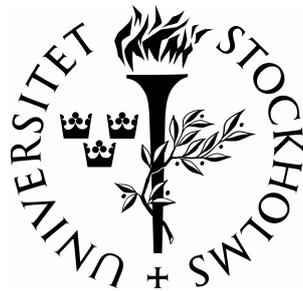


Distribution and abundance of genetic variation in the arctic fox

Genetic variation in the arctic fox (Lepus arcticus) is characterized by high levels of polymorphism across the genome. This variation is distributed across the species' range, with distinct patterns of genetic differentiation and gene flow. The distribution of genetic variation is influenced by historical processes such as population expansion, contraction, and migration, as well as contemporary factors like habitat fragmentation and human impact. The abundance of genetic variation is also affected by these factors, with higher levels of variation typically found in larger, more stable populations. The study of genetic variation in the arctic fox is important for understanding its evolutionary history and for developing conservation strategies to protect this species and its genetic diversity.

Distribution and abundance of genetic variation in the arctic fox

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Stockholm 2005

Distribution and abundance of genetic variation in the arctic fox
Doctoral dissertation 2005

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Abstract

This thesis investigates how changes in population size and spatial movements of individuals have shaped the distribution and abundance of neutral genetic variation in the arctic fox (*Alopex lagopus*). This is done through mitochondrial and microsatellite DNA analyses on samples covering most of the species' distribution, but with special emphasis on Scandinavia. On the species level, nucleotide diversity was relatively low, which indicated a historical expansion in population size in connection with the onset of the last Ice Age. It is thus possible that the glacial cycles have affected the arctic fox, and other cold-adapted species, in a way opposite to their effect on temperate species. Gene flow seemed to be high among arctic fox populations on a circumpolar scale, especially between populations where lemmings are the main food source, which could be explained by the spatial synchrony in lemming fluctuations. In Scandinavia, the arctic fox went through a severe demographic bottleneck in the beginning of the 20th century. Although some genetic variation was lost during this bottleneck, the loss was much smaller than expected, probably due to post-bottleneck gene flow from Russia. The arctic fox in Scandinavia is divided into four relatively isolated populations. Within each population, dispersal seemed to be high despite the high availability of empty territories close to natal dens, which supported the hypothesis that lemming fluctuations influence arctic fox dispersal. Genetic analyses on samples collected between 1989 and 2004 indicated an ongoing genetic drift and inbreeding within the Scandinavian populations. Furthermore, individual genetic variation was negatively associated with fitness, which could be attributed to an ongoing inbreeding depression. Analyses on faecal samples suggested that arctic foxes move higher up in the mountains and farther from the tree-line during summer compared to winter. This seasonal shift in distribution is probably caused by interspecific competition from the red fox, which is likely to be higher during summer due to red fox predation on arctic fox cubs. The results presented in this thesis have several implications for the conservation of the Scandinavian arctic fox. The finding of four isolated populations within Scandinavia and an ongoing inbreeding depression suggests that the risk of extinction is higher than previously thought. Conservation actions need to be taken in all populations to be effective, and could include genetic restoration through translocation.

List of papers

- I 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.
- II Nyström V, Angerbjörn A, Dalén L.** Genetic consequences of a demographic bottleneck in the Scandinavian arctic fox. *Provisionally accepted, Oikos*.
- III Dalén L, Elmhagen B, Angerbjörn A.** Microsatellite diversity and fitness: testing the local and general effect hypotheses in an endangered carnivore. *Submitted manuscript*.
- IV Dalén L, Kvaløy K, Linnell JDC, Elmhagen B, Strand O, Tannerfeldt M, Henttonen H, Fuglei E, Landa A, Angerbjörn A.** Population structure, genetic variation and dispersal in a critically endangered arctic fox population. *Submitted manuscript*.
- V Dalén L, Götherström A, Angerbjörn A.** 2004. Identifying species from pieces of faeces. *Conservation Genetics* 5: 109-111.
- VI Dalén L, Elmhagen B, Angerbjörn A.** 2004. DNA analysis on fox faeces and competition induced niche shifts. *Molecular Ecology* 13: 2389-2392.
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Introduction

Genes through time and space

The distribution and abundance of genetic variation in an organism is a result of past events. The two processes involved in these past events may be described as the movement of genes through time and space.

The movement of genes through time is propelled by reproduction. As genes move through time, new genetic variants may arise through mutation (*e.g.* point mutation, insertion/deletion, recombination), whereas others are lost through selection or random genetic drift. Mutation rates vary among different gene loci, but are thought to be relatively constant over time for any given locus. Furthermore, a large proportion of an organism's genome is considered as being more or less selectively neutral (Ohta 1992). Thus, the number of neutral genes in an isolated finite population is a balance between the mutation rate and the amount of genetic drift, where the latter is a function of the effective population size (Kimura & Crow 1964). Changes in population size will therefore lead to a change in the number of neutral genes in a population.

