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Population history and genetic structure of a circumpolar species: the arctic fox

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The circumpolar arctic fox *Alopex lagopus* thrives in cold climates and has a high migration rate involving long-distance movements. Thus, it differs from many temperate taxa that were subjected to cyclical restriction in glacial refugia during the Ice Ages. We investigated population history and genetic structure through mitochondrial control region variation in 191 arctic foxes from throughout the arctic. Several haplotypes had a Holarctic distribution and no phylogeographical structure was found. Furthermore, there was no difference in haplotype diversity between populations inhabiting previously glaciated and unglaciated regions. This suggests current gene flow among the studied populations, with the exception of those in Iceland, which is surrounded by year-round open water. Arctic foxes have often been separated into two ecotypes: 'lemming' and 'coastal'. An analysis of molecular variance suggested particularly high gene flow among populations of the 'lemming' ecotype. This could be explained by their higher migration rate and reduced fitness in migrants between ecotypes. A mismatch analysis indicated a sudden expansion in population size around 118 000 BP, which coincides with the last interglacial. We propose that glacial cycles affected the arctic fox in a way opposite to their effect on temperate species, with interglacials leading to short-term isolation in northern refugia. *Biological Journal of the Linnean Society*, 2005, **84**, 79–89.

ADDITIONAL KEYWORDS: *Alopex lagopus* – bottleneck – ecology – gene flow – mitochondrial DNA – phylogeography.

INTRODUCTION

The Quaternary cold periods are considered to have had a strong influence on the geographical distribution and genetic variation of organisms worldwide. In continental Eurasia and North America, repeated glaciations caused multiple periods of isolation in southern refugia and resulted in increased intraspecific genetic divergence (Taberlet *et al*., 1998; Hewitt, 2001). Several mammal species display phylogeographical patterns predicted by the expansion/contraction model with, for example, a high divergence between phylogroups from different refugia and genetic signatures of late Pleistocene expansions in population size (Hewitt, 1996). However, in highly mobile species gene flow during interglacials could lead to an admixture of genotypes from different refugia (Cruzan & Templeton, 2000). Furthermore, the impact of glaciation would have been different in species that were well adapted to cold climates compared

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with temperate species (Hewitt, 2001). Arctic species will not have been in southern temperate refugia and should thus not display the expansions/contractions associated with them. Arctic species may, however, have gone through range changes and they could have had different glacial and/or interglacial refugia.

The arctic fox *Alopex lagopus* is well adapted to arctic conditions (Fuglei & Øritsland, 1999) and in winter fur tolerates ambient temperatures below –40 °C without having to increase its metabolic rate significantly to keep a constant body temperature (Scholander *et al*., 1950). Its diet is composed of a variety of vertebrates (Audet, Robbins & Larivière, 2002), but two ecotypes are generally recognized: 'lemming foxes' that feed mainly on lemmings (*Lemmus* spp. and *Dicrostonyx* spp.) and 'coastal foxes' that feed mainly on eggs, birds and carrion from the marine system (Braestrup, 1941). Lemming foxes are found in continental Eurasia, North America, the Canadian archipelago and east Greenland, whereas coastal foxes are found in Iceland, Svalbard and south, west and northwest Greenland (Tannerfeldt & Angerbjörn, 1998). The difference between a highly fluctuating food source (lemming) and one that is more stable (coastal) has led to a number of different life-history strategies, where lemming foxes undergo an enormous reproductive output during lemming peaks compared with coastal foxes (Tannerfeldt & Angerbjörn, 1998). Furthermore, there are significant differences in migration patterns between the two ecotypes, with lemming foxes migrating further than coastal foxes (Angerbjörn, Hersteinsson & Tannerfeldt, 2004a).

Several studies suggest a high migration rate in *A. lagopus*, and that they are capable of long (> 1000 km) movements over the polar pack ice (e.g. Eberhardt & Hansson, 1978). Several subspecies of *A. lagopus* have been proposed, for example *A. l. fuliginosus* (Iceland), *A. l. groenlandicus* (Greenland), *A. l. spitzbergenensis* (Svalbard) and *A. l. ungava* (Canada) (Audet *et al*., 2002). Frafjord (1993) found some latitudinal differences in morphology between populations on a circumpolar scale, but pointed out that more information was needed on the genetic differentiation among *A. lagopus* populations.

