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Population structure in an isolated Arctic fox, *Vulpes lagopus*, population: the impact of geographical barriers

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The genetic composition of a population reflects several aspects of the organism and its environment. The Icelandic Arctic fox population exceeds 8000 individuals and is comprised of both coastal and inland foxes. Several factors may affect within-population movement and subsequent genetic population structure. A narrow isthmus and sheep-proof fences may prevent movement between the north-western and central part and glacial rivers may reduce movement between the eastern and central part of Iceland. Moreover, population density and habitat characteristics can influence movement behaviour further. Here, we investigate the genetic structure in the Icelandic Arctic fox population ($n = 108$) using 10 microsatellite loci. Despite large glacial rivers, we found low divergence between the central and eastern part, suggesting extensive movement between these areas. However, both model- and frequency-based analyses suggest that the north-western part is genetically differentiated from the rest of Iceland ($F_{ST} = 0.04$, $D_S = 0.094$), corresponding to 100–200 generations of complete isolation. This suggests that the fences cannot be the sole cause of divergence. Rather, the isthmus causes limited movement between the regions, implying that protection in the Hornstrandir Nature Reserve has a minimal impact on Arctic fox population size in the rest of Iceland.

ADDITIONAL KEYWORDS: coastal – dispersal – divergence – genetic variation – Iceland – inland – isthmus – microsatellites – substructure.

INTRODUCTION

Movement is the major determinant of population structure (Slatkin, 1987; Eckert, Samis & Lougheed, 2008) and the pattern of movement is influenced by both biotic factors such as inter- and intra-specific interactions (e.g. Dias, 1996; Nathan, 2001) and abiotic factors in the form of geographical barriers (e.g. Goldman, 1937; Rueness *et al.*, 2003; Dalén *et al.*, 2005; Miller *et al.*, 2006). The Arctic fox (*Vulpes lagopus*) is a circumpolar specialist predator with high capacity for long-distance movement (e.g. Garrott & Eberhardt, 1987). Geffen *et al.* (2007) concluded that sea ice was the primary factor determining Arctic fox migratory behaviour and subsequent genetic divergence between populations. Arctic fox movement patterns are likely influenced by availability and distribution of resources as well, with long-distance movement less common in habitats with high resource predictability (Angerbjörn, Hersteinsson & Tannerfeldt, 2004). In agreement with these findings, Carmichael *et al.* (2007) recorded extensive gene flow between Arctic fox populations in the Svalbard archipelago and North America, proposing that the genetic homogeneity primarily is as a result of the presence of sea ice and differing foraging behaviours in coastal and inland habitats. However, the Arctic fox population in Iceland is bordered by constant open water that functions as a barrier to immigration from neighbouring populations (Dalén *et al.*, 2005). Except for comparisons of mitochondrial DNA variation between Iceland and other Arctic fox populations

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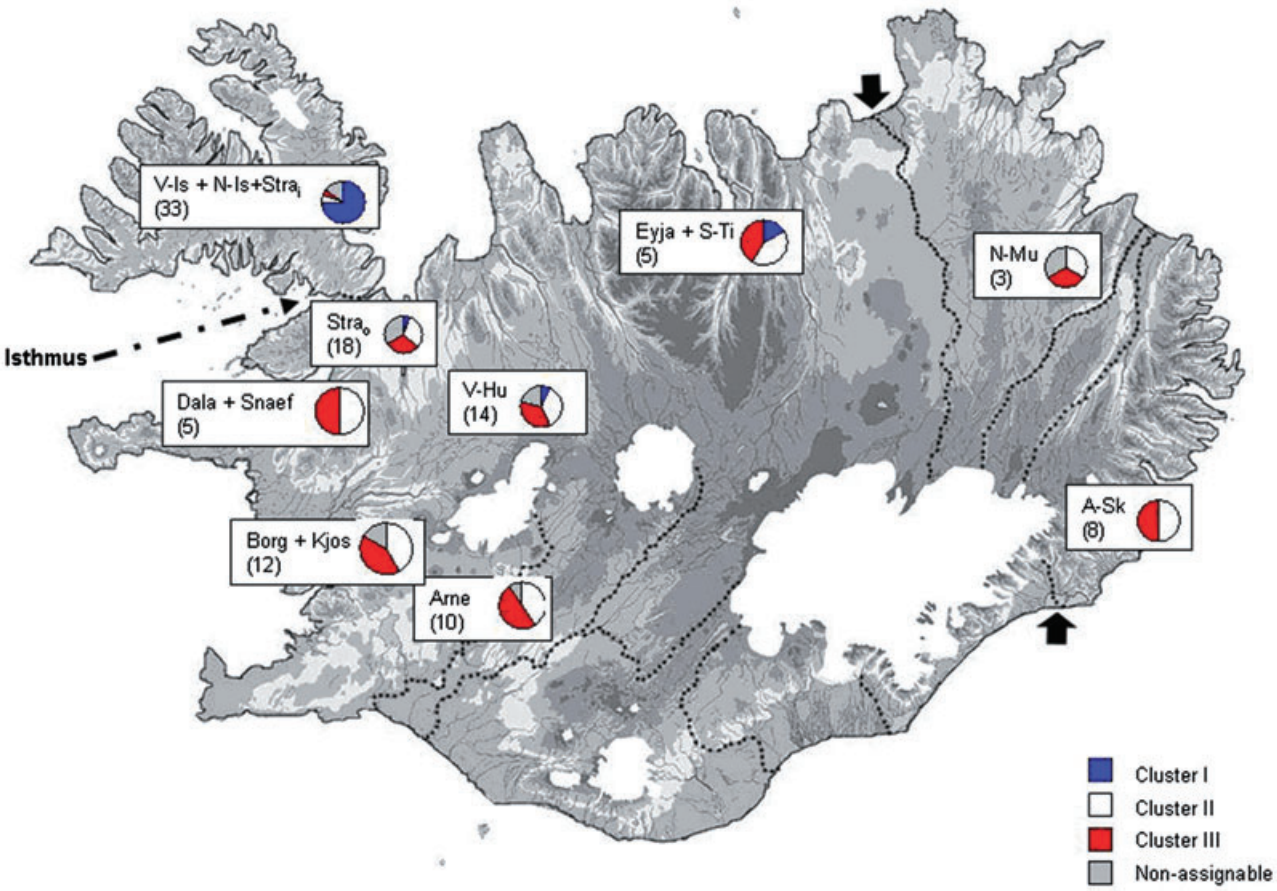