Organisms live in a constantly changing environment, and it is thus not surprising that they go through changes in population size. In a longer time perspective, changes in climate are likely to have had a major impact on the population size of organisms world-wide. Many species have for example gone through contractions in population size during the Ice Ages and expansions during warm periods (Webb & Bartlein 1992). Changes in interspecific competition and predation pressure, sometimes associated with climate change, may also cause changes in population size. Species can decline in numbers if competitors and predators increase. Similarly, a decrease in competition or predation could result in ecological release and a subsequent expansion in population size. In more recent times, human activity has led to over-exploitation of species, changes in the amount of available habitat and introduction of new

competitors and predators. In a small scale, genetic variation may in itself cause changes in population size (*e.g.* Lynch *et al.* 1995). Small populations may go through a feedback loop where high levels of genetic drift results in fixation of deleterious alleles, which in turn will decrease the overall fitness in the population, leading to a decrease in population size and a subsequent increase in genetic drift.

The movement of genes through space is caused by both active and passive movements of the individuals or gametes that carry them. These spatial movements of individuals can take many forms. Individuals disperse, for example from their birth place, and whole groups of individuals may migrate between different habitats. If individuals disperse or migrate from one population to another and reproduce successfully, this will lead to gene flow between the populations. A species or population may also expand its range. Range expansions and long distance gene flow can be considered as spatio/temporal processes in that the movement of genes from point A to point B may take several generations.

There are numerous factors that affect the spatial movements of individuals (*e.g.* Baker 1978). Changes in climate, such as the ones discussed above, have led to an increase or decrease in the amount of available habitat for species. Decreases in the amount of available habitat are likely to have a relatively small impact on gene flow since it would involve a directional movement of individuals into patches already inhabited by conspecifics, whereas an increase in available habitat would have a much larger impact since empty territories are easy to occupy (Hewitt 1999).

Another factor that has strong influence on the spatial movements of individuals are geographical barriers. These comprise everything from oceans and mountain ranges to small streams or patches of habitat with low quality. Biotic factors, for example competition and predation, can also have an effect on individual movements. This can be both in a directional sense, as a competitor or pre-

dator changes its distribution, or that the presence of competitors or predators in some areas act as geographical barriers.

There is also a direct interaction between population size and the spatial movement of individuals. Dispersal is often associated with population density, which in turn may be related to population size. Dispersal can be both positively and negatively density dependent (Murray 1967). In cases where dispersal is positively density dependent, there is a possibility for a feed-back loop between population size, dispersal and genetic variation. A reduction in population density could then lead to a decrease in dispersal. This would decrease the rate of gene flow among subpopulations, which in turn would increase the effect of genetic drift within each of the subpopulations. Genetic drift may lead to lowered fitness and subsequently a further decrease in population size and density.

In conclusion, the distribution and abundance of neutral genetic variation in an organism is governed by the movement of genes through time and space. How they do this is a consequence of the population size and the spatial movements of the organisms that carry them. Several factors, both biotic and abiotic, affect the population size and spatial movements of organisms. This thesis investigates the temporal and spatial processes of how genes move through time and space and how this has shaped the distribution and abundance of neutral genetic variation in the arctic fox (*Alopex lagopus*). The temporal and spatial processes can be viewed at different scales in terms of how far the genes have 'moved' in time and space, where time is the unit for the temporal process and geographical distance is the unit for the spatial process.

The arctic fox

The earliest remains from arctic foxes are found in the Olyorian fauna of northeast Siberia, which suggests a Beringian origin of the arctic fox, no later than 500 000 years before present (BP; Sher 1986 *as cited in* Kahlke 1999). The earliest appearance of arctic foxes in Europe date to approximately

200 000 BP (Kurtén 1968). Its closest relative is the North American swift fox (*Vulpes velox*) and it has been suggested that the arctic fox evolved from a swift fox-like ancestor (Geffen *et al.* 1992), possibly as a result of vicariance caused by expanding ice sheets. During the last Ice Age, arctic foxes were widely distributed in continental Eurasia and North America (Kurtén 1968, Kurtén & Anderson 1980, Sommer & Benecke 2005). Today, the arctic fox has a circumpolar distribution and inhabits the tundra regions of North America and Eurasia as well as most arctic islands, including Greenland, Iceland and Svalbard (Audet *et al.* 2002). The southern distribution of the arctic fox has been suggested to be limited by competition from the red fox (*Vulpes vulpes*), whose northern distribution in turn is limited by climatic factors (Hersteinsson & Macdonald 1992). The arctic fox, on the other hand, is well adapted to cold temperatures, displaying several physiological and morphological adaptations to the harsh arctic environment (Prestrud 1991, Fuglei & Øritsland 1999) and tolerates temperatures below -40° C in winter without having to increase its metabolic rate significantly to keep the body temperature constant (Scholander *et al.* 1950).

