 1989; Clark 1971).

Conservation of Arctic Island wolves in a changing climate

Management decisions should consider the status of Baffin and northern Arctic Island wolves as a whole, because extinctions and recolonizations among these populations during the last century are consistent with metapopulation dynamics (Elmhagen and Angerbjorn 2001). Population fluctuations have likely occurred throughout the entire history of island wolves, and during the Pleistocene, could have encompassed the entire region. This latter scenario would be comparable to that experienced by Beringian brown bears (*Ursus arctos*), whose range expanded and contracted with each glacial cycle (Barnes et al. 2002). Barnes et al. (2002) demonstrated that bear population genetic structure following each recolonization was similar, implying spatial overlap of dispersal barriers throughout time. In our study area, physical and ecological barriers could have resulted in consistent isolation of Arctic island from mainland barren-ground wolves following each colonization of the archipelago. If so, contemporary Arctic Island wolf populations may embody a repetitive long-term process that should be recognized as endemic and unique, regardless of their taxonomic status.

Island metapopulation cycles seem to be influenced by both anthropogenic and ecological variables. Despite high rates of harvest occurring on some islands (Carmichael et al. 2001), variation in prey density is currently perhaps most critical, as wolves cannot persist in the absence of large ungulates. 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 and Nagy 2001b; Mech 2005). 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 are present in at least some regions.

However, our results suggest Arctic island wolves may soon face genetic, as well as ecological threats to persistence. Island populations 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 large, continuous mainland populations. 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 (Johnston 2002; Charron 2005). Facilitation of this traffic with icebreakers might further reduce the opportunity for mainland wolves to reach the Arctic Islands, disrupting gene flow which may be critical to persistence of the island metapopulation. 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.

Wolves are the only large terrestrial carnivore in the Arctic Archipelago, and thus fill a unique niche in the ecosystem. As observed in a wolf-free Yellowstone (Ripple and Larsen 2000), “ecosystems are dynamic, and loss of a species in one place may cause unexpected trouble elsewhere” (Pratchett et al. 2002). It is unclear whether combined climatic, demographic, ecological, genetic, and anthropogenic factors will result in wolf-free Arctic Islands, but if island wolves are to persist, anthropogenic intervention may yet be key.

Acknowledgements Thanks to all those who contributed samples or facilitated their collection: Alaska Raw Fur; D. Bewick and North

American Fur Auctions; G. Jarrell at the University of Alaska Museum; P. Merchant; P. Clarkson; R. Otto; G. Bihun; D. Berezanski; R. Brenneman; and the numerous Hunters and Trapper’s Associations and wildlife officers across Manitoba, the Northwest Territories and Nunavut. Thanks to G. A. Wilson for updates to his program BAYESSASS, assistance with interpretation of results, and helpful comments on the manuscript. We also appreciate the comments of S. Moore, R. K. Wayne, D. Coltman, D. Hik, and two anonymous referees on earlier drafts of the paper. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada, the Alberta Ingenuity Fund, the Government of Nunavut, and the Northern Scientific Training Program.