In this study, we analysed mitochondrial DNA (mtDNA) variation in *A. lagopus* on a circumpolar scale to investigate the genetic structure and population history of the species. Concerning the population history, we did not expect to find the patterns of a rapid postglacial increase in population size which have been observed in more temperate species, since the wide distribution of *A. lagopus* during the last Ice Age (Kurtén, 1968; Kurtén & Anderson, 1980) suggests that *A. lagopus* were at least as abundant during this period as they are today. Instead, it is more probable that the warm interglacials have had a negative effect on the abundance of *A. lagopus*. We did, however, expect to see phylogeographical patterns from a postglacial range expansion in *A. lagopus* since they must have colonized formerly glaciated areas at the end of the last Ice Age. Past fragmentation events may be inferred from genetic distance among haplotypes, and their spatial distribution provides information on current gene flow among populations (Avise *et al*., 1987). Based on the high migration rate and long-distance movements observed in *A. lagopus*, we hypothesized that there is gene flow between most sampled populations that are connected via land or the polar sea ice (i.e. all populations except that in Iceland). We therefore predicted little phylogeographical structure, low Φ_{ST} values between all populations except that in Iceland and that populations in previously glaciated regions should have a haplotype diversity similar to those in continuously unglaciated regions. We also examined the long-term effective female population size and compared this with current estimates of the worldwide population size.

MATERIAL AND METHODS

DNA samples were collected from 191 *A. lagopus* from 13 regions throughout the arctic. The regions sampled were Svalbard (SVA), Iceland (ICE), east Greenland (EG), south Greenland (SG), west Greenland (WG), north-west Greenland (NWG), Churchill Manitoba (CHU), Cambridge Bay (CMB), Bathurst Island (BAT), Banks Island (BAN), Alaska (ALA), Siberia (SIB) and Fennoscandia (FEN) (Fig. 1). For statistical analyses concerned with geographical distances, we divided Siberia into east and west Siberia (two samples from Taimyr, which is halfway between east and west Siberia, were excluded from these analyses along with one sample for which it was not clear whether it was from east or west Siberia). Cambridge Bay, Banks Island and Bathurst Island were in some instances pooled into Canadian Archipelago (CA) in order to increase statistical power (there was no significant genetic differentiation among the regions within each pooling). Thirty-two of the samples were from the previous study by Dalén *et al*. (2002). The samples from Greenland were those previously used for microsatellite analysis by Meinke, Kapel & Arctander (2001). Tissue samples from Alaska were obtained from the University of Alaska Museum (UAM AF371–AF377, AF379, AF4012–AF4014, AF4039, AF21094).

Whole genomic DNA was extracted using Qiagen's Dneasy tissue kit (Qiagen). Faecal DNA ($N = 4$) was extracted from *c.* 200 mg dried faecal matter using the Qiaamp DNA stool mini kit (Qiagen). An approximately 320-bp fragment of the mitochondrial control region was amplified as previously described in Dalén *et al*. (2002). Sequencing of both the heavy and light