Its diet is composed of a variety of vertebrates (Audet *et al.* 2002), but two ecotypes are generally recognised: 'lemming' foxes that mainly feed on lemmings (*Lemmus spp.* and *Dicrostonyx spp.*) and 'coastal' foxes that mainly feed on eggs, birds and carrion from the marine system (Bræstrup 1941). 'Lemming' foxes are found in continental Eurasia, North America, the Canadian archipelago and eastern Greenland, whereas 'coastal' foxes are found in Iceland, Svalbard as well as southern, western and northwestern 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 to 'coastal' foxes (Tannerfeldt & Angerbjörn 1998). Furthermore, there are

significant differences in dispersal patterns between the two ecotypes, where ‘lemming’ foxes disperse further than ‘coastal’ foxes (Angerbjörn *et al.* 2004a).

The arctic fox is an unusually mobile species that has a high dispersal rate (Shilyaeva 1968) and is capable of long distance movements of over more than 1000 km (Pulliainen 1965, Garrott & Eberhardt 1987, Strand *et al.* 2000), including long passages over the polar sea ice (Nansen 1897, Eberhardt & Hanson 1978). Several sub-species have been proposed for the arctic fox, but Frafjord (1993) found little difference in morphology among populations on a circum-polar scale.

The world population of arctic foxes is large, and the species is therefore not considered as threatened on a global scale. On a regional scale, however, arctic fox numbers are low in Fennoscandia (Sweden, Norway, Finland and the Kola Peninsula) and on Mednyi Island and the Pribilof Islands (Angerbjörn *et al.* 2004b). In Sweden, Norway and Finland, it is classified as critically endangered (Rassi *et al.* 2001, Gärdenfors 2005, Directorate for Nature Management 2003).

The arctic fox in Fennoscandia

Several of the studies in this thesis are focused on the arctic fox in Fennoscandia, and a more detailed description of the situation in this region therefore seems motivated. It is considered one of the oldest species in Fennoscandia. The arctic fox was present along the Norwegian coast during the Ice Age (Frafjord & Hufthammer 1994), and fossil records suggest that it also followed the retreating ice edge in early Holocene (Ronnie Liljegren *pers. comm.*). Today, the arctic fox inhabits the mountain tundra in Sweden, Norway, Finland and the Kola Peninsula. Arctic foxes used to be a common sight in the mountains and the population size in Scandinavia probably exceeded 10 000 individuals during peak years (Tannerfeldt 1997). However, at the end of the 19th century arctic fox numbers started to decline as a result of heavy hunting pressure. As the population

became smaller and smaller during the first decades of the 20th century, fur prices skyrocketed which in turn caused the hunting to become even more intense. The population size in Scandinavia after this demographic bottleneck is likely to have been only a few hundred individuals (Lönnerberg 1927). Despite being protected by law in Sweden (1928), Norway (1930) and Finland (1940) the population did not recover. The population size in Sweden in the 1970’s was estimated to approximately 100 individuals (Haglund & Nilsson 1977). Since then, the population size has continued to decrease and a recent estimate suggests a maximum population size in Sweden, Norway and Finland of 120 individuals (Elmhagen *et al.* 2004). The situation on the Kola Peninsula is unclear, but the population size is possibly somewhat larger (*pers. obs.*).

A range of explanations for the arctic fox’s non-recovery have been proposed. Inter-specific competition with red foxes seems to have resulted in a reduction in the amount of available habitat and that the remaining habitat is of relatively low quality (Elmhagen *et al.* 2002, Tannerfeldt *et al.* 2002). Other proposed explanations include food shortage due to irregularities in lemming fluctuations and decreasing densities of large carnivores, as well as human disturbance and changes in habitat (Hersteinsson *et al.* 1989, Tannerfeldt *et al.* 1994). Furthermore, there are concerns that the small population size may have led to genetic drift, inbreeding depression and a decrease in population growth due to the Allee effect (Linnell *et al.* 1999, Loison *et al.* 2001). Inbreeding depression has been shown to cause a decrease in litter size and juvenile survival in farmed arctic foxes (Nordrum 1994).

Materials & methods

DNA sampling

The DNA samples analysed in this thesis have been collected from a variety of locations covering most of the arctic fox’s distribution.

The names of geographical regions sometimes vary between the Papers and a clarification is thus needed. In Papers **I**, **II** and **IV**, we refer to the Russian region west of the Yamal Peninsula as West Siberia, North Russia and northwest Russia. Since Siberia is defined as the region between the Urals and the Pacific Ocean, northwest Russia seems to be the most appropriate name, and I will use this from now on. Fennoscandia is the geographic region comprising Sweden, mainland Norway, Finland and the Kola Peninsula, whereas Scandinavia refers to Sweden and mainland Norway. For several reasons, which will become apparent later, there is a need to group the arctic foxes in Sweden, mainland Norway and Finland together. Since mountain tundra only exists in the far northern reaches of Finland (Fig. 7), I will refer to these areas as belonging to Scandinavia.

The source material of the DNA has varied. For the circumpolar samples most of the samples consisted of soft tissues such as muscle, liver and brain tissue. Samples from Scandinavia were collected between 1989 and 2004 and mainly consisted of ear biopsies, faeces and hair samples. Soft tissues were stored frozen, sometimes in ethanol. Hair samples were stored dry in room temperature and faecal samples were collected in jars containing silica pellets and were stored in -80° C.

