



GENETICS OF NORTH AMERICAN ARCTIC FOX POPULATIONS:

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Final Report

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POPULATIONS**

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Executive Summary

The arctic fox (*Alopex lagopus*) is a polar adapted species that was widely distributed during the Pleistocene glaciation. Since the last glacial maximum, as suitable habitat has contracted and the larger red fox (*Vulpes vulpes*) has expanded its distribution northwards, arctic foxes have retreated towards the pole. In North America, the species is currently found throughout the mainland barren ground tundra and the islands of the Canadian Arctic Archipelago. Arctic foxes also occur in Scandinavia, Siberia, and numerous additional islands in the Pacific and Atlantic, including Svalbard (Norway).

Arctic foxes are the only canid species with fur on their foot pads, and which undergoes a seasonal colour molt. In addition, they have developed flexible behavioral strategies to cope with variations in their food supply. While arctic foxes form smaller social groups than many other canid species, large families may be sustained when food resources are plentiful. However, it is less clear how often non-alpha adults in these families are able to mate. Arctic foxes can also travel distances up to 2300km, often over sea ice or through the boreal forest where breeding populations do not normally occur. These long-distance movements are thought to be an adaptation to large-scale synchrony in lemming population declines, but are also likely advantageous to coastal foxes which may supplement their diet by scavenging from polar bear kills.

Population genetic studies of arctic foxes are rare and have never been conducted in North America. 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. Since arctic fox pelts are a valuable source of income for many northern residents, and since foxes are the major vector of rabies and canine distemper in the north, identification of the factors influencing fox movement may be of additional practical significance. The goals of this study were: 1) to determine the genetic status of island arctic foxes and their relationship to mainland populations and 2) to identify the influence of ecology on movement and gene flow in arctic foxes. In addition, mating patterns of arctic foxes on Bylot Island, Nunavut, were investigated.

1700 fox samples were collected throughout the North American range of the species, and from the Svalbard Archipelago. Samples originated from fur houses, museums, previous research projects, and many were also collected directly from hunters and trappers in Nunavut and the Northwest Territories. DNA was extracted from all samples and 12 bi-parentally inherited microsatellite loci PCR amplified to create a DNA fingerprint of each individual. After the database was tested for duplicate genotypes, 1514 samples remained for analysis. Capture locations of each fox were plotted using ArcGIS and samples divided into populations based on gaps in the sampling distribution. A combination of classical population genetic methods and newer, Bayesian inference techniques were used to explore genetic relatedness, genetic variation and population genetic structure between foxes in different geographical regions.

A variety of mating patterns were detected among foxes sampled at known dens on Bylot Island. At most dens, single pairs of mated foxes could have produced offspring with all genotypes observed. However, two mated pairs produced cubs at one den, and cubs found at the

final den may have arisen through multiple paternity (one female mated by two male foxes, producing a single litter). The flexible social structures observed on this island most likely reflect the abundance of available food, consisting of both lemmings and large numbers of birds and their eggs.

Arctic foxes populations, regardless of location on islands or the mainland, possessed high and equal levels of genetic variation (78% heterozygosity and >6 alleles per locus). Since arctic foxes frequently travel over sea ice, migration from mainland populations into island populations likely prevents accelerated genetic drift and loss of variation common to island populations of many other species. Foxes also show greater variation than mainland grey wolves (*Canis lupus*) and significantly more variation than island wolves. These differences likely reflect both divergent glacial histories, and differences in contemporary effective population sizes of island canid populations.

Arctic foxes in all regions in North America show generally homogeneous allele frequencies. Assignment indices in all populations overlapped, and there was no correspondence between genetic relationships of populations and their position in physical space. Furthermore, Bayesian clustering analysis of all fox samples (performed in Structure) suggested that a single genetic cluster is most appropriate for North American fox populations, with most Svalbard foxes also assigning to this cluster. In combination, these results indicate that arctic foxes in the study area may be acting as a single, panmictic population.

Panmixia in foxes is likely a result of three factors: their widespread distribution during the Pleistocene; their current continuous distribution in North America (absence of population bottlenecks or habitat fragmentation), and; the long-distance foraging movements undertaken by contemporary foxes, apparently resulting in long distance gene flow. Sex-biased dispersal was not detected, and foxes of both sexes appear to travel equivalent distances, at least in North America. Apparent panmixia is in contrast to arctic fox populations in Greenland and Scandinavia, may be unique within the canid family, and is therefore particularly interesting. However, this genetic homogeneity among North American foxes unfortunately precludes identification of particular movement corridors or directional migrations, and regional ear-tagging or radio-collaring studies may be more effective at answering such questions.

At the present time, there appear to be no genetic threats to persistence of arctic fox populations in North America, whether island or mainland. However, this may change as the climate of the arctic continues to warm; sea ice corridors for movement may gradually be restricted or lost, thus restricting gene flow, and red foxes may continue to expand their range northward, competitively excluding the smaller arctic fox. The results of the present study therefore represent an important baseline for monitoring future genetic changes in North American arctic fox populations.

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 arctic foxes; for discussion of wolves, please see Carmichael (2006).

Fossil (Kurtén & Anderson 1980), morphological (Bisaillon & Deroth 1980; Frafjord 1993) and molecular phylogeographical studies (Dalén *et al.* 2005) suggest arctic foxes expanded their range during cooling cycles, retreating to a compact but continuous polar distribution during warm interglacials. Gradual range contraction is consistent with the species' present occurrence: continuous throughout circumpolar tundra regions, with remnant populations on various islands in the polar oceans (Goltsman *et al.* 2005; Kurtén & Anderson 1980). Current arctic fox distribution reflects both the progressive contraction of species-suitable habitat towards the pole and the northward expansion of their primary competitor, the red fox (*Vulpes vulpes*, Dalén *et al.* 2004; Dalén *et al.* 2005; Kurtén & Anderson 1980; Tannerfeldt *et al.* 2002). The Canid Specialist Group of the International Union for the Conservation of Nature and Natural Resources (IUCN) recognizes four subspecies of arctic fox globally, with *A. l. lagopus* occupying most northern circumpolar regions and the remaining subspecies restricted to single small ice-free islands in the Bering Sea (Angerbjörn *et al.* 2004a).

The Arctic Fox

Arctic foxes display sexual size dimorphism, with males weighing up to 5 kg and females as much as 4 kg. They are the only canid species with fur covering their foot pads (*lagopus* meaning "hare foot") and the only canid to undergo a seasonal colour molt (Prestrud 1991). Summer fur is generally a grayish-brown, with winter fur either white or blue. The white morph is predominant throughout most of the species' range, but the frequency of blue foxes increases in coastal regions and on islands (Angerbjörn *et al.* 2004a). Since coastal and inland foxes also tend to use different food resources, this difference has historically prompted recognition of two ecotypes: "coastal" and "lemming" (Braestrup 1941).