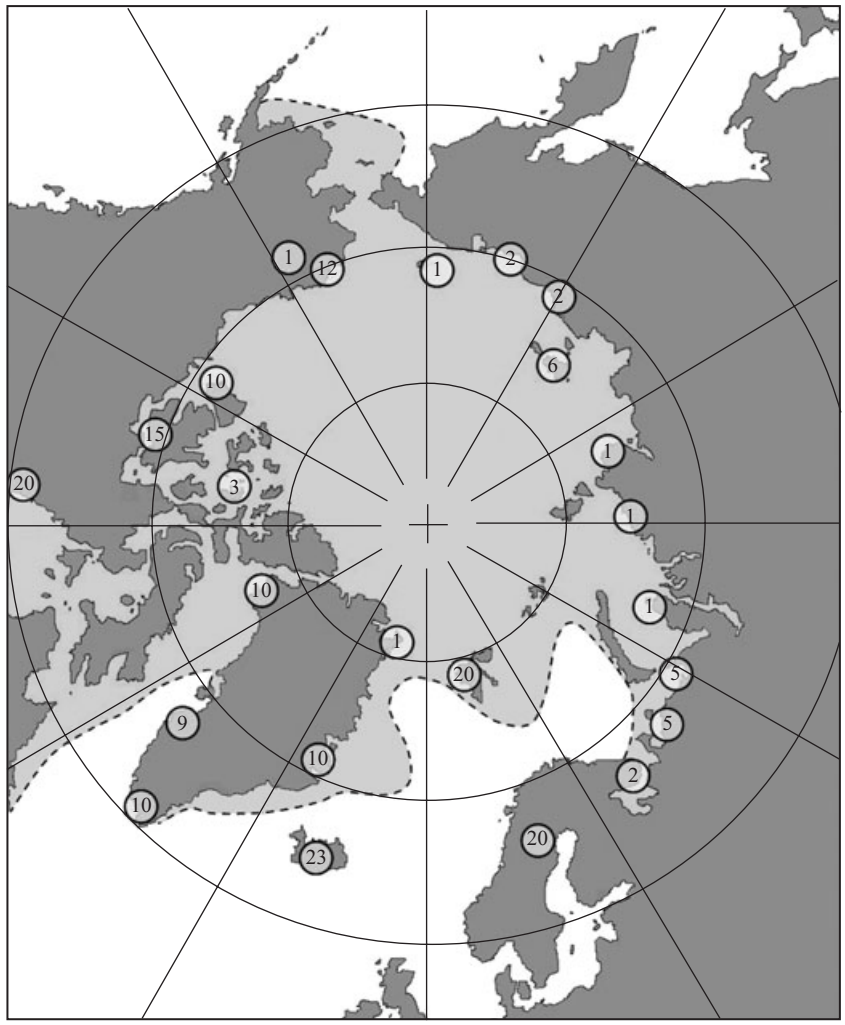

Figure 1. Sample sites and number of samples (indicated within each circle) from each location. Populations clockwise from Greenwich Mean Time are: Iceland (ICE), east Greenland (EG), south Greenland (SG), west Greenland (WG), northwest Greenland (NWG), Churchill (CHU), Bathurst Island (BAT), Cambridge Bay (CMB), Banks Island (BAN), Alaska (ALA), Siberia (SIB), Fennoscandia (FEN) and Svalbard (SVA). The light grey area inside the dashed line illustrates the extent of polar sea ice in January (data from EOSDIS NSIDC Distributed Active Archive Center, http://nsidc.org/data/index.htm).

strands was carried out using a CEQ 2000 automated sequencer (Beckman Coulter) following the manufacturer's instructions.

Sequences were aligned in BioEdit version 5.0.9 (Hall, 1999), checked by eye and assigned to haplotypes, which were named after their origin (see Fig. 2). We used the program ModelTest (Posada & Crandall, 1998) to evaluate which model of nucleotide substitution gave the best fit to the data. Sequence variability and population pairwise comparisons were computed with the software ARLEQUIN version 2.0 (Schneider, Roessli & Excoffier, 2000). Of the nucleotide substitution models supported in Arlequin, the Tamura & Nei (1993) model gave the lowest log likelihood score (with a gamma parameter of 0.7), and this was subsequently used in further analyses. Sequence variability was estimated as haplotype diversity (H), nucleotide diversity (π; Nei, 1987) and the mean number of pairwise differences (Tajima, 1993). Historic demographic expansions of population size were investigated through a mismatch analysis where the distribution of pairwise differences was compared with the expected distribution under a model of sudden expansion (Rogers & Harpending, 1992; Schneider & Excoffier, 1999). The estimated time of sudden expansion can be calculated from the equation $\tau = 2\mu t$ (Rogers, 1995), where μ is the mutation rate for the sequence and t is the time since expansion (confidence intervals for τ were obtained from 2000 bootstrap replicates). We also performed Fu's test of selective neutrality with 10 000

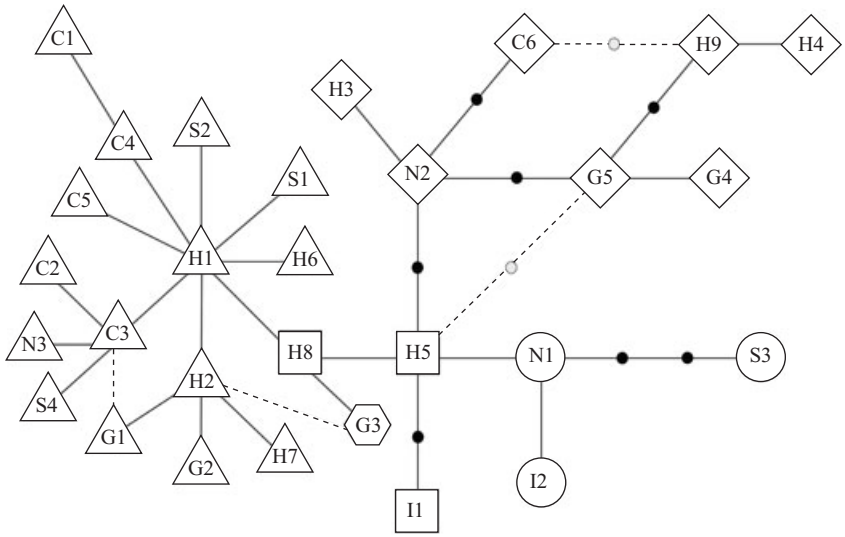

Figure 2. The minimum spanning network. Haplotypes are named after geographical origin: Holarctic (H), Nearctic (N), Canada (C), Siberia (S), Greenland (G) and Iceland (I). Each branch represents one mutational step; missing haplotypes are represented by a dot. Equally parsimonious branches are shown with dashed lines. The shape of the haplotypes illustrates the second nesting level in the nested clade analysis. Haplotype G3 was not nested until the third nesting level.

bootstrap replicates, where a significant negative Fs value (at $P < 0.02$) would indicate an expansion in population size (Fu, 1997). The long-term effective female population size (N_f) was approximated using the equation: $N_f = 10^6(p/s)/g$ where p is the nucleotide diversity, s is the rate of sequence divergence and g is the generation time in years (Wilson *et al*., 1985). For the above calculations, we assumed a rate of sequence divergence of 14.2% Myr^{-1} ($\mu = 2.073 \times 10^{-5}$), a rate that was recently estimated for wolves and coyotes (Savolainen *et al*., 2002), and a generation time of 2 years.