Laboratory analyses

DNA extractions of modern samples were carried out using commercial kits (Qiagen), while historical bone samples were extracted using a silica-based method modified from Yang *et al.* (1998) and described by Bouwman *et al.* (2002). Polymerase chain reactions (PCR) were used to amplify a 332 base pair (bp) fragment of the mitochondrial DNA (mtDNA) control region (Dalén *et al.* 2002) or 10 microsatellite loci (*see* Paper **IV** for details). Sequencing products and microsatellite amplicons were scored on a CEQ 8000 automated sequencer (Beckman Coulter) or an ABI 310 Genetic Analyzer (Applied Biosystems), using fluorescently labelled dyes or primers.

Early on in the analyses, it became apparent that we needed a method to separate arctic fox faeces from those of red foxes. This would allow us to choose samples for subsequent genetic analyses, as well as to identify the current distribution of the arctic fox and compare it to that of the red fox. We therefore developed a PCR-based method to separate faeces from these two species and from wolverines, since these also might present a problem (Paper **V**). Since the methods available in the scientific literature were either expensive and time-consuming, or had problems with false positives and negatives, we opted for a PCR method based on a simultaneous use of several species-specific primers. The species-specific primers were designed to bind at different distances from a general primer. Thus, the simultaneous application of all four primers on a DNA extract of unknown origin will result in PCR-products of different length depending on which species the faecal sample originates from. The applicability of the method was tested on a number of samples of known origin, and gave the expected results (Paper **V**).

As DNA in faeces and historical samples occurs in low numbers and may be degraded (Wayne *et al.* 1999), we took several precautions when analysing this kind of material. Pre-PCR analyses were done using sterile equipment and work surfaces. For faecal samples, these analyses were done in a separate sterile bench. The historical samples were analysed in a laboratory dedicated to ancient DNA research. Negative controls were continually used to monitor for contamination (this was done also for modern tissue samples). For the historical samples, several specimens were amplified and sequenced three times to identify possible misincorporated bases. Multiple amplifications were also done in the microsatellite analyses to control for allelic dropout and the probability of scoring a false homozygote after *n* replicates was calculated according to Gagneux *et al.* (1997).

Statistical analyses

The details of the statistical methods are given Papers I-VI, but I will here give a brief overview of those used in this thesis, which are specific for genetic data. For sequence data, the most detailed measure is the nucleotide diversity (Nei 1987), which is based on the number of nucleotide differences among haplotypes (when several individuals have identical sequences, each unique variant is called a haplotype). Since this measure is an estimate of the number of mutations that have occurred since the divergence of a common ancestor, it can be used to infer population history under the assumption of neutrality. For example, the distribution of pairwise differences among sequences, the mismatch distribution (Rogers & Harpending 1992), can be used to test hypotheses on historical changes in population size. The nucleotide diversity, in combination with a rate of molecular divergence for that particular mtDNA region and the generation time for the species in question, can also be used to estimate the effective population size (Wilson *et al.* 1985). The evolutionary relationships between sequences can be illustrated in a phylogeny or a minimum spanning network and can be combined with the geographical distribution of each taxa to infer the spatial movements of genes (*e.g.* Avise *et al.* 1987, Templeton 1998). The spatial distribution of genes can also be used to estimate population differentiation, for example through F_{ST} or Φ_{ST} statistics, and to determine the geographical structuring of the genetic variation (Excoffier *et al.* 1992). The frequency of each haplotype can be used to calculate a population's haplotype diversity, which is a measure of its genetic variation (Nei 1987).

The potential for microsatellites as a tool to study population structure has been known for more than ten years (*e.g.* Roy *et al.* 1994). Microsatellites have a high mutation rate (Sunnucks 2000) and are therefore appropriate to infer recent events. Since an individual has two alleles for every locus, it can either be heterozygous or homozygous. An individual's genetic variation can thus be

measured as the proportion of heterozygous loci (or as d^2 , which takes into account size difference among alleles; Coulson *et al.* 1998). Similarly, the observed heterozygosity (H_O) in a population can be calculated as the proportion of individuals that are heterozygous for a given locus. Alternatively, the allele frequencies in a population can be used to calculate an expected heterozygosity (H_E) under the assumption of Hardy-Weinberg equilibrium. Deviations from Hardy-Weinberg equilibrium (*i.e.* $H_O \neq H_E$) may be caused by a number of processes, for example inbreeding, presence of null alleles and population subdivision. Such deviations can thus be exploited to infer, for example, population structure (*e.g.* Wahlund 1928, Pritchard *et al.* 2000). The difference in allele frequencies among populations can be used to estimate genetic divergence, which for example can be measured as F_{ST} . Genetic differentiation may reflect gene flow among populations, if they are in migration/drift equilibrium (Wright 1951). The allele frequencies within and among populations can further be used to calculate the probability of two individuals having identical genotypes (Taberlet & Luikart 1999), as well as from which population a genotype is most likely to originate from (Paetkau *et al.* 1995). The latter can thus be used to estimate the amount of dispersal among populations. Genetic similarity between individuals can be expressed as relatedness (*e.g.* Queller & Goodnight 1989), and the association between pairwise relatedness and geographic distance between individuals can be used to investigate dispersal patterns within populations.