Figure 1. Map of Iceland with sample sizes and geographic location of the nine largest glacial rivers (dotted lines), the two glacial rivers west of which rabies never spread in the 18th century (thick arrows) and the narrow isthmus between the north-west and rest of Iceland (dashed arrow). Pie graphs show the proportion of individuals from each locality assigned to each of the three clusters inferred by STRUCTURE.

(Dalén *et al.*, 2005; Geffen *et al.*, 2007), little is known about the genetic composition in Iceland. Because of genetic isolation, Iceland is ideal for studying the impact of within-population movement on population genetic structure. Possible factors influencing within-population movement in Iceland are geographical barriers, spatially variable population density and habitat characteristics.

Because of the purported killing of lambs, the Arctic fox in Iceland has been considered a pest species and is subjected to intense hunting pressure by man. The population went through a bottleneck in the 1970s where its numbers declined to less than 1300 individuals in autumn (Angerbjörn *et al.*, 2004; Hersteinsson, 2006). Today, the population has recovered and its contemporary numbers exceed 8000 individuals in autumn (Angerbjörn *et al.*, 2004; Hersteinsson, 2006). Iceland offers both coastal and inland Arctic fox habitats where inland foxes rely largely on ptarmigan as a food resource during winter and migratory birds during summer, whereas coastal foxes mainly utilize seabirds in all seasons (Hersteinsson & Macdonald, 1996). Consequently, food availability is relatively predictable interannually compared with areas where lemmings are the main component of the diet (Angerbjörn *et al.*, 2004). Coastal foxes are mostly found in the western and eastern part of Iceland, whereas inland foxes primarily are found in the interior regions in between (Fig. 1). In inland habitats, food resources are relatively evenly distributed in space, while resources are more aggregated and productivity is higher in coastal habitats (Hersteinsson, 1984). Therefore, the density of occupied dens in coastal areas is high and coastal foxes are highly territorial (Hersteinsson & Macdonald, 1982).

In the north-western part of Iceland, Arctic fox population density is 10 times higher than in large

parts of the central highlands (Hersteinsson, 1984). Furthermore, the Hornstrandir Nature Reserve, where Arctic foxes have been totally protected since 1994, covers about 7% of the surface area of the north-western part of the country. In all, this may result in density-dependent dispersal from high-density to low-density areas (Hersteinsson, 1999; Hersteinsson, Th & Unnsteinsdóttir, 2000). Because of the combined effect of high population density and resource productivity, the north-western part of Iceland may function as a source population, with extensive movement to the central part where population density is lower, creating a homogenous population structure (prediction I). However, movement distances in coastal habitats are shorter than in inland habitats, likely as a result of the distribution and density of resources (Dalén *et al.*, 2005; Carmichael *et al.*, 2007). Further, Pagh & Hersteinsson (2008) concluded that Arctic foxes rarely settled in habitats with unfamiliar food resources, possibly because of habitat training. In all, this implies that movement between habitats may be rare.

Within Iceland, there are also geographical barriers that may reduce movement. The north-western part is connected to the rest of the country by a 9-km isthmus, which may impede movement between the areas (Fig. 1). Furthermore, since the 1940s, Iceland has been divided into 30 quarantine areas by sheep-proof fences and natural boundaries such as rivers and glaciers in order to eradicate lentiviral diseases of sheep and paratuberculosis of sheep and cattle (Georgsson, Sigurdarson & Brown, 2006). Two such fences partition north-western Iceland from the rest of the country. Accumulation of snow facilitates crossing these fences, but as movement mainly occurs during autumn prior to extensive snow accumulation (Audet, Robbins & Larivière, 2002), it is likely that the fences restrict movement. In contrast to prediction I, we thus predict that the north-west is genetically divergent to the inland areas (prediction II).