References

- Barnes I, Matheus P, Shapiro B, Jensen D, Cooper A (2002) Dynamics of Pleistocene population extinctions in Beringian brown bears. *Science* 295:2267–2270
- Bennike O, Andreasen C (2005) New dates of musk-ox (*Ovibos moschatus*) remains from northwest Greenland. *Polar Rec* 41:125–129
- Carmichael LE, Nagy JA, Larter NC, Strobeck C (2001) Prey specialization may influence patterns of gene flow in wolves of the Canadian Northwest. *Mol Ecol* 10:2787–2798
- Carmichael LE, Krizan J, Nagy JA, Fuglei E, Dumond M, Johnson D, Veitch A, Berteaux D, Strobeck C (2007) Historical and ecological determinants of genetic structure in arctic canids. *Mol Ecol*. doi:10.1111/j.1365-294X.2007.03381.x
- Castric V, Bernatchez L (2004) Individual assignment test reveals differential restriction to dispersal between two salmonids despite no increase of genetic differences with distance. *Mol Ecol* 13:1299–1312
- Charron A (2005) The Northwest passage—is Canada’s sovereignty floating away? *Int J* 60:831–848
- Clark KRF (1971) Food habits and behavior of the tundra wolf on central Baffin Island. Ph.D. Dissertation, University of Toronto
- di Rienzo A, Peterson AC, Garza JC et al (1994) Mutational processes of simple sequence repeat loci in human populations. *Proc Natl Acad Sci USA* 91:3166–3170
- Elmhagen B, Angerbjorn A (2001) The applicability of metapopulation theory to large mammals. *Oikos* 94:89–100
- England J (1999) Coalescent Greenland and Innuitian ice during the last glacial maximum: revising the Quaternary of the Canadian High Arctic. *Quat Sci Rev* 18:421–456
- England J, Atkinson N, Bednarski J, Dyke AS, Hodgson DA, Cofaigh CÓ (2006) The Innuitian ice sheet: configuration, dynamics, and chronology. *Quat Sci Rev* 25:689–703
- Environment Canada (2000) Canadian Climate Normal Data. Government of Canada. http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html. Cited July 2006
- Fedorov VB, Stenseth NC (2002) Multiple glacial refugia in the North American Arctic: inference from phylogeography of the collared lemming (*Dicrostonyx groenlandicus*). *Proc R Soc Lond B* 269:2071–2077
- 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: Hall E (ed) People and Caribou in the Northwest Territories. Department of Renewable Resources, Government of the Northwest Territories, Yellowknife, pp. 141
- Frankham R (2005) Genetics and extinction. *Biol Conserv* 126:131–140