Fox genes in time and space

Temporal – large scale

Neutral genetic variation is generated through mutation and is lost through genetic drift. In a longer time perspective, populations that are stable in size will reach an equilibrium both in terms of the number of alleles that are maintained (Kimura & Crow 1964) and the

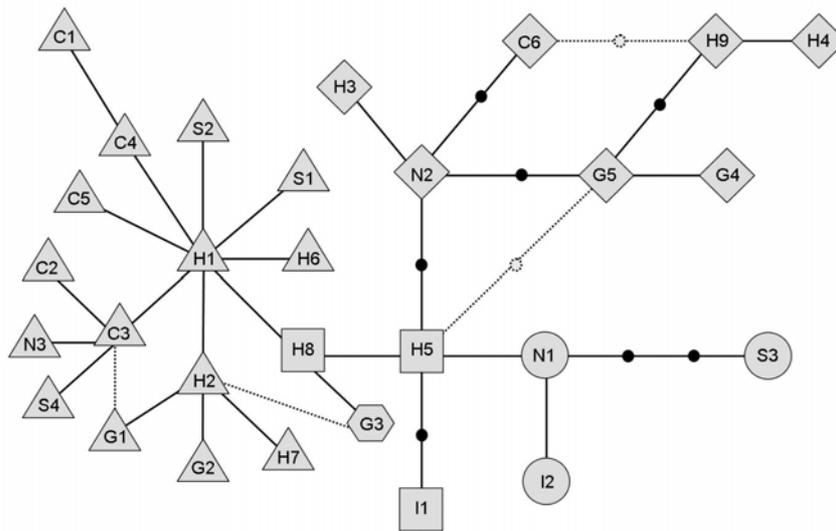


Figure 1. Minimum spanning network with haplotypes named after geographic origin: Holarctic (H), Nearctic (N), Canada (C), Siberia (S), Greenland (G) and Iceland (I). Each branch represents one mutational step; missing haplotypes are represented by a dot. Equally parsimonious branches are shown with dashed lines. The shape of the haplotypes illustrates the second nesting level in the nested clade analysis. Haplotypes H1 and H2 were found in 42% of all individuals.

genetic relationship among the alleles themselves (Fu 1997, Rogers & Harpending 1992). Consequently, deviations from these equilibria can be used to infer historical changes in population size.

Among the most important historical factors that have influenced the distribution and abundance of organisms are the glacial cycles (Taberlet *et al.* 1998, Hewitt 2001). Glaciations lasting some 100 000 years (*i.e.* Ice Ages) have come and gone over the last 2.4 million years (Webb & Bartlein 1992), with relatively short warm periods in between. The cold periods have forced temperate species in continental North America and Europe to endure repeated isolations in southern refugia, whereas the warmer interglacials have allowed them to expand northwards to recolonise previously glaciated regions (Hewitt 1996). Indeed, several temperate mammals display genetic signatures of post-glacial expansions in population size (Lessa *et al.* 2003). However, arctic species are likely to show different responses to the glacial cycles compared to temperate species (Hewitt 2004).

In Paper I, we investigated mtDNA variation in 191 arctic foxes in a sample

covering most of the species' distribution range. Since the arctic fox's current distribution is smaller than it was during the last Ice Age (Kurtén 1968, Kurtén & Anderson 1980, Sommer & Benecke 2005), we did not expect to find the patterns of post-glacial expansions in population size that are associated with temperate species. In total, we found 29 mtDNA haplotypes, where two haplotypes, H1 and H2, were found in 42% of all individuals (Fig. 1). The overall nucleotide diversity was relatively low ($\pi = 0.009$) and a significantly negative F_S value (Fu 1997) together with a mismatch analysis (Rogers & Harpending 1992) suggested that the arctic fox has gone through a rapid expansion in population size, which presumably was preceded by a demographic bottleneck. The time of this expansion, as suggested by the mismatch analysis, was 118 000 years before present. Although the confidence interval was large, this time coincides with the end of the last interglacial, which was approximately 5°C warmer than at present (Funder *et al.* 1998).

These results indicated that the previous interglacial had a negative impact on arctic foxes, and we therefore proposed that arctic

foxes respond to the glacial cycles in the opposite way to temperate species, contracting during interglacials and expanding during glaciations (Paper I). It has been suggested that the southern distribution of the arctic fox is limited by the red fox (Hersteinsson & Macdonald 1992), and it is therefore possible that increasing temperatures during interglacials have allowed red foxes to expand northwards, forcing arctic foxes to contract into northern refugia. Considering the higher temperatures during the last interglacial, and the presence of forest remains as far north as northern Siberia (Sher 1991), it is possible that the arctic fox was extinct in continental Eurasia and North America and only persisted in high-latitude islands. This reasoning also implies that the arctic fox currently is in a contraction phase, and that the onset of the Holocene was accompanied by a loss in genetic variation. Indeed, genetic analyses on Late Pleistocene arctic fox remains from central Europe and southern Russia (Dalén *et al. unpublished*) suggest a loss of haplotype diversity over the Pleistocene-Holocene boundary.