Where lemmings (*Lemmus* and *Dicrostonyx* spp.) are present, as common in northern Canada, they compose up to 90% of the arctic fox's diet (Macpherson 1969). In coastal regions

(e.g. Bylot Island, Nunavut), and in islands like Svalbard (Norway) that do not contain small mammals, foxes also eat nesting birds and their eggs, and will scavenge from both marine and terrestrial carrion (Eide *et al.* 2005; Roth 2002). When resources are abundant, foxes hunt in excess and cache prey for future use, and will also raid each other's caches when opportunity presents (Samelius & Alisauskas 2000). During periodic crashes of North American lemming populations, when caches are depleted and live prey unavailable, arctic foxes undertake vast foraging movements in search of alternative food and may migrate distances up to 2300 km (Eberhardt *et al.* 1983). Long-range movements have also been documented through regions which do not support breeding populations, such as sea ice (640 km) and the southern boreal forest (1000 km, Wrigley & Hatch 1976). These seasonal migrations mean that North American arctic foxes are territorial primarily during breeding season, with pair bonds perhaps dissolving in winter. They also suggest that "normal" dispersal distances of 40-60 km, typical of European alpine foxes, may not be applicable to large, continuous populations in North America (Landa *et al.* 1998; Strand *et al.* 2000).

In large, continuous populations, arctic foxes do not typically form social groups containing more than two adults (Angerbjörn *et al.* 2004a; Eide *et al.* 2004). Where additional adults occur, they may be littermates of the dominant pair or offspring from a previous season, but are less likely than wolves to care for or provision young (Strand *et al.* 2000; but see Goltsman *et al.* 2005 for exceptions). It is not clear whether additional adult foxes "help" by contributing to territorial defense, but they may increase success of the breeders indirectly by caching food within the shared home range (Eide *et al.* 2004). Indeed, supernumerary adults appear to be best tolerated when food resources are abundant, and may produce secondary litters under these circumstances (Goltsman *et al.* 2005). In addition to the potential for plural breeding, arctic foxes display a second reproductive adaptation to vagaries in their food supply: "lemming" foxes, with periodic access to superabundant food resources, have larger litters (6.3 ± 3.3 , max 19) in all years than "coastal" foxes (4.2 ± 1.5 , max 10), whose food resources are more predictable but less rich (Angerbjörn *et al.* 2004b).

Recent History and Current Status of Arctic Foxes

Since arctic foxes are naturally restricted to remote and largely inaccessible northern areas, human impact on the species – throughout most of their range – has occurred only recently. Trapping for fur became common in the early 1900s, but current harvests are likely less than 20% of the total North American fox population. Given the species' high fecundity, these rates are likely sustainable over the long term (Geffen *et al.* 1996). However, climate change is also expected to have a negative impact on arctic foxes. In Svalbard, reindeer (*R. t. platyrhynchus*) are susceptible to winter mortality, and the effect of reindeer density declines on arctic foxes, who hunt reindeer calves and scavenge from carcasses (Prestrud 1992), may mimic that of lemming population crashes (Fuglei *et al.* 2003). In North America, a greater threat to arctic fox persistence is the northward expansion of the red fox (*Vulpes vulpes*), which limits reproductive success of this species via both resource competition and direct aggression (Bailey 1992; Dalén *et al.* 2004; Tannerfeldt *et al.* 2002).

Arctic foxes are an important economic resource for many northern residents. They are also the primary vector for rabies and distemper in the Canadian Arctic. An understanding of

their population status and movement patterns could therefore have great significance for management of this species.

Project Objectives

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 arctic foxes in the Canadian Arctic Archipelago, which are capable of traversing annual sea ice, has not been previously examined. 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 major goal of this work was thus to determine the genetic nature and status of island arctic fox populations, relative to those on the mainland.

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); genetic analyses of arctic foxes are considerably less common, and with the exception of a single circumpolar phylogeographic investigation (Dalén *et al.* 2005), have never been conducted for the North American population. Furthermore, most population-level studies previously conducted have been devoted to historical, topographical or geological influences on genetic structuring of canids, 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 second major goal of this work is to identify the influence of ecology on the genetics of arctic foxes.

Field work conducted by other researchers on Bylot Island resulted in samples of adults and juveniles taken from known dens. Mating systems of arctic foxes in this population were therefore examined as an addition to the major focus of the project.

All results described in this report are based on the use of nuclear microsatellite DNA markers. Initially, sequencing of mitochondrial and Y chromosome DNA was planned to allow reexamination of morphologically-defined subspecies classifications in the arctic fox. However, recent work by other authors (Angerbjörn *et al.* 2004; Dalén *et al.* 2005) made this aspect of the project redundant, and it was therefore dropped.

Methods

Sample Collection

Contemporary samples of 1700 arctic foxes, distributed throughout the North American range of the species and the Svalbard Archipelago, were collected (Fig. 1). In communities across Nunavut (NU) and the Northwest Territories (NT), local hunters and trappers were asked to provide a 0.5cm x 8cm strip of fox pelts harvested. In NU, hunters were paid \$10 for each fox sample contributed, including information regarding harvest date, location, sex of the animal if known and a subjective estimate of local lemming density (high, average, low) at time of harvest. In future studies, it may be necessary to specify more clearly that each sample must come from a separate fox, as a number of samples were found to have originated from the same individual once DNA fingerprinting was complete. Sample collection began in March 2001, and continued through May 2004. Samples collected directly from hunters were supplemented with those obtained through fur auction houses, museums, and other research projects.

All samples were taken from killed foxes, except those from Bylot Island where, in the summer of 2003, other researchers performed an extensive den survey by foot and snowmobile over a study area of approximately 425 km² (Fig. 2). Foxes were trapped at eight occupied dens using methods described elsewhere (Carmichael *et al.*, submitted). Twenty to 40 summer hairs were collected from the back or flank of each animal. Foxes were released and samples were sent to the University of Alberta, where all laboratory analysis described in this report was conducted.

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). Twelve biparentally inherited microsatellite loci were PCR-amplified using fluorescently-labeled primers from domestic dogs (locus names and reaction conditions given in Carmichael *et al.*, in prep.). 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, 1514 arctic foxes remained for analysis (genotypes are given in Carmichael *et al.* in prep.).

Population Delineation and Preliminary Analysis

Capture locations of all arctic foxes were mapped using ARCGIS 9.1 (Environmental Systems Research Institute 1999-2004) and samples were grouped based on gaps in the sampling distribution (Fig. 1). 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.

Assignment of Parentage and Calculation of Relatedness

For Bylot Island samples collected at known den sites, an inclusion-exclusion test of parentage was conducted based on simple Mendelian heredity of co-dominant microsatellite markers, whereby offspring inherit one allele at each locus from each parent. Although Baker *et al.* (2004) and Roemer *et al.* (2001) considered single-locus mismatches adequate for full parental exclusion, for this project, they were interpreted as “potential exclusion,” allowing for the possibility of germ-line mutation. Mismatches at two or more loci were interpreted as full exclusion (Kitchen *et al.* 2006). For full details of this analysis, see Carmichael *et al.* (submitted).