Using a function implemented in ARLEQUIN, we constructed a minimum spanning network based on pairwise differences among haplotypes (including indels). This network was subsequently used in a nested clade analysis (NCA) in an attempt to discriminate between phylogeographical patterns caused by the current restricted gene flow and patterns caused by historical events (Templeton, 1998). Nesting of the minimum spanning network followed the basic rules by Templeton, Boerwinkle & Sing (1987). Nesting of ambiguities and intermediate haplotypes was carried out according to Templeton & Sing (1993) and Crandall (1996). Geographical distances between regions were obtained using the distance calculator at http://www.wcrl.ars.usda.gov/cec/java/lat-long.htm (2003-01-28, Byers, 1997). The null hypothesis of no geographical associations of clades was tested and computation of clade distances and nested clade distances were carried out using the program GeoDis (Posada, Crandall & Templeton, 2000) with 10 000 permutations. Interpretation of the results obtained in the NCA was obtained using the inference key in GeoDis.

We employed an exact non-parametric procedure (1 000 000 steps in the Markov chain and 50 000 dememorization steps) to test for differentiation between pairs of populations (Raymond & Rousset, 1995). In order to investigate geographical structuring of genetic variation, we used an analysis of molecular variance (AMOVA) with 10 000 permutations (Excoffier, Smouse & Quattro, 1992). We performed six AMOVAs with different hierarchical groupings: [Palaearctic vs. Nearctic], [Palaearctic vs. Nearctic vs. Atlantic islands], [mainland vs. islands], [above 68°N vs. below 68°N], [lemming fox populations vs. coastal fox populations] and [lemming fox populations vs. each coastal fox population]. We then assumed that the most probable geographical structure was represented by the groupings that maximized values of Φ_{CT} (Vila *et al*., 1999), which is a measure of the proportion of genetic variation among groupings of populations. Population pairwise Φ_{ST} values (a measure analogous to F_{ST}) were generated and tested for significance through 10 000 permutations (Schneider *et al*., 2000). The resulting matrix of Φ_{ST} values between the different populations was visualized with a UPGMA tree constructed in PAUP (Swofford, 1998). To investigate the effect of postglacial gene flow, we compared H for populations in formerly glaciated areas with those inhabiting regions not glaciated during the last Ice Age. This was done with a one-way ANOVA, as implemented in the software STATISTICA (StatSoft Inc., 1999). For this analysis we

excluded samples from Bathurst Island due to low sample size. A Mantel test with 10 000 replicates (Smouse, Long & Sokal, 1986) was used to test if there was a correlation between genetic and geographical distances among populations.

RESULTS

We sequenced 292 bp of the control region for each of the 191 individuals. The sequenced region contained 21 variable sites, which defined 29 different haplotypes (Table 1). All the observed variation was in the form of single base-pair substitutions or indels, except for haplotype S3, in which a 16-bp deletion was observed (since this region was present in all other haplotypes, as well as in kit and swift foxes (*Vulpes macrotis* and *V. velox*), it was presumably a deletion). This deletion was confirmed by a second amplification and sequence analysis using two additional primers, H1F (5′-GCCATCAACTCCCAAAGCT-3′) and P1R (5′-GAGGCATGGTGATAAATCC-3′). The whole deletion was treated with the same weight as substitutions and indels in further statistical analyses. The mean number of pairwise differences between all samples was 2.65 (SD, 1.42), and π in the total sample was 0.009 (SD, 0.005). Fu's test of selective neutrality gave a significantly large negative Fs value (Fs = –8.15, $P = 0.014$).

The distribution of pairwise differences between all individuals did not deviate from the expected distribution under a model of sudden expansion ($P = 0.45$). The extent of divergence was measured as $\tau = 4.889$ (95% CI, 1.674–9.298), giving an estimated time of expansion at 118 000 BP (95% CI, 40 000–224 000).