Moreover, the eastern part of Iceland is bordered by an ice cap and the largest glacial rivers of the country (Fig. 1). Most likely, these rivers can only be traversed during late winter when snow bridges have formed in some locations and may thus act as a barrier to movement for much of the year. During the rabies epizootic (1765–1766), the disease was never documented west of these glacial rivers (Fig. 1; Fooks *et al.*, 2004), suggesting that crossing the glacial rivers is rare. Accordingly, we predict that eastern Iceland is genetically distinct compared with the other areas (prediction III). Here, we use 10 polymorphic microsatellite loci in order to investigate the movement patterns and subsequent population structure in the Icelandic Arctic fox.

MATERIAL AND METHODS

Samples and genetic analyses

Muscle and brain tissue samples from 108 Icelandic Arctic foxes were collected during 1999–2007 (Fig. 1). Known relatives were excluded from the sample. We extracted DNA from muscle and brain tissue by using the DnEasy Tissue Kit (Qiagen) or the Purgene Kit (Gentra) according to the manufacturer's protocol. To monitor for contamination, extractions were conducted in a laboratory exclusively used for DNA extractions and, for every tenth sample, one negative control was included.

All samples were analysed for variation in 10 microsatellite loci (Dalén *et al.*, 2006) according to Norén *et al.* (2005). The PCR thermal cycler used was the PTC-100 Programmable Thermal Controller (MJ Research Inc.). Each allele was size determined by visualization on a CEQ 8000 automated sequencer.

Data analysis

Firstly, we grouped the individuals into three populations predicted from geography (Fig. 1), termed Central ($STRA_{outside\ isthmus}$, SNAEF, DALA, V-HU, BORG, ARNE, KJOS, EYJA, S-TI; $N = 64$), North-west (V-IS, N-IS, $STRA_{inside\ isthmus}$; $N = 33$) and East (N-MU, A-SK; $N = 11$) and calculated population pairwise F_{ST} (Weir & Cockerham, 1984) using the software Arlequin (Excoffier & Schneider, 2005). We calculated the likelihood that each individual's multilocus genotype originated from each of the three geographically predicted populations using a frequency-based population assignment test (Patkeau *et al.*, 1995) in the software GeneClass2 with a missing data frequency of 0.01 (Piry *et al.*, 2004). Based on Nei's standard genetic distance (DS) (Nei, Maruyama & Chakraborty, 1975), we constructed a UPGMA tree with 200 bootstrap replicates in Populations (Langella, 1999) and TreeView (Page, 1996). To investigate the impact of geographic distance on genetic differentiation, we tested for isolation by distance in GeneClass2 using a Mantel test with 10 000 permutations. Because of the low sample size from some localities, we arranged our 13 sample sites into nine population samples based on geography according to; BORG+KJOS, DALA+SNÆF, V-IS+N-IS+$STRA_{inside\ isthmus}$, $STRA_{outside\ isthmus}$, V-HU, EYJA+S-TI, N-MU, A-SK and ARNE (Fig. 1).

However, using these methods requires prior information of each individual's origin which might bias the results. We further investigated the population structure using the Bayesian Markov Chain Monte Carlo (MCMC) approach without any prior information of geographic origin to assess the number of populations within Iceland, given the genetic data.

For this, we set the number of clusters (K) between 1 and 7 and used 10^4 burn-in steps, followed by 10^6 MCMC replicates (Pritchard, Stephens & Donelly, 2000). For each setting of K, we repeated the simulation 10 times. The likelihood plateaued at the most likely number of genetic clusters (Pritchard *et al.*, 2000) and a Mann–Whitney U-test (StatSoft Inc., 2004) was used to test at which value of K the likelihood was highest. We used a threshold value (q) of 0.7 for assigning an individual to a cluster, meaning that > 70% of that individual's genome originates from that cluster. Individuals displaying likelihoods ranging from $0.3 < q < 0.7$ for two clusters were jointly assigned to both, whereas individuals displaying equal likelihoods of belonging to all three clusters were classified as non-assignable.

We used simulations in the software EASYPOP 1.7 (Balloux, 2001) to investigate the possible causes of the concluded population structure. Assuming two populations organized in a linear stepping stone model, we compared three scenarios (Table 4). For all scenarios, we assumed two populations consisting of 1600 (north-west) and 6400 individuals respectively, displaying the same level of diversity as suggested by empirical data and assumed no impact of mutations. Each simulation was replicated 10 times. Firstly, we assumed one originally panmictic population that was fragmented into two completely isolated subpopulations because of the sheep-proof fences (scenario 1). Secondly, we assumed two subpopulations created by the isthmus between the north-west and the rest of Iceland. Here, we used a constant degree of migration between the subpopulations (scenario 2). Thirdly, in order to investigate the combined effect of the isthmus and the sheep-proof fences, we assumed two subpopulations initially connected for a number of generations and later followed by complete isolation ($m = 0$) for 25 generations (scenario 3). We used the software MIGRATE 2.4.3 (Beerli & Felsenstein, 1999) to estimate migration rates per generation (m) through a maximum likelihood approach. We used the full migration matrix model, Brownian motion and constant mutation rate over all loci. To calculate m, we used mutation rates of 10^{-3} and 10^{-5} per locus and generation (Jarne & Lagoda, 1999). We included the migration rate (m) obtained from MIGRATE in EASYPOP for 100–5000 generations (Table 4). A total of 1750 generations corresponds to the earliest recorded findings of Arctic foxes in Iceland (Hersteinsson *et al.*, 2007), whereas 5000 generations corresponds to the time since the last Ice Age. The software Arlequin (Excoffier & Schneider, 2005) was used to calculate the expected population differentiation (F_{ST}).