Relatedness coefficients (R , Queller & Goodnight 1989) are indices of the proportion of alleles identical by descent between two individuals, accounting for the frequencies of those alleles in the population. A pair of individuals with R between -1 and 0 are less related on average than two randomly chosen individuals, while those with R between 0 and +1 are more related than average; $R \approx 0.5$ is expected for first degree relationships (parent-offspring or full sibling), while $R \approx 0.25$ is predicted for half-siblings or other similarly related pairs. The midpoint 0.375 can be used as a cutoff to distinguish between first and second degree relatives (Blouin *et al.* 1996). Pairwise R was calculated between all foxes using SPAGeDi version 1.2 (Hardy & Vekemans 2002). Average values and standard deviations (SD) were also calculated among foxes at each den, and these results used to provide additional support for conclusions based on inclusion/exclusion analysis.

Genetic Variation and Genetic Distance

Expected heterozygosity H_E (Nei & Roychoudhury 1974) 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 20 allele copies (Table 1).

One thousand bootstrap pseudoreplicates of fox regions were generated using PHYLIP 3.65. Nei’s D_S was calculated for each replicate, and a neighbor-joining majority-rule consensus tree constructed (Felsenstein 1985; Saitou & Nei 1987). Euclidean distance was calculated among populations within species using average latitude and longitude and the “Geographic Distances” subroutine of MANTEL 4.0 (Casgrain & Legendre 2001). A Mantel test (Mantel 1967) with 9999 permutations was used to assess isolation by distance.

Assignment and Sex-Biased Dispersal

Paetkau *et al.*’s assignment test (1995) was conducted with allele frequencies adjusted to avoid zeros (Titterton *et al.* 1981). To identify levels of cross-assignment greater than those expected due to correlation of allele frequencies between clusters, 10,000 replicates were performed, creating new individuals and assuming Hardy-Weinberg Equilibrium (Carmichael *et al.* 2001). In addition to providing estimates of the relative number of migrants between two

populations, assignment indices can be used as an indicator of relative differentiation, and were employed to explore contrasts between wolves in different habitat types. The variance of corrected assignment indices (vAIC) method, implemented in FSTAT (Goudet 1995), was used to test for sex-biased dispersal. This method was chosen as it is most sensitive to recent and rare dispersal events (Goudet 1995; Goudet *et al.* 2002; Prugnolle & de Meus 2002).

Genetic Clustering Analysis

STRUCTURE 2.1 was used to perform Bayesian clustering of genotypes, including all loci and without any prior spatial information (Pritchard *et al.* 2000). Initial runs for arctic foxes consisted of 100,000 burn-in cycles followed by 1,000,000 iterations of the Markov Chain. The admixture model was selected and a unique α estimated for each cluster; λ , describing the allele frequency distribution of each locus, was also inferred. Setting the number of clusters, K , to vary between 1 and 4, indicated that an appropriate value for λ was 0.5 and that α was unequal between clusters and often small, requiring ALPHAPROPSD to be reduced to 0.1. These final parameters were used to conduct two replicates each of $K=1-7$.

Results

Mating Patterns of Foxes on Bylot Island

Two adult females, four adult males, and 42 juvenile foxes were sampled from a total of eight dens (Fig. 2). An additional male, BY08, was sampled near the greater snow goose nesting colony near the den sites (Carmichael *et al.*, submitted), but was genetically excluded as a potential father for all juveniles in the study. One cub from den 145 could not be genotyped due to poor quality DNA and was excluded from further analysis. Genotyping of the remaining 48 foxes was 99.7% complete, and no fox was typed for fewer than 11 loci. Among adult foxes, no microsatellite deviated significantly from HWE. Taken together, these results suggest that null alleles were rare or absent in our sample.

The genetic data presented below could support a number of possible mating configurations, but we present the most parsimonious solutions, involving the smallest number of possible parents for each litter (Fig. 3). Genotypes of foxes included in parentage analysis are given in Appendix 1.

Single Breeding Pairs

Adult foxes were not sampled at dens 108, 112, or 327. However, despite the fact that 9 of 12 loci had more than 5 alleles in the adult sample, the cubs from each den contained no more than 4 unique alleles at any locus; therefore, a single male-female pair would be adequate to explain offspring at each den. Relatedness among cubs averaged 0.53 ± 0.14 at den 108, 0.54 ± 0.14 at den 112, and 0.4 at den 327, supporting the status of each litter as full siblings. However, no male in our sample shared one or more alleles per locus with any of these cubs, and therefore their paternity is unknown.

One adult male and one cub were sampled from den 137; the male was included as a possible father of this cub. At den 010, a single male BY15 was captured and included as a father for all 6 cubs. Although adult females were not sampled, no more than two putative maternal alleles were observed at any locus, and therefore a single mother could explain all cubs in this litter. One adult female and one unrelated adult male ($r = -0.13$) were sampled at den 106, which contained 4 juvenile foxes. This pair of adults was included as a parental set for all cubs at this den. Single breeding pairs of adult foxes therefore existed at 6 of 8 dens (75%).

Plural Breeding

Adult male BY04 was included as a father for 2 of the 5 pups found at den 145 ($r = 0.45 \pm 0.03$), but excluded at 8 or more loci for the remaining 3: a second male would thus be required to explain these juveniles. This social group may also have included two adult females; at locus 173, offspring attributed to BY04 contained putative maternal alleles 124 and 130, while one cub attributed to the second, unknown male was homozygous for allele 128. Polyandry and multiple paternity with a maternal germ-line mutation is possible, but plural breeding of two mated pairs seems more likely.

Polyandry with Multiple Paternity

Adult female BY07 was sampled at den 101 and included as a mother for the 9 cubs found there. However, a second, unidentified female was observed suckling cubs at this den (M-A Giroux, pers. obs.). This female may have lost her litter but remained with the family group (White 1993) or may have been a yearling helper female experiencing induced lactation (Goltsman et al. 2005a).

No sampled male was included as the father of any cub at den 101, however, the cubs attributed to female BY07 possessed 3 putative paternal alleles at locus CXX250, CXX733, CXX745, and CXX758. Relatedness among the cubs ranged from -0.14 to 0.75 ($r = 0.31 \pm 0.22$). Therefore, polyandry with multiple paternity is the most parsimonious explanation for the 9 cubs found at this den.

Genetic Structure of North American Arctic Fox Populations

Variation

H_E averaged 78% in all fox populations, regardless of their origin on islands or the mainland (Table 1). Allelic richness results confirmed this trend.

Relationships Among Populations

Allele frequencies were generally homogeneous across geographic regions; Svalbard foxes were the only population to display consistent significant differences (data not shown). There was no association, visual or statistical, between geography and D_S in arctic foxes (Fig. 4, $r = 0.15$, $P = 0.24$). Indeed, subpopulations located on the same island appear on opposite sides of the tree (Fig 5). These observations suggest that arctic foxes form a single genetic unit.