Table 1. Geographical distribution and GenBank accession numbers for *Alopex lagopus* haplotypes

		Geographical region												
Haplotype	GenBank #	FEN	SIB	ICE	BAT	CHU	CMB	WG	EG	NWG	SG	ALA	SVA	BAN
H1	AY321121	8	12			9	6	1	3		1	3	7	3
H2	AY321125		1	2	1	4			5	7		2	4	2
H3	AY321120	9	1						1					
H4	AY321124		1				1					1		
H5	AY321127	1	1	1								2		
H6	AY321128				2								3	
H7	AY321129	4	4								1			
H8	AY321132			2		1	2							1
H9	AY321134							6				1	6	
N1	AY321136					1		1				2		
N2	AY321138						2		1			2		
N3	AY321140										3			1
S1	AY321123		1											
S2	AY321133		1											
S3	AY321122		2											
S4	AY321126		1											
I1	AY321131			4										
I2	AY321130			14										
G1	AY321135							1						
G2	AY321137								1					
G3	AY321139									3				
G4	AY321141										2			
G5	AY321142										3			
C1	AY321143					3	1							
C2	AY321144					1								
C3	AY321145					1	1							2
C4	AY321146						1							
C5	AY321147						1							
C6	AY321148													1
Total		22	25	23	3	20	15	9	11	10	10	13	20	10
H		0.70	0.76	0.61	–	0.76	0.84	0.58	0.76	0.47	0.84	0.91	0.76	0.89

The number of samples and haplotype diversities (H) are indicated for each geographical region (abbreviations as in Fig. 1).

The observed nucleotide diversity suggested a long-term female effective population size of 32 000 (± 17 000) individuals in the sampling area (i.e. the world population).

The minimum spanning network of the different haplotypes revealed no major branching events (Fig. 2). Two haplotypes, H1 and H2, were observed in 42% of all individuals. These two haplotypes, together with several less common haplotypes, had a widespread geographical distribution. The remaining haplotypes were generally site-specific and occurred in low frequencies (Table 1). Haplotypes specific to certain geographical regions did not form monophyletic groups but instead appeared to be randomly distributed in the network (Fig. 2). The NCA did, however, indicate a significant geographical association for a majority of the nested clades (data not shown). We inferred that the overall phylogeographical pattern in the NCA was caused by recurrent but restricted gene flow. This pattern was dominant at the second and third (total network) nesting levels. At the first nesting level the pattern was more complicated, with indications of past fragmentations, range expansions and restricted gene flow (see Appendix for a complete listing of NCA results).

There was no significant correlation between genetic and geographical distances among populations (Mantel test: $r = -0.19$, $P = 0.90$). The exact test of population differentiation indicated that most populations were differentiated although there were exceptions, especially within North America (Table 2). The most probable geographical grouping of populations in the AMOVA was when lemming fox populations were grouped against each of the coastal fox populations ($P < 0.002$), where 25.4% of the variation was observed among groups (Φ_{CT} values for other groupings were all below 3%). The total proportion of variation among all populations (Φ_{ST}) was 30%, and the proportion of variation among populations within groups (Φ_{SC}) was 6.8%. Among the populations, the Φ_{ST} values were generally low with the exception of Iceland and to some extent west Greenland (Table 2). The H in the different populations varied between 0.47 and 0.91 (Table 1). There was no significant difference in H between previously glaciated and non-glaciated regions (one way ANOVA, $N = 13$, $F = 2.44$, $P = 0.15$), where Banks Island, Alaska and East Siberia were considered as having been unglaciated during the latest Ice Age.

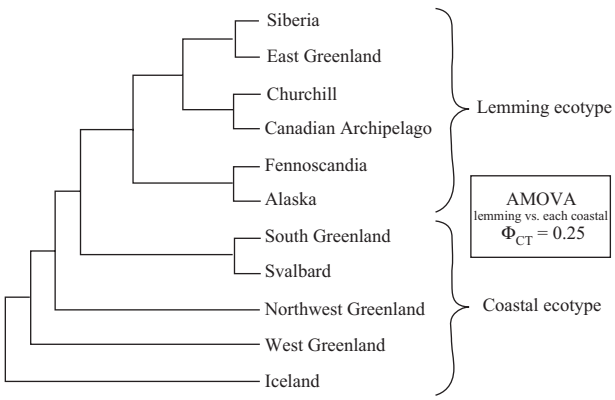

Figure 3. Population tree based on Φ_{ST} values, illustrating the most probable geographical structure in the analysis of molecular variance (AMOVA). The results suggest that there is high gene flow between populations belonging to the lemming ecotype, whereas gene flow seems to be lower between populations of the coastal ecotype as well as between the two ecotypes.