We also used the variation among mtDNA haplotypes to estimate the female long-term effective population size (Paper I). This was estimated at 32 000 females, which would correspond to an approximate world population of 160 000 adults. Since this estimate is not a major deviation from the current census population size of 330 000 - 930 000 individuals (Angerbjörn *et al.* 2004b), there was no indication of recent changes in global population size as have been reported for other canids (Vilà *et al.* 1999). However, on a local level, there have been recent changes in population size, most notably in Scandinavia where the arctic fox population declined from several thousand individuals (Tannerfeldt 1997) to a few hundred (Lönnberg 1927) in the beginning of the 20th century.

Temporal – mesoscale

Over a shorter time perspective, novel mutations are too rare to have any major impact on the neutral gene frequencies of a

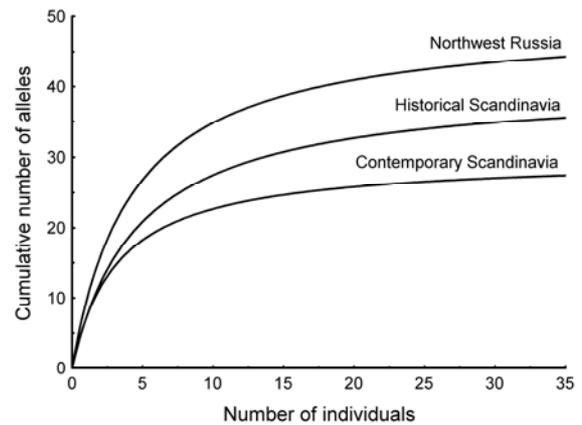


Figure 2. Cumulative number of microsatellite alleles with increasing sample size for northwest Russia, historical and contemporary Scandinavia. The estimates are based on averages from 5000 randomised iterations.

population and, if the population is large, genetic drift is negligible. Thus, over a time span of 25-50 generations, populations may display genetic continuity, which was empirically shown by Thomas *et al.* (1990). However, on a population level, new genetic variation can arise as a result of gene flow from neighbouring populations. Furthermore, in populations that go through demographic bottlenecks, genetic variation can be lost both through the bottleneck effect and subsequent genetic drift (Nei *et al.* 1975, Garza & Williamson 2001, *but see* Matocq & Villablanca 2001).

To evaluate the effect of the demographic bottleneck in the Scandinavian arctic fox, we analysed mitochondrial and microsatellite DNA variation in pre-bottleneck museum samples collected between 1831 and 1924 (Paper II). Comparisons with the contemporary population showed that the bottleneck had an impact on the genetic composition in Scandinavia. Four out of seven mtDNA haplotypes and 10-25% (Papers II and IV) of the microsatellite alleles have been lost (Fig. 2). Furthermore, a significant differentiation over time ($F_{ST} = 0.035$) suggests a shift in allele frequencies, probably due to genetic drift. Interestingly, although four mtDNA haplotypes had been lost, the remaining three had changed so much in frequency that the

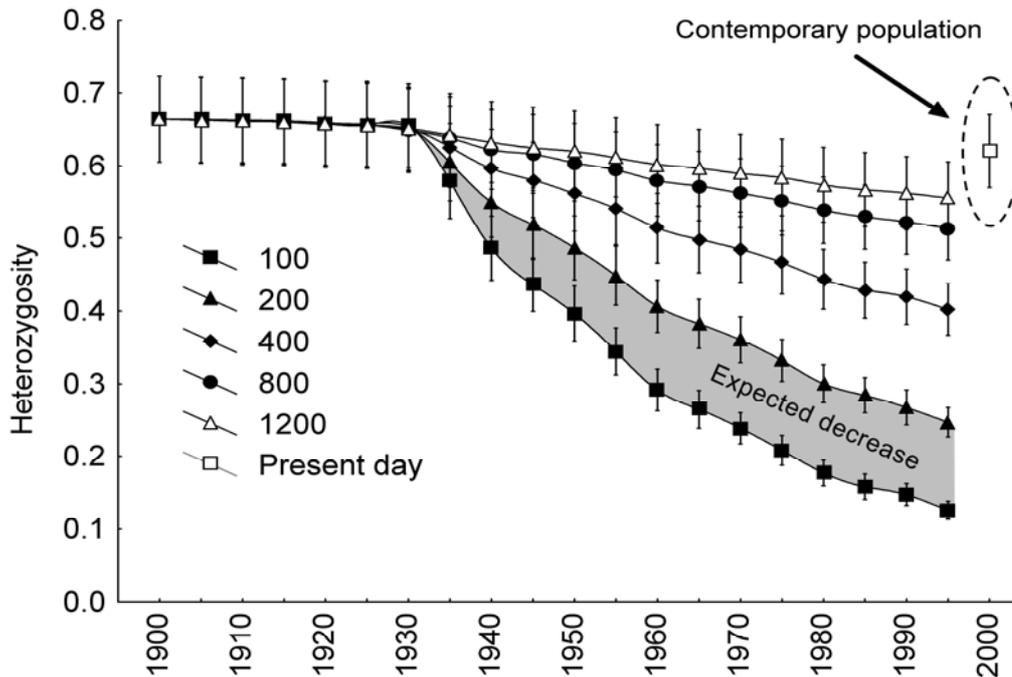


Figure 3. Results from the simulations using the pre-bottleneck microsatellite data. Error bars represent standard error. Five different post-bottleneck population sizes were used ranging from 100 to 1200 individuals. The results show that approximately 1200 individuals were needed to retain a heterozygosity similar to the one observed in the present day population, which is almost tenfold the estimated actual post-bottleneck population size of 100-200 individuals.