Assignment indices (Paetkau *et al.* 1995) overlapped among all fox populations (data not shown), and self-assignment rates below 14% were observed in North America (42% in Svalbard). Low differentiation in foxes could potentially be attributed to high male-mediated gene flow, however, no signal for sex-biased dispersal was detected.

Genetic Clustering

STRUCTURE analysis was conducted using all loci. $\ln\text{Prob}(D)$ for arctic foxes increased only slightly as K was increased (Fig. 6). However, for $K = 2$, an average of 97% of the individuals in each geographic region assigned to a single cluster, and this trend persisted as K was increased. While some genuine complexity seemed to exist within the Svalbard group, this population also consistently assigned to the single cluster containing the vast majority of North American arctic foxes (Carmichael *et al.* in prep). It is therefore most likely that the increase in probability with larger K resulted from over-parameterization of the model, and that STRUCTURE was segregating rare alleles, rather than partitioning individuals according to true genetic discontinuities. A single panmictic unit including North America and Svalbard thus seems most likely for arctic foxes.

Fig. 6 illustrates differences in results for arctic foxes, which appear to have no true structure, and wolves, which display genuine population genetic subdivision (Carmichael 2006).

Discussion

Complex Mating Patterns of Bylot Island Foxes

Field studies indicate that social structure in arctic foxes is variable and can be complex (Audet *et al.* 2002; Goltsman *et al.* 2005; Hersteinsson & MacDonald 1982; Korhonen & Alasuutari 1994; Strand *et al.* 2000). While groups including multiple adults have been observed, previous studies often suggest that breeding is restricted to the dominant pair (e.g., Eide *et al.* 2004; Korhonen & Alasuutari 1994; Kullberg & Angerbjörn 1992); our work provides preliminary genetic support for plural breeding, polygyny, and polyandry with multiple paternity in the arctic fox.

Breeding season territoriality of arctic foxes has been linked to spatio-temporal resource abundance in a social group's home range (Eide *et al.* 2004). Arctic foxes are known to cache lemmings and bird eggs for winter consumption (Careau *et al.* 2006; Eide *et al.* 2004; Samelius & Alisauskas 2000) and subordinate animals of social groups, who do not often provision cubs directly (Strand *et al.* 2000), have been observed caching food within the territory of the breeding pair (Eide *et al.* 2004). This behavior suggests a possible energetic advantage to the dominant pair that may permit formation of larger social groups (Eide *et al.* 2004); plural breeding may thus be elevated in resource-rich habitats. Our study was conducted in an area of Bylot Island which includes both lemmings and avian nesting grounds, and it is worth noting that 3 out of 4 dens with potential plural breeding (101, 106, and 145) were clustered near the snow goose nesting colony.

Explanations for polyandry and its associated multiple paternity are varied, including both material benefits and genetic advantages such as assurance of compatibility between maternal and paternal genomes (Zeh & Zeh 2001). Multiple paternity also allows a female to increase the genetic variation contained in a single season's reproductive output. This increase in variation might result in an increased probability that at least one cub in a litter will be optimally adapted to its current environment, or better equipped to deal with changes in its environment over time. The reproductive output of arctic foxes is closely tied to the productivity of their habitat in any given year (Angerbjörn *et al.* 1995), and multiple paternity may provide an additional adaptive advantage to both recurrent ecological fluctuations and incipient climate-induced changes in the polar habitat of the arctic fox.

Genetic Variation in Arctic Canid Species

Arctic foxes averaged 78% heterozygosity regardless of the type of population (Table 1); heterozygosity in mainland wolves averaged 74%, while island wolves were significantly less diverse (Carmichael 2006). We observed similar trends in the average number of alleles per population, and the pattern likely results from both historical and contemporary events.

Wolves persisted in small populations in a number of distinct refugia during the last glaciation (Brewster & Fritts 1995), while arctic foxes were widely distributed, and would not have experienced the bottlenecks undergone by wolves (Dalén *et al.* 2005; Kurtén & Anderson 1980). In addition, arctic foxes occur at higher density than wolves, (Angerbjörn *et al.* 2004; Mech & Boitani 2004), and likely possess a higher effective population size. Whereas only 2 wolves normally breed in a pack of 6-8 individuals (but see Mech & Boitani 2003), foxes form smaller social groups, and a higher proportion of adults thus breeds each generation (Macpherson 1969); litter sizes in foxes are also greater (Geffen *et al.* 1996; Moehlman 1989). Given their respective species and life histories, it is unsurprising that arctic foxes in general possess more genetic variation than wolves. Differences in home range sizes and energetics may also contribute to differences in variation between wolf and fox populations on arctic islands.

Since arctic foxes can travel long distances over sea ice, it is also unsurprising that island and mainland populations are equally variable (Table 1). More interesting is the fact fox populations surveyed here are more variable than populations in Greenland ($H_e = 0.54-0.73$ Meinke *et al.* 2001) and Scandinavia ($H_e = 0.58-0.77$), while equal to the large Russian population ($H_e = 0.83$ Dalén 2005). Russian foxes, like North American ones, have likely persisted at high density since the Pleistocene, while Scandinavian foxes have endured recent, severe, and prolonged bottlenecks (Dalén 2005). The lower variation in Greenland foxes is more difficult to explain, but portions of the Greenland coast are ice-free year round, perhaps impeding gene flow; drift-in-isolation may therefore be higher in this population (Dalén *et al.* 2005).

Absence of Genetic Structure in Arctic Foxes

North American and Svalbard foxes formed a single genetic cluster. Dalen *et al.* (2005) attributed this pattern in mtDNA phylogeography to the inverse response of polar-adapted species to climatic cycles: expanding during ice ages and contracting into a single circumpolar population during interglacials. With the exception of foxes in alpine habitats and on sea ice-free

islands like Iceland, world-wide arctic fox populations have likely been physically continuous since the Pleistocene (Dalén *et al.* 2005).

Spatial synchrony of lemming population cycles has selected for development of long-distance migrations in foxes, allowing them to escape areas devoid of adequate prey (Audet *et al.* 2002; Dalén 2005); high levels of gene flow resulting from these movements would maintain homogeneous allele frequencies across large geographic areas. Mitochondrial DNA studies have suggested low-level differentiation between lemming and coastal foxes, with higher gene flow occurring within the lemming ecotype (Dalén *et al.* 2005). Our study area included only one coastal population, Svalbard, which assigned predominantly to the North American genetic cluster. Furthermore, while foxes in coastal regions of North America use marine food resources, particularly when lemmings are at low abundance (Roth 2002; Roth 2003), no significant genetic differentiation was detected in the North American range of this species. This may not be surprising, however, as coastal-dwelling foxes often follow polar bears long distances in search of carrion, and these movements would result in long distance gene flow, just as lemming population declines do. Fox scavenging on wolf-killed migratory caribou in inland areas would also produce a similar outcome (J. Akat, pers. comm.). It is therefore likely that no population in our sampling range has experienced significant genetic isolation since initial colonization. Large population sizes, in combination with this physical and temporal continuity, would effectively suppress genetic differentiation in these regions.