Table 2. Population differentiation test (*P*-values; above diagonal) and cross-wise Φ_{ST} values for each population (below diagonal)

	FEN	SIB	ICE	CHU	CA	WG	EG	NWG	SG	ALA	SVA
FEN		0.030	<0.001	<0.001	<0.001	<0.001	0.001	<0.001	<0.001	<0.001	<0.001
SIB	0.116		<0.001	0.021	0.010	<0.001	0.029	<0.001	0.002	0.029	0.001
ICE	0.280	0.365		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
CHU	0.195	0.025†	0.467		0.557	<0.001	0.235	0.001	<0.001	0.079	0.010
CA	0.080	0.007†	0.357	0.008†		0.001	0.343	0.002	0.003	0.193	0.024
WG	0.390	0.417	0.537	0.555	0.419		0.001	<0.001	0.001	0.055	0.046
EG	0.094†	0.004†	0.410	0.084†	0.028†	0.399		0.053	0.002	0.349	0.030
NWG	0.361	0.197	0.564	0.397	0.286	0.505	0.144		<0.001	0.004	<0.001
SG	0.135	0.183	0.407	0.282	0.130	0.256	0.219	0.466		0.004	<0.001
ALA	0.043†	0.074†	0.204	0.179	0.052†	0.210	0.076†	0.272	0.063†		0.026
SVA	0.187	0.110	0.439	0.201	0.101	0.155†	0.088†	0.216	0.090†	0.063†	

†Φ_{ST} values not significantly different from zero. Population abbreviations as in Fig. 1.

DISCUSSION

Population history

The earliest historic event that can be inferred from the mitochondrial DNA variation is that of a sudden expansion in population size. This was presumably preceded by a population bottleneck. The occurrence of a historic bottleneck and subsequent expansion is further supported by the significantly negative Fs value (Fu, 1997) and by the low nucleotide diversity (0.009) in *A. lagopus*. The nucleotide diversity in the control region was considerably lower than that in other mammals, for example wolves (*Canis lupus*; $\pi = 0.026$; Vila *et al*., 1999), coyotes (*Canis latrans*; $\pi = 0.046$; Vila *et al*., 1999) and moose (*Alces alces*; $\pi = 0.025$; Hundertmark *et al*., 2002). The time of the expansion, as suggested by the mismatch analysis, was estimated at approximately 118 000 BP. Bearing in mind the large confidence interval (40 000–224 000 BP), this estimate coincides with the last interglacial which ended in 117 000 BP (Kukla *et al*., 2002). A similar expansion in connection with the last interglacial was recently observed in a study on reindeer (Flagstad & Røed, 2003). Considering that the last interglacial was approximately 5 °C warmer than temperatures are at present (Funder *et al*., 1998), it is probable that *A. lagopus* (along with other arctic organisms, such as reindeer) was adversely affected during this period. This may, for example, have been through indirect effects, such as a northern expansion of the red fox *Vulpes vulpes*, as it has been proposed that the southern distribution of *A. lagopus* is limited by *V. vulpes* (Hersteinsson & Macdonald, 1992). The presence of forest remains from previous interglacials in northern Siberia (Sher, 1991) suggests a suitable habitat for *V. vulpes*. *A. lagopus* may therefore have been extinct in continental Eurasia and North America during the last interglacial, persisting only in high-latitude islands, and then expanding south as temperatures started to fall some 117 000 years ago. This hypothesis predicts a high current genetic diversity in high-latitude islands that were not glaciated during the ensuing Ice Age, since these are the only areas that would have been continuously inhabited by *A. lagopus* for at least 130 000 years (the low sample sizes from these islands in our study did not allow us to test this hypothesis). It can also be expected that any sequences recovered from fossil remains less than 100 000 years old would fall within the scope of the mismatch distribution.

During the Ice Age that followed, *A. lagopus* was widely distributed in Eurasia and Beringia (Kurtén, 1968; Kurtén & Anderson, 1980). The structure of the minimum spanning network, without distinct phylogroups, indicates a lack of significant geographical barriers during this period (Fig. 2). This is further supported by the lack of evidence of past fragmentation at the higher nesting levels in the NCA (Appendix). At the end of the Ice Age it is probable that there was a range expansion into formerly glaciated areas such as Greenland, Iceland, Svalbard and Fennoscandia. Although the second nesting level in the NCA showed some support for a range expansion, this was not as strong as might have been expected. There could be several explanations for this; for example, that these areas were colonized by *A. lagopus* from local refugia (e.g. Frafjord & Hufthammer, 1994), as has been suggested for other arctic species (Fedorov & Stenseth, 2001, 2002). A high postglacial gene flow could also explain the weak support in the NCA as it may have erased phylogeographical patterns created by an initial range expansion. At the lowest nesting level, the NCA gave a rather ambiguous picture, possibly due to small sample sizes in the nested clades. There may also be problems with the interpretation of NCA results using the inference key (see Knowles & Maddison, 2002).