For estimating the degree of genetic variation, we used the number of populations concluded from the above described analyses. We tested for deviations from Hardy–Weinberg proportions using a Markov chain with a chain length of 10^5 and 3000 dememorization steps (Guo & Thompson, 1992) and calculated the average numbers of alleles per locus using the software Arlequin version 3.0 (Excoffier & Schneider, 2005). To correct for sample size, we also calculated allelic richness (El Mousadik & Petit, 1996) using the software FSTAT version 2.9.3.2 (Goudet, 2001). We tested for linkage disequilibrium using a permutation test with 16 000 permutations and 10 initial conditions (Slatkin & Excoffier, 1996). The significance level was adjusted for multiple testing using the Bonferroni correction (Rice, 1989). We used the software BOTTLENECK (Cornuet & Luikart, 1996) to investigate whether there were any signatures from the bottleneck in the 1970s. A Wilcoxon sign rank test was used to test if there were a significant number of loci with heterozygote excess relative to the number of alleles which is a common effect of drastic declines in population size.

RESULTS

Population structure

Genetic differentiation (F_{ST}) was significant ($P < 0.0001$) between all three populations that were predicted from the geographical barriers. Differentiation between central and eastern Iceland was 0.023, and 0.035 between central and north-western Iceland. Between the north-western and the eastern part, genetic differentiation was 0.061. The same pattern is shown by Nei's standard genetic distance (D_S) (Fig. 2). Moreover, the population assignment test showed that 85% of the individuals had highest likelihood of originating from the area they had been sampled in (Table 1). There was no correlation between geographic distance and degree of differentiation (one-tailed $P = 0.192$).

According to the Bayesian MCMC approach, the highest likelihood was obtained for $K = 3$ (Table 2) that was significantly different from $K = 2$ ($P = 0.0045$) and $K = 4$ (Mann–Whitney U-test:

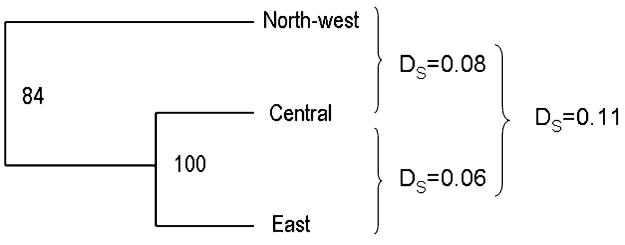

Figure 2. UPGMA tree with bootstrap values based on Nei's standard genetic distance (DS) between the populations predicted from geographical barriers.

Table 1. Results from the population assignment test (filled columns) and Bayesian approach (transparent columns) showing the proportion of individuals assigned to each population or cluster respectively. Each row represents samples from each of the study areas

	Sample size	Central	North-west	East	Cluster I	Cluster II	Cluster III	Not assigned
Central	64	0.844	0.047	0.109	0.016	0.453	0.453	0.079
North-west	33	0.061	0.848	0.091	0.776	0.048	0.048	0.129
East	11	–	0.09	0.909	0.071	0.358	0.358	0.214

Table 2. Mean estimated likelihoods for different numbers of clusters (*K*) inferred by STRUCTURE

K	Mean ln Pr(X/K)
1	–2634.9
2	–2592.9
3	–2546.4
4	–2625.8
5	–2685.1
6	–2777.6
7	–2913.5

$P < 0.00001$). Of the individuals sampled in the north-western part, 77.4% were assigned to cluster I (Table 1), whereas only 2.6% of the individuals sampled in the central or eastern part were assigned to cluster I. A vast majority of the individuals sampled in the central and eastern part had almost equal likelihoods of originating from cluster II and III, displaying no consistency between which cluster they were assigned to and in which area they had been sampled (Table 1, Figs 1, 3). Interestingly, one of the individuals sampled in the central region was assigned to the same cluster as individuals sampled in the north-western part in both the assignment test and the clustering analysis ($q_I = 0.85$), which implies that it might be a migrant. Another individual was likely an immigrant from the central part into the north-west ($q_I = 0.068$) according to both the assignment test and the clustering analysis ($q_{II+III} = 0.392 + 0.540$).

Assuming that the central and eastern part is one population, we calculated an F_{ST} value of 0.04 between the north-west and the rest of Iceland. Between 100–200 generations of complete isolation were required to obtain the observed magnitude of differentiation (Table 4, scenario 1). Simulations in MIGRATE suggested that migration rate (m) between the two populations was 4×10^{-5} when setting mutation rate to 10^{-5} and 0.0049 when setting migration rate to 10^{-3} per locus and generation. A migration rate of 0.0049 per generation is not sufficient to obtain the observed magnitude of differentiation during the period between the last Ice Age (5000 generations) and the present, whereas a migration rate of 4×10^{-5} per generation would require about 200 generations to obtain the empirical divergence (Table 4).