No fox populations were separated by F_{ST} above 0.02, and our pairwise values averaged 0.002 (data not shown). In contrast, pairwise F_{ST} ranged from 0.06-0.2 in Scandinavian foxes (Dalén 2005), while Meinke *et al.* observed values from 0.07 to 0.262 among coastal Greenland populations (Meinke *et al.* 2001). Higher differentiation, like low variation, is expected among alpine foxes in Scandinavia; Greenland foxes are tundra foxes, but restricted to coastal regions (Meinke *et al.* 2001). If fox movement occurs only around Greenland's circumference, gene flow between populations may therefore be restricted; greater resource stability may also reduce the number of long distance movements made by Greenland foxes relative to North American populations.

The absence of genetic structure observed in our arctic fox populations appears to be unique among canids studied to date. Coyotes (*Canis latrans*) were once considered genetically homogeneous (Roy *et al.* 1994), but recent work suggests existence of previously undetected genetic subdivisions (Sacks *et al.* 2004). F_{ST} ranged from 0.009-0.015 in red foxes (Lade *et al.* 1996; Wandeler *et al.* 2003), had a global value of 0.043 in kit foxes (*Vulpes macrotis*, Schwartz *et al.* 2005), and was 0.11 between Channel Island foxes (*Urocyon littoralis*) separated by only 13 km (Roemer *et al.* 2001). The Channel Island fox population, founded by mainland grey foxes (*Urocyon cinereoargenteus*), has also diverged into a unique species after a time since founding equivalent to that of Svalbard arctic foxes, which remain largely indistinguishable from those in North America. While unique, our results are however consistent with the minimal social structure and larger litter sizes observed in arctic foxes relative to other fox species (Geffen *et al.* 1996; Moehlman 1989).

Implications of the Present Work

Population structure in arctic foxes appears to be strongly influenced by adaptation of these carnivores to variability in their prey base. Arctic foxes in coastal regions of Greenland show levels of differentiation comparable to the isolated and depleted Scandinavian subpopulations; arctic foxes inhabiting the large, continuous landscape of North America show no differentiation whatsoever. Panmixia is likely maintained through long distance movements in response to spatiotemporal changes in availability of prey, and may be unique among canid species.

Response to historical climate change is another potential contributor to the absence of structure observed in arctic foxes. While temperate species like wolves are thought to have been isolated in multiple, widely spaced refugia during the Pleistocene, arctic foxes enjoyed an extensive range expansion. During the current interglacial, wolf populations have expanded and intermingled, while foxes have retreated, following arctic temperatures toward the pole and avoiding intra-guild competition with temperate-adapted red foxes (Dalén *et al.* 2004; Tannerfeldt *et al.* 2002). As the arctic climate continues to warm and sea ice becomes scarcer, arctic foxes may persist only in those isolated high arctic islands red foxes cannot reach. The fox populations surveyed here may then begin to resemble currently isolated populations (such as Iceland), with higher differentiation and lower genetic variation. A greater future threat to the persistence of the species than increased risk of inbreeding may be the inability of foxes to escape crashes in lemming population density; however, as long as sea birds nest on the arctic islands (Bety *et al.* 2001; Samelius & Alisauskas 2000), and carrion from polar bear kills is available, arctic foxes are likely to persist. The present study provides an important baseline for monitoring future, potentially climate-induced changes in the genetic variation and structure of this species.

Recommendations for Future Research

When this project began, one hope was that genetic analysis would detect directional gene flow, and perhaps identify factors influencing the orientation of arctic fox movements. Specifically, we wished to examine the impact of the lemming cycle on fox migration, with the goal of predicting or mediating the spread of fox-borne diseases like rabies and canine distemper. Unfortunately, because foxes in all geographic regions were genetically similar, such inferences could not be made. Furthermore, as we were unable to collect adequate samples in each year, or sufficient data on lemming population dynamics, we could not separate samples by year to check for changes over time or their relationships to shifting prey distributions. These questions cannot therefore be answered by the present results.

Regional studies may be able to shed more light on these issues. A more intensive sampling of live foxes, with both genetic samples and ear tags for physical tracking, could be informative. Alternatively, radio-collaring would provide more detailed information regarding movements of individual arctic foxes.

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Table 1 Genetic variation in arctic foxes

Region *	N [†]	H_E [§]	H_E SD	A^R (20) [¥]
Alaska	50	0.78	0.04	6.84
Mackenzie	20	0.76	0.03	6.49
Karrak	50	0.77	0.03	6.52
Kivalliq	304	0.79	0.03	6.80
Manitoba	46	0.78	0.03	6.50
NE Main	99	0.79	0.03	6.75
James Bay	16	0.77	0.05	6.67
Atlantic	25	0.76	0.04	6.57
Mainland		0.78		6.64
AK Islands	30	0.78	0.05	7.90
Banks	10	0.80	0.03	7.00
Victoria W	71	0.79	0.03	6.64
Victoria E	24	0.78	0.04	6.80
High Arctic	19	0.76	0.05	6.52
N. Baffin	68	0.78	0.03	6.69
S. Baffin	27	0.78	0.03	6.56
Svalbard	636	0.78	0.03	6.48
Island		0.78		6.80

* Averages for population type are given in bold. Regions are shown in Figure 1.

[†] number of individuals sampled in each region

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

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



Figure 1 Sampling range of arctic foxes, with treeline indicated by a black line. Fox samples are shown grouped into geographic regions. Svalbard foxes are considered coastal foxes, with all other populations belonging to the lemming ecotype.

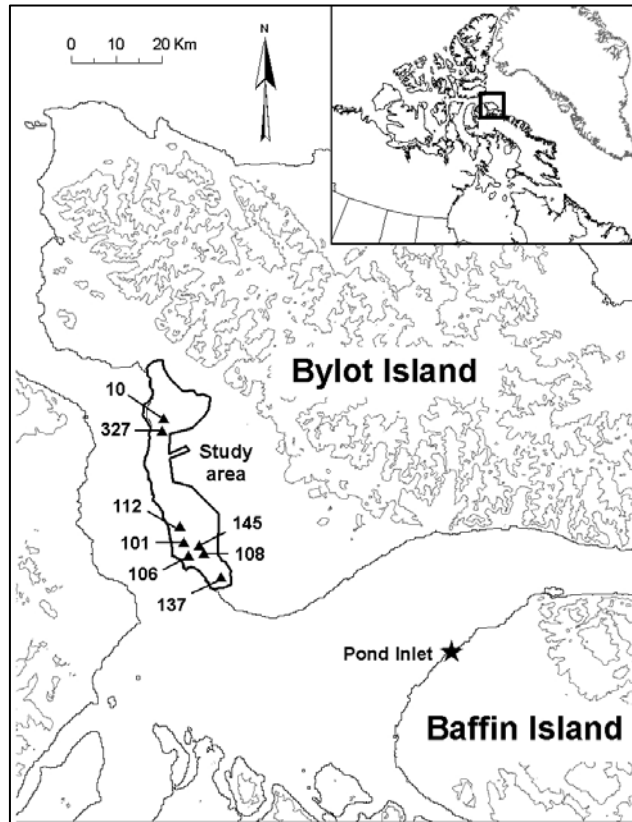


Figure 2 Study area on Bylot Island (73°0'N, 80°0'W), Nunavut. Triangles represent occupied fox dens (2004) and den numbers are given.