The female long-term effective population size was estimated at 32 000 individuals. Assuming a 1 : 1 sex ratio and that 40% of all female adult *A. lagopus* breed during their lifetime (Angerbjörn *et al.*, 2004a), this would correspond to an approximate world population size of *c*. 160 000 (± 85 000) adults. This is lower than the census population size of 330 000–930 000 adults (Angerbjörn, Hersteinsson & Tannerfeldt, 2004b), but is within the margins of what can be expected for a species with a large variance in reproductive success (Creel, 1998; Bensch & Hasselquist, 1999). Thus, we did not find any indication of recent changes in the world-wide population size of *A. lagopus* as have been reported for other canids (e.g. Vila *et al*., 1999).

Current genetic structure

Although most populations seemed to be significantly differentiated from each other, several analyses suggested that currently there is restricted gene flow between the majority of the populations. There was no phylogeographical structure in the minimum spanning network, where presumed ancestral haplotypes were frequent and widespread and newly arisen haplotypes have not yet spread throughout the range of the species. Therefore, *A. lagopus* appears to be a species with intermediate gene flow and no long-term zoogeographical barriers (category V in Avise *et al*., 1987). A similar lack of phylogeographical structure has previously been observed in fish (e.g. Rocha-Olivares, Garber & Stuck, 2000), and to some extent wolves (*Canis lupus*; Vila *et al*., 1999). The predominantly low Φ_{ST} values among populations on such a large geographical scale, compared with Φ_{ST} values of 0.75 in kit foxes, 0.50 in swift foxes (Mercure *et al*., 1993), 0.46 in Mediterranean *V. vulpes* (Frati *et al*., 1998) and 0.69 in wolves (Vila *et al*., 1999), also indicate current gene flow. Yet low Φ_{ST} values and poor phylogeo-

graphical structuring of haplotypes could also be the result of a postglacial range expansion. However, the high Φ_{ST} values between Iceland and the other populations suggest that Iceland is particularly isolated, as would be expected under the hypothesis that there is current gene flow between all populations except that in Iceland. The observation of equal haplotype diversities in populations inhabiting formerly glaciated and unglaciated areas further supports the gene flow hypothesis, although it should be noted that colonization of a formerly glaciated region from several different refugia can also result in high haplotype diversity (Hewitt, 1996). Taken together, these results suggest that there is gene flow among most populations, which is in agreement with previous studies reporting that *A. lagopus* travels long distances (e.g. Eberhardt & Hanson, 1978) and illustrates the importance of the polar sea ice for terrestrial arctic mammals.

We could not, however, find a correlation between genetic and geographical distances, implying that there is no genetic isolation by distance between the populations. There could be a number of explanations for this, such as ice movements, geographical barriers or *A. lagopus* following polar bears (however, we could find no relationship between *A. lagopus* and polar bear genetic distances; Paetkau *et al*., 1999). A more likely explanation can be found in the relationship between the different populations and the geographical structuring of the genetic variation as suggested by the AMOVA. *A. lagopus* from east Greenland, Siberia, Churchill, the Canadian Archipelago, Fennoscandia and Alaska formed a group of populations that were genetically more closely related to each other than to any of the other populations. This former group consisted of populations with lemming foxes, whereas the latter populations were all of the coastal fox ecotype. As indicated by the AMOVA, only 6.8% of the genetic variation could be explained by differences among lemming fox populations whereas 25.4% of the variation could be explained by differences between the lemming fox group and each of the coastal fox populations. It therefore seems that gene flow is substantially higher between populations of lemming foxes than it is between the two ecotypes or between coastal fox populations. The ecological causes for such a pattern could be that lemming foxes have a higher frequency of long-distance migrations (Angerbjörn *et al*., 2004a), and that migrants from one type of habitat to the other have a lower fitness compared with resident *A. lagopus*. That lemming foxes should migrate longer and more often than do coastal foxes actually makes evolutionary sense owing to the large-scale spatial synchrony of lemming populations (Krebs *et al*., 2002), which may force foxes feeding on lemmings to migrate longer and more frequently than do foxes in coastal areas where food resources are more stable. The hypothesis that immigrant foxes from a different habitat should have lower fitness compared with residents was originally proposed by Vibe (1967) as an explanation for the stable difference in fur colour frequency between *A. lagopus* in north-west Greenland and Canada, despite an influx of white foxes after lemming peaks in Canada. It has been suggested that different reaction norms in litter size have evolved in fluctuating and stable *A. lagopus* populations (Tannerfeldt & Angerbjörn, 1998). The observed pattern might thus be explained if food resource predictability affects selection pressure on reproductive output, giving lemming foxes a disadvantage under stable coastal conditions, or by the higher competition for territories in coastal fox populations (Angerbjörn *et al*., 2004a).

These results agree well with what is known on the biology of *A. lagopus*, in particular the extraordinary migration patterns facilitated by the polar sea ice, and the difference in life-history strategies between lemming and coastal *A. lagopus*. The generally high gene flow suggested by this study, in particular among lemming fox populations, should also be taken into account with respect to the spread of arctic disease, such as rabies.