Genetic variation

Average expected heterozygosity was 0.624, with an average of 6.8 alleles per locus for the entire sample. Average expected heterozygosity was not significantly different in the north-western part ($H_{Ea} = 0.676$) than in the rest of Iceland ($H_{Ea} = 0.575$) ($P = 0.217$). For both populations, all 10 loci were polymorphic, with an average number of alleles of 5.5–5.8 and allelic richness ranging from 4.7–5.5 (Table 3). We found significant deviation from Hardy–Weinberg proportions in five loci in the central-eastern population and in three loci for the north-western population (Table 3). When testing for linkage disequilibrium in entire Iceland, significant deviation, after applying the Bonferroni correction ($P < 0.001$) was recorded in 24 out of the 45 possible combinations. However, when dividing the sample into the two populations suggested above, there was disequilibrium in five combinations in the central-eastern population, whereas we recorded disequilibrium in 18 combinations in the north-western population. There was no significant signature of a bottleneck. The probability for heterozygote excess in relation to the number of alleles was $P = 0.999$ for the central-eastern population and $P = 0.530$ for the north-western population (one-tailed Wilcoxon test).

DISCUSSION

Population structure

Our results show that the Arctic fox population in Iceland is not genetically homogenous, contradicting prediction I. Firstly, we found significant linkage disequilibrium in a vast majority of the loci combinations when treating Iceland as one population, which implies an unknown substructure within a population (e.g. Carmichael *et al.*, 2007). Because the disequilibrium in the central-eastern population diminishes as

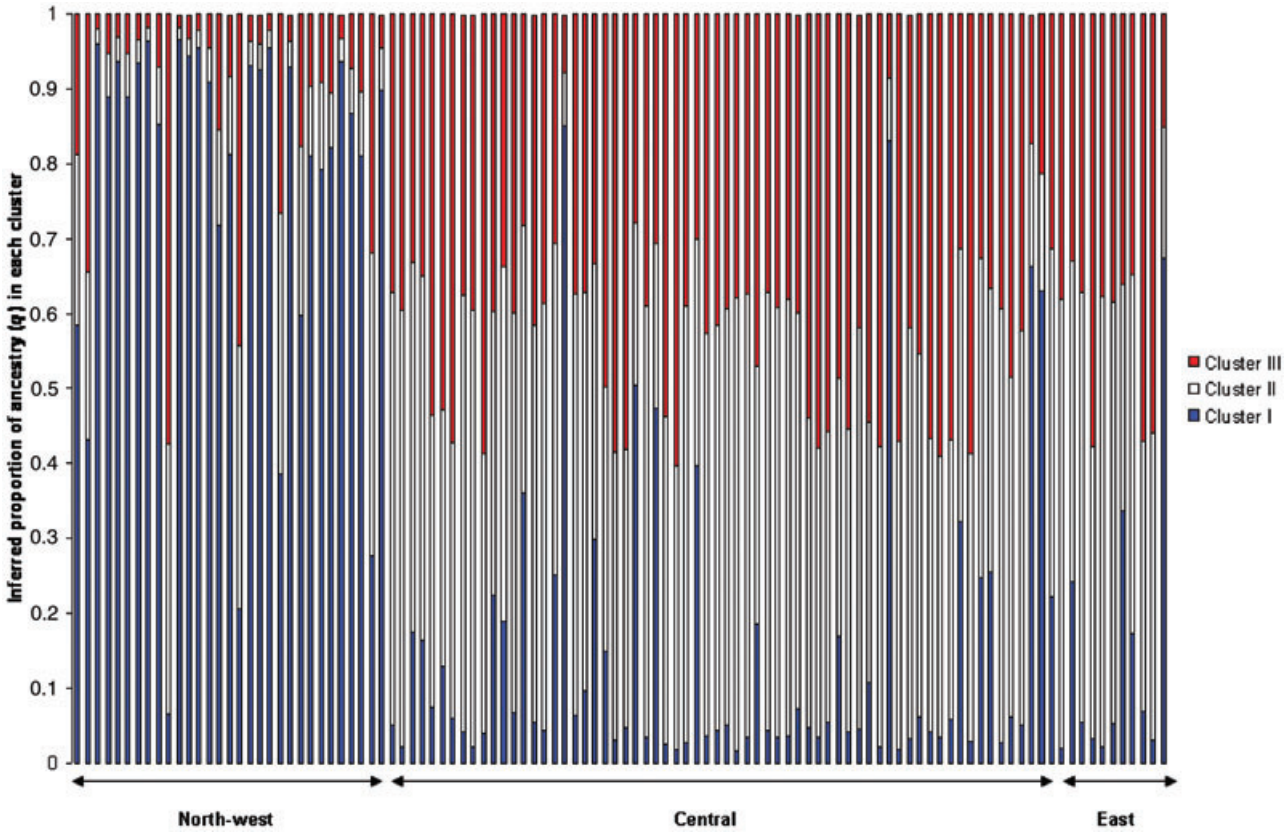

Figure 3. Proportion of ancestry in each inferred cluster ($K = 3$) for each individual using the MCMC approach without prior population information in STRUCTURE. Each individual is represented by a bar divided into sections corresponding to their inferred proportion of ancestry in clusters I, II and III.