Figure 3 Summary of inclusion/exclusion analysis. Each den is represented by a horizontal box. Sampled individuals are labeled with the letters BY; unsampled individuals predicted by exclusion analysis are indicated by ?'s and coded with den numbers and letters. Horizontal lines within den boxes indicate presence of multiple same-sex parents at a den. For example, in Den 145, male BY04 was included as the father of BY06 and BY12, but putative father 145A would be required to explain the remaining offspring; two unsampled females are also inferred at this den. Mean and standard deviation of cub mass (g) at time of capture are given.

Den	Male	Female	Offspring	Mass
010	BY15	? 010A	All	1965 ± 80
101 - Polyandry - Multiple Paternity	? 101A ? 101B (cubs cannot be divided among these males)	BY07	BY10 BY16 BY19 BY28 BY44 BY22 BY43 BY14 BY49	950 ± 97
106	BY01	BY21	All	1468 ± 67
108	? 108A	? 108B	All	1346 ± 117
112	? 112A	? 112B	All	1236 ± 24
137	BY34	? 137A	BY03	2900
145 - Plural breeding	BY04 ? 145A	? 145B ? 145C	BY06 BY12 BY05 BY13 BY26	1324 ± 177
327	? 327A	? 327B	All	1900 ± 71

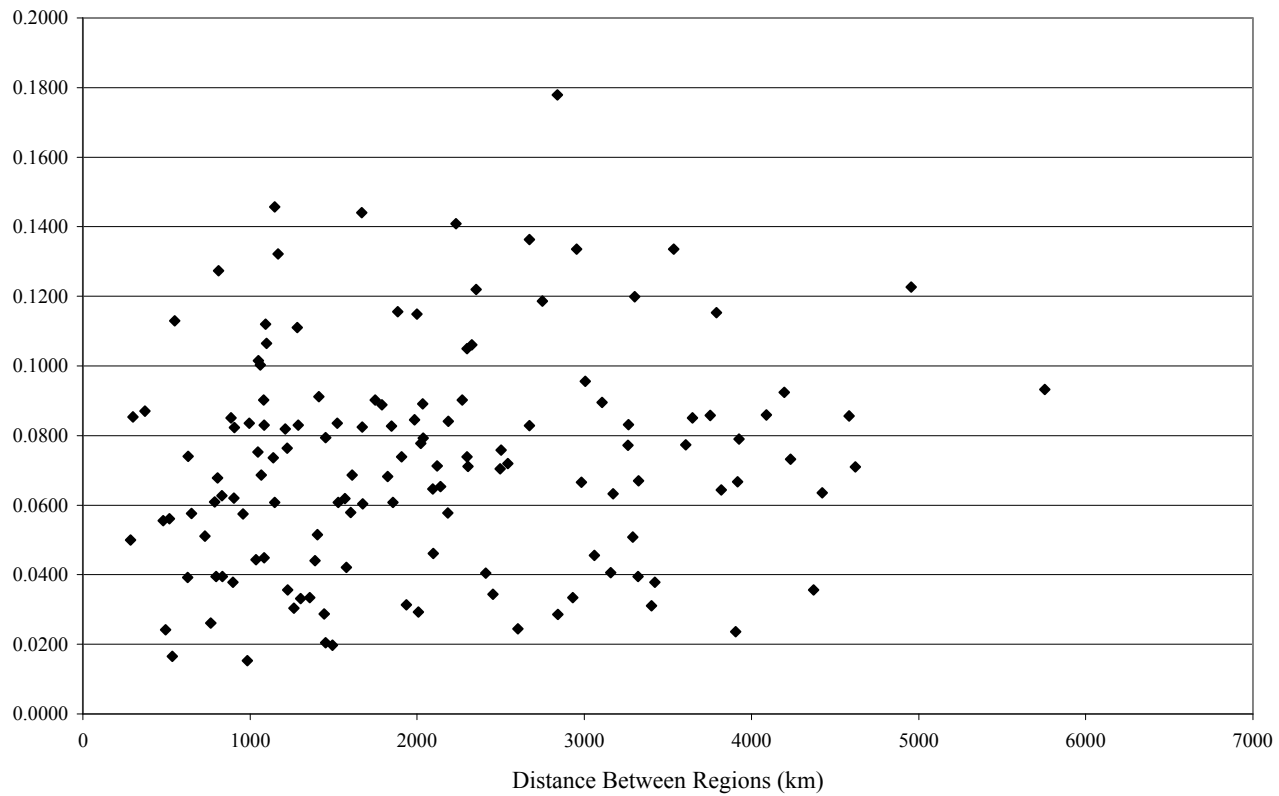


Figure 4 Nei's D_S between pairs of arctic fox regions, relative to the geographic distance between them. Mantel tests confirmed that isolation-by-distance does not occur in this species.