estimated haplotype diversity actually was higher after the bottleneck than before. There was no change in average heterozygosity over time, which is surprising considering the observed losses in other populations that have gone through demographic bottlenecks (Larson *et al.* 2002, Flagstad *et al.* 2003). The question, therefore, was whether the current level of genetic variation was higher than could be expected given the severity of the demographic bottleneck.

To resolve this, we performed a simulation of the bottleneck (Kuo & Janzen 2003) using the pre-bottleneck variation as input data (Paper II). The simulation suggested that the heterozygosity in the contemporary population was higher than could be expected given the known post-bottleneck population size (Fig. 3). This simulation assumed one single large population, and the observation in Paper IV of there being four relatively isolated populations in Scandinavia made the current high heterozygosity even more

surprising. It therefore seemed that new genetic variation must have been introduced to the population. Since mutation is unlikely to generate this amount of new variation over such a short time-span (Paper II), gene flow from another population after the bottleneck appeared as the most likely explanation (*e.g.* Hadly *et al.* 2004). The most probable source for this is the large and variable population in northwest Russia, although hybridisation with escaped farm foxes (*e.g.* Norén *et al.* 2005) should not be discounted, and needs to be better resolved.

Temporal – small scale

Variation in how genes are inherited will affect not only the gene pool of the population, but also the genetic variation within individuals. Genetic drift in a population can have an indirect effect on individual genetic variation, whereas inbreeding will reduce individual genetic variation directly (Wright 1921, Lande 1988).

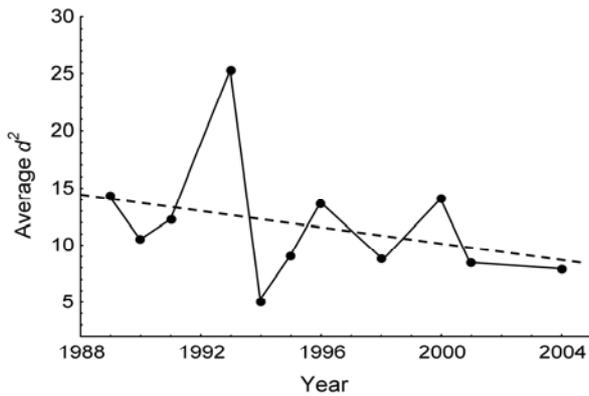


Figure 4. Average individual genetic variation (d^2) in juvenile arctic foxes born in the Vindelfjällen reserve between 1989 and 2004.

In species with large fluctuations in population size, the amount of genetic drift can be expected to vary among years and will be most pronounced during ‘low years’ which may act as genetic bottlenecks (*e.g.* Lindström *et al.* 2001). In Paper III, we analysed individual genetic variation in 156 juvenile arctic foxes born between 1989 and 2004 in the Vindelfjällen nature reserve. The amount of genetic variation, measured as d^2 , varied greatly among years (Fig. 4), but there was an overall decrease over time, which could be due to inbreeding or genetic drift.

Another small-scale temporal aspect involves the correlation in heterozygosity among loci. Such correlations can be caused by chromosomal proximity between the loci (*i.e.* linkage disequilibrium) or inbreeding (David 1998). Over the last decade, several studies have reported on correlations between heterozygosity in non-coding DNA markers and various fitness estimates (*reviewed in* Hansson & Westerberg 2002). Since non-coding DNA is thought to be selectively neutral, it has been suggested that such results are caused by an indirect correlation in heterozygosity between marker and fitness loci, a pattern that has been termed associative overdominance (Ohta 1971). Two hypotheses have been proposed to explain such associative overdominance, the general effect hypothesis (correlation caused by inbreeding) and the local effect hypothesis (correlation caused by linkage disequilibrium).