Table 3. Hardy–Weinberg proportions for the 10 microsatellite loci and genetic diversity measured as average expected heterozygosity, proportion polymorphic loci, average number of alleles per locus and allelic richness

	Central-eastern			North-western		
Locus	H_O	H_E	*P*	H_O	H_E	*P*
CPH3	0.762	0.826	0.012	0.742	0.811	0.000
CPH9	0.327	0.305	0.700	0.571	0.557	0.199
CPH15	0.248	0.274	0.039	0.258	0.291	0.250
CXX20	0.676	0.729	0.004	0.630	0.719	0.769
CXX140	0.413	0.657	0.000	0.724	0.694	0.042
CXX173	0.612	0.597	0.494	0.679	0.702	0.532
CXX250	0.352	0.513	0.000	0.621	0.587	0.352
377	0.295	0.648	0.000	0.633	0.801	0.001
758	0.562	0.579	0.053	0.774	0.768	0.000
771	0.690	0.611	0.024	0.621	0.750	0.032
Average expected heterozygosity		0.580			0.668	
Polymorphic loci (%)		100			100	
Average number of alleles/locus		5.8			5.5	
Allelic richness		5.9			4.7	

we separate it from the north-western one, this may indeed be the case. Secondly, according to the population pairwise F_{ST} values and the population assignment test, there is significant differentiation between the three populations predicted from the presumed geographical barriers. According to general guidelines, population differentiation in Iceland can be considered low (F_{ST}: 0–0.05) to moderate (F_{ST}: 0.05–0.15) (Wright, 1978). Thirdly, the degree of differentiation cannot be explained by geographic distance only.

The clustering analyses imply that, given our data, there are three subpopulations within Iceland. The majority of the individuals sampled in the north-western part were assigned to one separate cluster (I) and few individuals were assigned to areas other than the north-west in the population assignment test (Table 1). The F_{ST} value between the north-western and the rest of Iceland ($F_{ST} = 0.04$) is comparable with differentiation between Arctic fox subpopulations in Fennoscandia ($F_{ST} = 0.06–0.2$, Dalén *et al.*, 2006). Consequently, movement between the north-west and the rest of Iceland is low and probably occurs with a rate < 0.0049 per generation (Table 4).

Finding that the north-western part is genetically distinct from the rest of Iceland is in agreement with prediction II of geographical barriers impeding movement between the areas. The sheep-proof fences that were put up in the area about 25 generations ago are not sufficient to obtain the observed degree of divergence (Table 4, scenario 1). Rather, the divergence is because of the narrow isthmus between the north-west and central area (Fig. 1, scenario 2). Possibly, the genetic distinctiveness in this area may also be as a result of lower movement frequency in coastal habitats or the increased number of territories that have to be traversed during dispersal of a given distance. Notably, a high proportion of foxes in the north-west are infected with ear-canker mites (*Otdectes cynotis*), whereas infection is rarely diagnosed in other parts of Iceland (Gunnarsson, Hersteinsson & Adalsteinsson, 1991), supporting the notion that movement between the regions is rare. Possibly, the genetic divergence between the north-western area and the rest of Iceland is enhanced by the sheep-proof fences (Table 4: scenario 2 vs. 3).

We found low support for prediction III, where genetic divergence of the eastern part was suggested because of large glacial rivers. We found low resolution of the third subpopulation inferred by the clustering analyses (Table 2) as the majority of the individuals sampled in the central and eastern part displayed almost equal likelihoods of originating from both of these clusters (cluster II and III) (Fig. 3). We suggest that movement between these regions is extensive, possibly occurring during late winter when the glacial rivers are possible to cross.

Genetic variation

In general, isolated island populations are expected to display lower genetic diversity than mainland populations (Frankham, 1997). Compared with the populations in the Svalbard and North American archipelago ($H_E = 0.78$; Carmichael *et al.*, 2007), the degree of variability within Iceland is low ($H_E = 0.58–0.67$). The diversity within Iceland is equal to the severely bottlenecked population in Fennoscandia ($H_E = 0.58–0.63$; Dalén *et al.*, 2006), which is probably as a result of a founder effect, lack of immigration and/or genetic drift augmented by the population

Table 4. Results from simulations in EASYPOP using three different scenarios: (1) complete isolation ($m = 0$); (2) continuous movement ($m = 0.0049–4 \times 10^{-5}$); (3) continuous movement ($m = 0.0049–4 \times 10^{-5}$), followed by complete isolation ($m = 0$) for 25 generations. Bold text shows where the expected F_{ST} value corresponds to the observed ($F_{ST} = 0.04$)

	Expected F_{ST}				
Generations	Scenario 1	Scenario 2		Scenario 3	
	$m = 0$	$m = 0.0049$	$m = 4 \times 10^{-5}$	$m = 0.0049$	$m = 4 \times 10^{-5}$
25	0.02	–		–	
50	0.03	–		–	
100	0.03	0.01	0.02	0.02	0.02
200	**0.05**	0.02	**0.03**	0.02	**0.04**
1000		0.02	**0.13**	0.03	
1750*		0.02		0.03	
5000†		0.02		0.03	

*Earliest known presence of Arctic foxes in Iceland (Hersteinsson *et al.*, 2007).
†End of last Ice Age.

bottlenecks in the 1970s. Our results on nuclear genetic variation are in agreement with those from Dalén *et al.* (2005), demonstrating a lower mitochondrial variation in Iceland than in mainland Arctic fox populations.