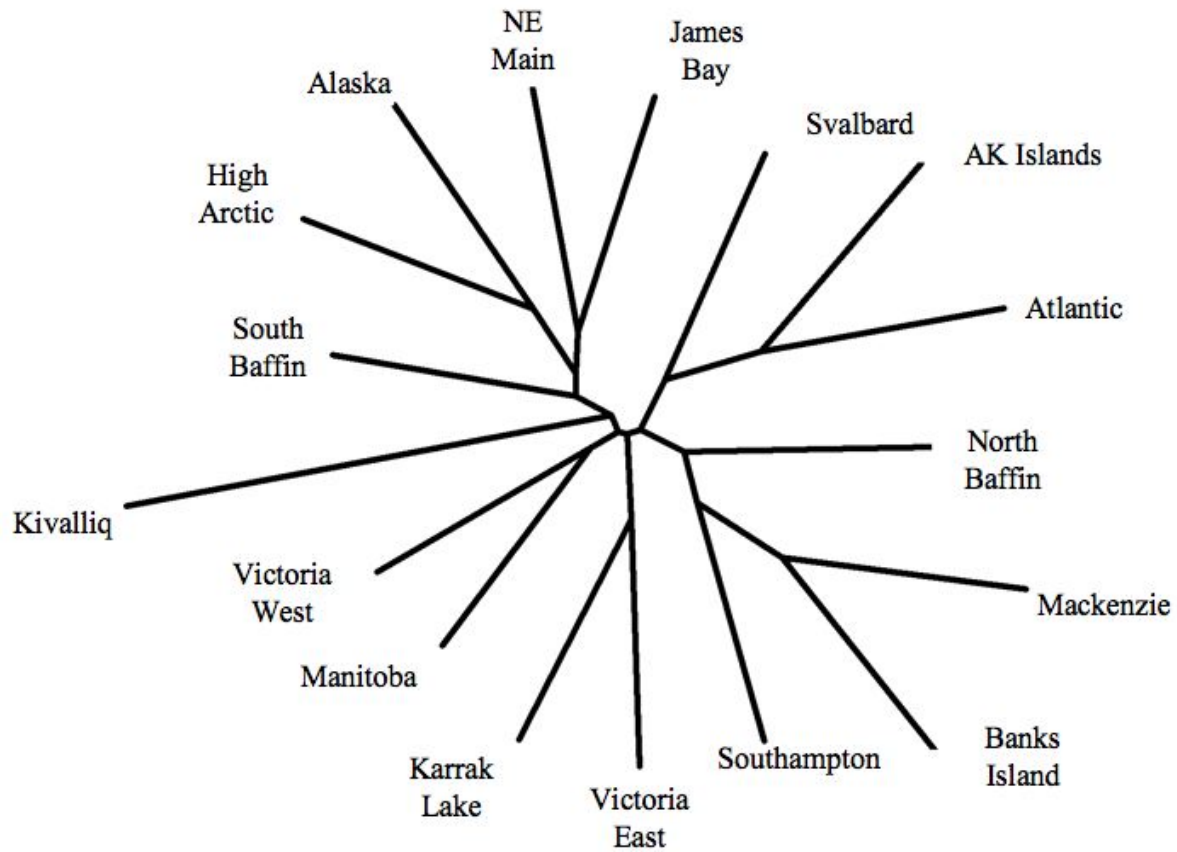


Figure 5 Majority rule consensus tree of arctic fox regions, based on Nei's D_S . Bootstrap support is not indicated, as no grouping occurred in more than 40% of trees.

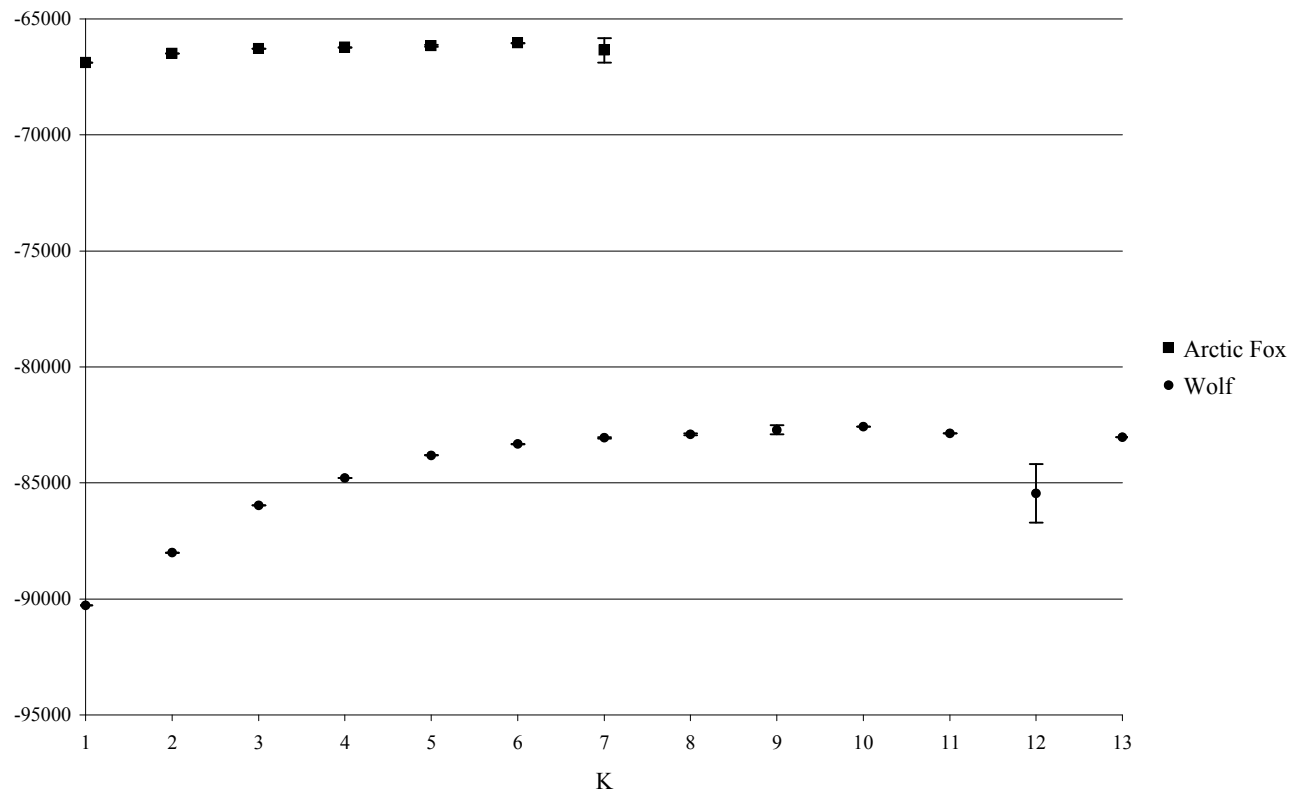


Figure 6 Average $\ln\text{Prob}(D)$ as number of clusters is increased during STRUCTURE analysis of arctic foxes. All values of K were similarly likely for arctic foxes, suggesting a single cluster was most appropriate. In contrast, probability of wolf data began to peak around $K=7$, suggesting existence of true genetic structuring (Carmichael 2006).

Appendix 1 Microsatellite DNA fingerprints of all arctic foxes sampled on Bylot Island. For each cub, presumed paternal alleles are given in bold and presumed maternal alleles in italics. Outlined alleles imply multiple female parents, shaded alleles imply multiple male parents.

Den	Age and Sex	Fox	5	9	15	140	147	173	250	671	733	745	758	771
?	Adult	BY08	113	151	157	142	177	126	127	207	250	273	-	102
	Male		131	157	157	144	177	128	133	211	250	277	-	102
010	Adult	BY15	125	151	153	146	171	122	127	203	250	271	239	100
	Male		133	157	157	148	179	124	129	209	256	277	245	106
010	Juvenile	BY25	125	151	157	148	179	122	123	209	256	271	241	106
	Male		131	155	161	148	179	124	127	209	262	277	245	106
010	Juvenile	BY35	125	151	153	148	179	122	123	203	256	277	239	96
	Male		131	157	159	148	183	122	129	209	262	277	241	106
010	Juvenile	BY42	131	151	157	144	171	122	123	207	250	277	239	96
	Male		133	157	159	146	179	122	129	209	256	277	241	106
010	Juvenile	BY45	125	151	157	146	179	122	127	209	250	271	239	106
	Male		133	151	161	148	179	126	129	209	256	275	245	106
010	Juvenile	BY47	125	151	157	146	171	122	123	203	250	271	245	100
	Male		131	157	161	148	179	124	127	209	262	275	245	106
010	Juvenile	BY48	131	151	157	148	179	124	123	209	250	271	245	96
	Male		133	155	159	148	179	126	127	209	262	277	245	106