Management implications

Our samples covered more or less the total distribution of *A. lagopus* except for the populations on the isolated Bering and Mednyi Islands. We found no support for the existence of any subspecies within the sampled area. Furthermore, based on the distribution of mtDNA haplotypes, we were unable to identify any Evolutionary Significant Units. Iceland may, however, be considered a Management Unit based on its isolation, as indicated by the high Φ_{ST} values. However, Management Units should not be based solely on genetic data. Fennoscandia, for example, is regarded as a Management Unit based on ecological data. In a previous study by Dalén *et al*. (2002) it was suggested that there is gene flow from Siberia into Fennoscandia, since the haplotype diversity and number of haplotypes in Fennoscandia was higher than expected for a small isolated population. Two observations in this study support that conclusion. First, the Φ_{ST} values between Fennoscandia and Siberia (0.12) was not particularly high compared with the difference between other populations. Second, the two haplotypes that had previously been observed only in Fennoscandia were in this study also found in western Siberia, which is to be expected if the haplotypes in Fennoscandia are the result of current gene flow from Siberia.

On a global level, the results of this study suggest that the high temperatures during the last interglacial may have had a severe impact on *A. lagopus* as a species. Given the increases in temperature predicted from models on global warming and the negative effect

of competition with the temperate *V. vulpes* (Chirkova, 1968; Tannerfeldt, Elmhagen & Angerbjörn, 2002), the range of *A. lagopus* will contract to the north. The local conservation problems for *A. lagopus* in Fennoscandia today may thus, in the near future, become a global issue.

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APPENDIX

Results of the nested clade analysis of geographical distances for control region haplotypes in *Alopex lagopus*

Haplotypes			1-Step Clades			2-Step Clades		
No.	D_c	D_n	No.	D_c	D_n	No.	D_c	D_n
C1	540$^{S.}$	620$^{S.}$						
C4	0	657						
I-T	–540$^{L.}$	37						
1-2-3-4No: RGF								
H1	2828$^{L.}$	2668						
C5	0	2702						
H6	667$^{S.}$	2130						
S1	0	4381	1-1	629$^{S.}$	2540			
S2	0	3060	1-2	2579$^{L.}$	2504$^{L.}$			
I-T	2411$^{L.}$	69	1-3	2041	2305			
1-2-3-4No: RGF			1-4	0	620			
C2	0	1815	1-5	1843$^{S.}$	1927$^{S.}$			
C3	620$^{S.}$	2223	I-T	846$^{L.}$	474$^{L.}$			
N3	1434	1357	1-2-3-4No: RGF					
S4	0	4544$^{L.}$						
I-T	–336	258						
1-2-11-12No: CRE								
H2	1451$^{S.}$	1639$^{S.}$						
G2	0	886				2-1	2260	2287$^{L.}$
H7	1311	2794$^{L.}$				2-2	2521	2583
I-T	272	–964$^{S.}$				2-3	1678	1914
1-2-11-12-13Yes: LDC						2-4	1838	1801$^{S.}$
I2	0$^{S.}$	1409$^{S.}$	1-7	1974	3990$^{L.}$	1-6	0$^{S.}$	1311
N1	1891	2246	1-8	1694	1223$^{S.}$	I-T	460	463
I-T	1891$^{L.}$	838	I-T	–279	–2767$^{S.}$	1-2-3-5-6-7-8Yes: RGF & LDD		
1-2-3-4-9No: PF			1-2-11-17No: Inconclusive					
H8	1408$^{S.}$	1946$^{S.}$	1-9	2412	2609			
H5	3322	3145$^{L.}$	1-10	0$^{S.}$	2083			
No tip clades			I-T	2412$^{L.}$	527			
1-2-11-17-4-9No: PF			1-2-3-4No: RGF					
H3	547$^{S.}$	1926						
N2	1465	2654	1-11	2210	2403$^{L.}$			
I-T	918	728	1-12	0	2977			
1-2-3-4-9No: PF			1-13	0$^{S.}$	890$^{S.}$			
H4	3860$^{L.}$	3568$^{L.}$	1-14	1674	1691			
H9	1184$^{S.}$	1248$^{S.}$	I-T	–1883$^{S.}$	–1185$^{S.}$			
I-T	–2676$^{S.}$	–2320$^{S.}$	1-2-11-12No: CRE					
1-2-11-12No: CRE								

Clade distances (D_c) and nested clade distances (D_n) are calculated for each clade within the nested group, and for the average difference in distances between interior and tip clades (I-T). Interior clades are shaded. Significantly large and small values of D_c and D_n are indicated by a superscript L and S, respectively. Results from the inference key are given below each nested group and are abbreviated as follows: RGF, restricted gene flow; LDD, long distance dispersal; CRE, contiguous range expansion; PF, past fragmentation; LDC, long distance colonization.