- Fredholm M, Wintero AK (1995) Variation of short tandem repeats within and between species belonging to the Canidae family. *Mamm Genome* 6:11–18
- Garza JC, Williamson EG (2001) Detection of reduction in population size using data from microsatellite loci. *Mol Ecol* 10:305–318
- Gravlund P, Meldgaard M, Paabo S, Arctander P (1998) Polyphyletic origin of the small-bodied, high-arctic subspecies of tundra reindeer (*Rangifer tarandus*). *Mol Phylogenet Evol* 10:151–159
- Guillot G, Estoup A, Mortier F, Cosso JF (2005) A spatial statistical model for landscape genetics. *Genetics* 170:1261–1280
- Gunn A, Shank C, McLean B (1991) The history, status and management of muskoxen on Banks Island. *Arctic* 44:188–195
- Hewitt GM (1996) Some genetic consequences of ice ages, and their role in divergence and speciation. *Biol J Linn Soc* 58:247–276
- Johnston DM (2002) The Northwest Passage revisited. *Ocean Dev Int Law* 33:145–164
- Kennedy LJ, Angles JM, Barnes A, Carmichael LE, Radford AD, Ollier WER, Happ GM (2007) DLA-DRB1, DQA1, and DQB1 alleles and haplotypes in North American gray wolves. *J Hered*. doi:10.1093/jhered/esm051
- Kimura M, Crow JF (1964) The number of alleles that can be maintained in a finite population. *Genetics* 49:725–738
- Krizan J (2005) Nunavut wolf morphology and diet study. Department of Environment, Nunavut Wildlife Management Division, Government of Nunavut, Iqaluit, p 59
- Kurtén B, Anderson E (1980) Pleistocene mammals of North America. Columbia University Press, New York
- Larter NC, Nagy JA (2000) Calf production and overwinter survival estimates for Peary caribou, *Rangifer tarandus pearyi*, on Banks Island, Northwest Territories. *Can Field Nat* 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 1986–1999. *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. *Arct Antarct Alp Res* 33:123–130
- Lamoureux SF, England J (2000) Late Wisconsinan glaciation of the central sector of the Canadian High Arctic. *Quatern Res* 54:182–188
- Leonard JA, Vila C, Wayne RK (2005) Legacy lost: genetic variability and population size of extirpated US grey wolves (*Canis lupus*). *Mol Ecol* 14:9–17
- MacPhee RDE, Tikhonov AN, Mol D, Greenwood AD (2005) Late quaternary loss of genetic diversity in muskox (*Ovibos*). *BMC Evol Biol* 5:49
- Manning TH, Macpherson AH (1958) The mammals of Banks Island. Arctic Institute of North America, Montreal
- McEwen EH (1955) A biological survey of the west coast of Banks Island. Canadian Wildlife Service, Ottawa
- 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: Mech LD, Boitani L (eds) *Wolves: behavior, ecology, and conservation*. University of Chicago Press, Chicago, p 1
- Mellersh CS, Langston AA, Acland GM, Fleming MA, Ray K, Weigland NA, Francisco LV, Gibbs M, Aguirre GD, Ostrander EA (1997) A linkage map of the canine genome. *Genomics* 46:326–336
- Miller FL (1995) Status of wolves on the Canadian Arctic Islands. In: Carbyn LN, Fritts SH, Seip DR (eds) *Ecology and conservation of wolves in a changing world*. Canadian Circumpolar Institute, Edmonton, p 35
- Miller FL, Reintjes FD (1995) Wolf sightings on the Canadian Arctic Islands. *Arctic* 48:313–323
- Nei M (1972) Genetic distance between populations. *Am Nat* 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: Carbyn LN, Fritts SH, Seip RD (eds) *Ecology and conservation of wolves in a changing world*. Canadian Circumpolar Institute, Edmonton, p 375
- Nowak RM (2003) Wolf evolution and taxonomy. In: Mech LD, Boitani L (eds) *Wolves: behavior, ecology, and conservation*. University of Chicago Press, Chicago, p 239
- Ostrander EA, Sprague GF, Rine J (1993) Identification and characterization of dinucleotide repeat (CA)_n markers for genetic mapping in dog. *Genomics* 16:207–213
- Paetkau D, Calvert W, Stirling I, Strobeck C (1995) Microsatellite analysis of population structure in Canadian polar bears. *Mol Ecol* 4:347–354
- Paetkau D, Waits LP, Clarkson PL, Craighead L, Strobeck C (1997) An empirical evaluation of genetic distance statistics using microsatellite data from bear (Ursidae) populations. *Genetics* 147:1943–1957
- Park SDE (2001) Trypanotolerance in West African cattle and the population genetic effect of selection. Ph.D. Dissertation, University of Dublin
- Petit RJ, El Mousadik A, Pons O (1998) Identifying populations for conservation on the basis of genetic markers. *Conserv Biol* 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. *J Hered* 90:502–503
- Pratchett T, Stewart I, Cohen J (2002) *The science of Discworld*, 2nd edn. Ebury Press, London
- Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics* 155:945–959
- Ripple WJ, Larsen EJ (2000) Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. *Biol Conserv* 95:361–370
- Saitou N, Nei M (1987) The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Mol Biol Evol* 4:406–425
- Sokal RR, Rohlf FJ (1995) *Biometry: the principles and practice of statistics in biological research*, 3rd edn. W. H. Freeman and Company, New York
- Spencer CC, Neigel JE, Leberg PL (2000) Experimental evaluation of the usefulness of microsatellite DNA for detecting demographic bottlenecks. *Mol Ecol* 9:1517–1528
- Stewart TG, England J (1986) An early Holocene caribou antler from northern Ellesmere Island, Canadian Arctic Archipelago. *Boreas* 15:25–31
- Titterton DM, Murray GD, Murray LS et al (1981) Comparison of discrimination techniques applied to a complex data set of head injured patients. *J Roy Stat Soc A Sta* 144:145–175
- 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*. *Mol Ecol* 8:2089–2103
- Waltari E, Demboski JR, Klein DR, Cook JA (2004) A molecular perspective on the historical biogeography of the northern high latitudes. *J Mammal* 85:591–600
- Walton LR, Cluff HD, Paquet PC, Ramsay MA (2001) Movement patterns of barren-ground wolves in the central Canadian Arctic. *J Mammal* 82:867–876

- Weckworth BV, Talbot S, Sage GK, Person DK, Cook J (2005) A signal for independent coastal and continental histories among North American wolves. *Mol Ecol* 14:917–931
- Wilson GA, Rannala B (2003) Bayesian inference of recent migration rates using multilocus genotypes. *Genetics* 163:1177–1191
- Wolfe AP, King RH (1999) A paleolimnological constraint to the extent of the last glaciation on northern Devon Island, Canadian High Arctic. *Quat Sci Rev* 18:1563–1568