Den	Age and Sex	Fox	5	9	15	140	147	173	250	671	733	745	758	771
101	Adult	BY07	121	151	157	152	177	124	123	211	246	279	228	100
	Female		129	155	157	154	179	126	133	213	260	283	241	108
101	Juvenile	BY10	121	155	157	148	179	122	125	207	260	275	224	100
	Female		127	155	159	152	183	126	133	213	270	279	228	100
101	Juvenile	BY16	121	151	157	148	177	122	133	209	246	279	228	108
	Female		129	155	157	152	179	126	133	211	250	283	234	108
101	Juvenile	BY19	121	155	157	146	177	122	125	209	252	275	224	100
	Female		127	155	159	152	185	124	133	213	260	283	228	100
101	Juvenile	BY22	127	153	157	146	179	126	123	207	246	275	241	100
	Female		129	155	159	154	183	126	123	211	252	279	241	108
101	Juvenile	BY43	121	151	157	148	177	122	123	207	246	275	241	100
	Female		127	155	159	154	183	124	123	213	270	279	241	100
101	Juvenile	BY14	127	151	157	146	177	122	123	209	260	273	241	100
	Male		129	155	159	152	185	124	123	211	270	283	241	100
101	Juvenile	BY28	121	155	157	146	179	122	123	207	246	275	228	108
	Male		127	155	159	154	183	126	133	211	252	279	241	108
101	Juvenile	BY44	121	155	157	146	177	122	123	209	252	273	228	100
	Male		127	155	159	154	183	126	133	211	260	283	241	108
101	Juvenile	BY49	127	155	157	146	179	122	123	207	246	275	241	108
	Male		129	155	159	152	183	126	123	211	252	283	241	108

Den	Age and Sex	Fox	5	9	15	140	147	173	250	671	733	745	758	771
106	Adult	BY21	121	151	157	148	177	122	133	203	250	267	234	104
	Female		131	155	165	148	179	122	133	209	256	277	241	108
106	Adult	BY01	113	155	157	146	177	124	125	209	250	273	222	108
	Male		131	155	159	148	183	124	135	213	252	281	234	112
106	Juvenile	BY23	131	155	157	146	177	122	133	203	250	267	222	108
	Female		131	155	165	148	177	124	135	209	252	281	234	112
106	Juvenile	BY32	131	155	157	148	177	122	133	203	250	273	222	104
	Female		131	155	165	148	183	124	135	209	256	277	241	108
106	Juvenile	BY20	113	151	157	146	177	122	133	209	250	277	222	104
	Male		121	155	165	148	177	124	135	213	252	281	234	112
106	Juvenile	BY40	121	151	157	148	177	122	133	209	250	273	222	104
	Male		131	155	165	148	179	124	135	209	252	277	241	112
108	Juvenile	BY02	121	155	157	146	177	122	125	203	250	267	222	104
	Female		129	155	165	148	183	122	131	211	250	277	245	104
108	Juvenile	BY11	123	151	157	148	179	122	125	203	250	277	222	102
	Female		131	155	159	148	183	122	133	209	256	279	241	104
108	Juvenile	BY29	123	151	157	148	183	122	125	203	250	277	222	104
	Female		131	155	159	148	183	122	133	209	250	279	241	104
108	Juvenile	BY31	123	155	159	146	179	122	133	203	250	277	234	104
	Female		129	155	165	148	183	122	133	211	250	279	241	108
108	Juvenile	BY33	121	151	157	146	179	122	131	203	250	267	234	104
	Female		131	155	157	148	183	122	133	211	250	277	245	108
108	Juvenile	BY09	121	155	157	146	177	122	133	203	250	277	234	104
	Male		131	155	159	148	183	122	133	211	256	279	241	108
108	Juvenile	BY37	123	151	157	148	177	122	125	203	250	277	222	102
	Male		131	155	165	148	183	122	133	211	250	279	241	104

Den	Age and Sex	Fox	5	9	15	140	147	173	250	671	733	745	758	771
112	Juvenile	BY18	119	151	157	136	177	126	125	203	250	271	239	96
	Female		133	151	159	148	179	128	127	213	250	277	241	100
112	Juvenile	BY27	127	151	157	136	171	126	127	207	250	271	241	104
	Female		133	155	157	148	177	128	133	207	252	277	241	108
112	Juvenile	BY30	119	151	157	136	171	126	127	207	250	267	241	96
	Female		133	151	159	148	177	128	133	213	252	271	241	108
112	Juvenile	BY38	127	151	157	136	171	126	127	203	250	271	241	100
	Female		133	155	159	148	177	126	133	207	250	277	241	104
112	Juvenile	BY39	127	151	157	136	171	126	127	207	250	267	241	104
	Female		133	155	157	148	177	126	133	213	250	271	241	108
112	Juvenile	BY46	127	151	157	136	177	126	125	207	250	271	239	96
	Female		133	151	157	148	179	128	127	207	250	277	241	100
112	Juvenile	BY24	127	151	157	136	177	126	125	203	250	267	239	96
	Male		133	155	159	148	179	128	127	213	252	271	241	108
137	Adult	BY34	131	151	157	142	177	126	125	207	250	267	222	98
	Male		131	151	159	148	183	128	133	211	258	273	241	104
137	Juvenile	BY03	117	151	157	142	177	122	123	207	250	267	222	98
	Male		131	155	157	144	183	128	133	207	258	277	230	106

Den	Age and Sex	Fox	5	9	15	140	147	173	250	671	733	745	758	771
145	Adult	BY04	121	151	159	142	177	126	125	205	246	267	228	100
	Male		121	155	165	144	187	126	127	207	250	277	241	102
145	Juvenile	BY05	131	151	157	148	167	128	125	207	250	271	237	98
	Female		133	157	161	152	171	130	133	209	254	279	243	104
145	Juvenile	BY06	121	151	153	140	179	126	123	207	246	277	-	100
	Female		129	151	165	142	187	130	127	207	250	279	-	102
145	Juvenile	BY13	131	155	153	146	171	128	123	203	250	271	237	104
	Female		133	157	157	152	179	128	133	209	254	279	237	104
145	Juvenile	BY12	121	155	159	140	167	124	125	207	250	277	228	100
	Male		129	155	161	144	177	126	125	207	250	279	243	100
145	Juvenile	BY26	131	151	153	140	179	124	123	207	246	271	224	104
	Male		133	157	157	146	183	128	125	209	250	279	243	104
327	Juvenile	BY36	113	151	155	148	175	122	123	203	250	271	239	102
	Female		133	151	157	148	179	128	127	207	250	275	245	104
327	Juvenile	BY41	119	151	153	146	175	122	123	203	250	271	241	102
	Male		133	155	157	146	183	128	127	207	256	275	245	104