We recorded deviations from Hardy–Weinberg proportions in both population samples (Table 3). As we have excluded all known relatives in the samples, found no significant signatures of a bottleneck and excluded isolation by distance, these deviations are more likely as a result of other factors. For instance, genetic isolation or a non-random mating system because of resource distribution and/or dispersal behaviour may produce such deviations.

CONCLUSIONS

On the one hand, movement between the central and eastern part of Iceland seems to occur frequently, resulting in a homogenous distribution of genetic variation. On the other hand, the north-western part is genetically divergent from the rest of Iceland. As was shown by our simulations, the sheep-proof fences have not been in the area long enough to be the sole cause of the recorded degree of divergence. Rather, the divergence is most likely as a result of the effect of geographical barriers where the narrow isthmus causes restricted movement (Table 4: scenario 2). The observed pattern may also reflect the findings by Dalén *et al.* (2005), where inland foxes were suggested to undertake more extensive movement than coastal foxes, or be an effect of habitat training. Accordingly, our results suggest that Arctic fox protection in the Hornstrandir Nature Reserve has minimal effects outside the north-western part of Iceland.

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REFERENCES

Angerbjörn A, Hersteinsson P, Tannerfeldt M. 2004. Europe and North and Central Asia (Palearctic): Arctic fox, Alopex lagopus. In: Sillero-Zubiri C, Hoffman M, Macdonald W, eds. *Canids, wolves, jackals and dogs. status survey and conservation action plan*. Gland, Switzerland: IUCN/SSC Canid Specialist Group, 117–123.

Audet AM, Robbins CB, Larivière S. 2002. Alopex lagopus. *Mammalian Species* **713:** 1–10.

Balloux F. 2001. EASYPOP (version 1.7), (2001) A computer program for the simulation of population genetics. *Journal of Heredity* **92:** 301–302.

Beerli P, Felsenstein J. 1999. Maximum likelihood estimation of migration rates and population numbers of two populations using a coalescent approach. *Genetics* **152:** 763–773.

Carmichael LE, Krizan J, Nag JA, Fuglei E, Dumond M, Johnson D, Veitch A, Bertreaux D, Strobeck C. 2007. Historical and ecological determinants of genetic structure in arctic canids. *Molecular Ecology* **16:** 3466–3483.

Cornuet JM, Luikart G. 1996. Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. *Genetics* **144:** 2001–2014.

Dalén L, Fuglei E, Hersteinsson P, Kapel CMO, Roth JD, Samelius G, Tannerfeldt M, Angerbjörn A. 2005. Population history and genetic structure of a circumpolar species: the arctic fox. *Biological Journal of the Linnean Society* **84:** 79–89.

Dalén L, Kvaløy K, Linnell JDC, Elmhagen B, Strand O, Tannerfeldt M, Henttonen H, Fuglei E, Landa A, Angerbjörn A. 2006. Population structure in a critically endangered arctic fox population: does genetics matter? *Molecular Ecology* **15:** 2809–2819.

Dias PC. 1996. Sources and sinks in population biology. *Trends in Ecology and Evolution* **11:** 326–330.

Eckert CG, Samis KE, Lougheed SC. 2008. Genetic variation across species' geographical ranges: the central-marginal hypothesis and beyond. *Molecular Ecology* **17:** 1170–1188.

El Mousadik A, Petit RJ. 1996. High level of genetic differentiation for allelic richness among populations of the argan tree (Argania spinosa (L.) Skeels) endemic to Morocco, *Theoretical and Applied Genetics* **92:** 832–839.

Excoffier LGL, Schneider S. 2005. Arleqin ver. 3.0: an integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online* **1:** 47–50.

Fooks AR, Roberts DH, Lynch M, Hersteinsson P, Runólfsson H. 2004. Rabies in the United Kingdom, Ireland and Iceland. In: King AA, Fooks AR, Aubert M, Wandeler AI, eds. *Historical perspectives of rabies in Europe and the Mediterranean basin*. Paris: World Organisation for Animal Health, 25–32.

Frankham R. 1997. Do island populations have less genetic variation than mainland populations? *Heredity* **78:** 311–327.

Garrott RA, Eberhardt LE. 1987. Arctic fox. In: Novak M, Baker JA, Obbard ME, Malloch B, eds. *Wild furbearer management and conservation in North America*. Ontario: Ministry of Natural Resources, 395–406.

Geffen E, Waidyaratne S, Dalén L, Angerbjörn A, Vilà C, Hersteinsson P, Fuglei E, White P, Goltsman M, Kapel CMO, Wayne RK. 2007. Sea ice occurrence predicts genetic isolation in the arctic fox. *Molecular Ecology* **16:** 4241–4255.

Georgsson G, Sigurdarson S, Brown P. 2006. Infectious agent of sheep scrapie may persist in the environment for at least 16 years. *Journal of General Virology* **87:** 3737–3740.

Goldman EA. 1937. The Colorado river as a barrier in mammalian distribution. *Journal of Mammalogy* **18:** 427–435.

Goudet J. 2001. FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9.3) (2001). Available at http://www2.unil.ch/popgen/softwares/fstat.htm

Gunnarsson E, Hersteinsson P, Adalsteinsson S. 1991. Prevalence and geographical distribution of the ear canker mite (*Otodectes cynotis*) among arctic foxes (*Alopex lagopus*) in Iceland. *Journal of Wildlife Diseases* **27:** 105–109.

Guo SW, Thompson EA. 1992. Performing the exact test of Hardy-Weinberg proportion for multiple alleles. *Biometrics* **48:** 359.

Hersteinsson P. 1984. The behavioural ecology of the Arctic fox (*Alopex lagopus*) in Iceland. DPhil thesis, Oxford University, p. 286.

Hersteinsson P. 1999. *The Arctic foxes of hornstrandir*. Reykjavik: Ritverk,.

Hersteinsson P. 2006. *Íslenski tófustofninn [The Icelandic arctic fox population]. Veididagbók 2006*. Reykjavik: The Environment Agency of Iceland, 6–15 (in Icelandic).

Hersteinsson P, Björnsson Th.B, Unnsteinsdóttir ER, Ólafsdóttir AH, Sigthórsdóttir H, Eiríksson Th. 2000. The Arctic fox in Hornstrandir: number of dens occupied and dispersal of foxes out of the reserve. *Náttúrufræðingurinn* **69:** 131–142 (in Icelandic with English Summary).

Hersteinsson P, Macdonald DW. 1982. Some comparisons between red and Arctic foxes, *Vulpes vulpes* and *Alopex lagopus*, as revealed by radio-tracking. *Symposium of Zoological Society of London* **49:** 259–289.

Hersteinsson P, Macdonald DW. 1996. Diet of arctic foxes (*Alopex lagopus*). *Iceland. Journal of Zoology* **240:** 457–474.

Hersteinsson P, Nyström V, Jóhannsson JH, Guðjónsdóttir B, Hallsdóttir M. 2007. The oldest known remains of Arctic foxes in Iceland. *Náttúrufræðingurinn* **76:** 13–21 (in Icelandic with English summary).

Jarne P, Lagoda PJL. 1999. Microsatellites from molecules to populations and back. *Trends in Ecology and Evolution* **11:** 424–429.

Langella O. 1999. POPULATIONS. Available at http://www.cnrs-gif.fr/pge/bioinfo/populations

Miller MP, Bellinger MR, Forsman ED, Haig SM. 2006. Effects of historical climate change, habitat connectivity, and vicariance on genetic structure and diversity across the range of the red tree vole (*Phenacomys longicaudus*) in the Pacific Northwestern United States. *Molecular Ecology* **15:** 145–159.

Nathan R. 2001. The challenges of studying dispersal. *Trends in Ecology and Evolution* **9:** 481–483.

Nei MT, Maruyama T, Chakraborty R. 1975. The bottleneck effect and genetic variability in populations. *Evolution* **29:** 1–10.

Norén K, Dalén L, Kvaløy K, Angerbjörn A. 2005. Detection of farm fox and hybrid genotypes among wild arctic foxes in Scandinavia. *Conservation Genetics* **6:** 885–894.

Page RDM. 1996. TreeView: An application to display phylogenetic trees on personal computers. *Computer applications in the biosciences* **12:** 357–358.

Pagh S, Hersteinsson P. 2008. Difference in diet and age structure of blue and white Arctic foxes (*Vulpes lagopus*) in the Disko Bay area, West Greenland. *Polar Research* **27:** 44–51.

Patkeau D, Calvert W, Stirling I, Strobeck C. 1995. Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology* **4:** 347–354.

Piry S, Alapetite A, Cornuet JM, Paetkau D, Baudouin L, Estoup A. 2004. GeneClass2: a software for genetic assignment and first-generation migrant detection. *Journal of Heredity* **95:** 536–539.

Pritchard JK, Stephens M, Donelly PI. 2000. Inference of population structure using multilocus genotype data. *Genetics* **155:** 945–959.

Rice WR. 1989. Analyzing tables of statistical tests. *Evolution* **43:** 223–225.

Rueness EK, Stenseth NC, O'Donaghue M, Boutin S, Ellegren H, Jakobsen KS. 2003. Ecological and genetic spatial structuring in the Canadian lynx. *Nature* **425:** 69–72.

Slatkin M. 1987. Gene flow and the geographic structure of natural populations. *Science* **236:** 787–792.

Slatkin M, Excoffier L. 1996. Testing for linkage disequilibrium in genotypic data using the EM algoritm. *Heredity* **76:** 377–383.

Weir BS, Cockerham CC. 1984. Estimating F-statistics for the analysis of population structure. *Evolution* **38:** 1358–1370.

Wright S. 1978. Variability within and among natural populations. In: *Evolution and the genetics of population*. Chicago, IL: University of Chicago Press, 649.