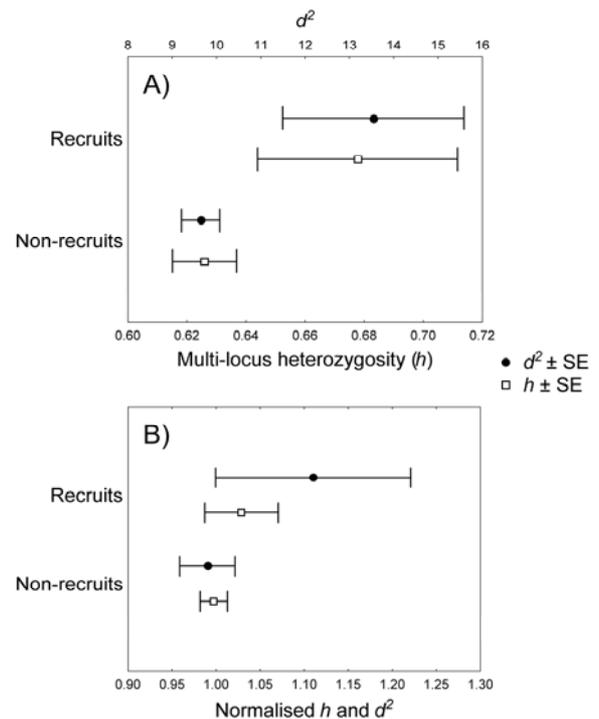


Figure 5. Microsatellite heterozygosity in Swedish arctic foxes comparing recruits ($n = 18$) and non-recruits ($n = 201$). Heterozygosity was measured as h and d^2 (A) and as normalised within-litter h and d^2 (B).

In an attempt to resolve these two hypotheses, we analysed microsatellite heterozygosity in 237 arctic foxes (Paper III). Recruits, defined as individuals that survived and reproduced, had significantly higher individual heterozygosity (measured both as h and d^2) than non-recruits, supporting an initial hypothesis of associative overdominance (Fig. 5). However, recruits were not more heterozygous than non-recruit siblings. In other words, the significant effect disappeared when individual heterozygosity was corrected for variance in the inbreeding coefficient. The results therefore favoured the general effect hypothesis, suggesting that the observed correlation was caused by inbreeding, which is not too surprising given the current small population size in Scandinavia.

Spatial – large scale

Genes travel through space by the movements of the individuals and gametes that carry

them. Therefore, the geographical distribution of neutral genes, and the genetic distance among them, provides information on gene flow and dispersal among populations (Avice *et al.* 1987). The connection between gene trees and geography, termed phylogeography, has also been frequently used to infer recolonisations and range expansions associated with the Ice Ages (Hewitt 1996).

On a circumpolar scale, the genetic relationships among arctic fox mtDNA haplotypes show that there are no distinct phylogroups (Paper I, Fig. 1). This indicates a lack of long-term geographical barriers during the last Ice Age. At the end of the Ice Age, arctic foxes must have recolonised formerly glaciated areas. Using a nested clade analysis (Templeton 1998), we could however find no clear genetic signatures of such range expansions (Paper I). There could be several explanations to this; for example, that these areas were colonised from local refugia (*e.g.* Frafjord & Hufthammer 1994), as has been suggested for other arctic species (Fedorov & Stenseth 2001). Alternatively, a high post-glacial gene flow could have erased the phylogeographical patterns of initial range expansions. In some instances, recolonisation may also have originated from regions where the arctic fox subsequently has gone extinct. In Fennoscandia, several carnivores display very low mtDNA variability, which has been suggested to be a consequence of their recolonisation history (Taberlet *et al.* 1995, Walker *et al.* 2001, Hellborg *et al.* 2002, Flagstad *et al.* 2003). In contrast, there were at least seven mtDNA haplotypes in the Scandinavian arctic fox prior to the 20th century bottleneck (Paper II). This high number of haplotypes could either be due to a high post-glacial gene flow, or that Scandinavia was colonised from several directions (Hewitt 1996).

The spatial distribution of mtDNA haplotypes suggested that there currently is a gene flow between the majority of the populations (Paper I). Presumed ancestral haplotypes were widespread and newly arisen haplotypes had yet not spread throughout the range of the species. Furthermore, there was

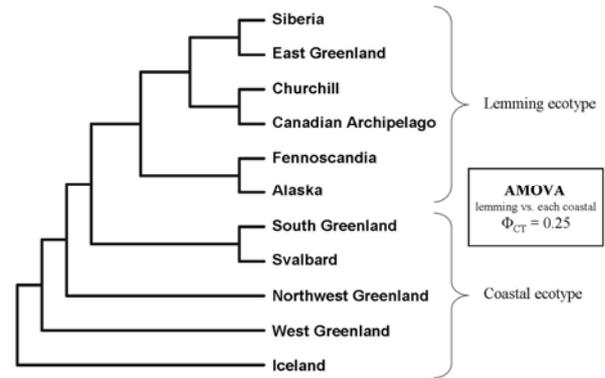


Figure 6. Population tree based on Φ_{ST} values, illustrating the most probable geographical structure in the analysis of molecular variance.

no phylogeographical structure in the minimum spanning network (Fig. 1), and estimates of genetic differentiation (measured as Φ_{ST}) among populations were predominantly low (Paper I). It is possible that the polar sea ice mediates gene flow among arctic fox populations. Iceland, which is the only population not connected to the other populations by the polar sea ice, also appeared to be the most isolated of the populations.

We could find no pattern of isolation by distance among the populations (Paper I). Instead, an analysis of molecular variance suggested that populations of the ‘lemming’ ecotype were more closely related to each other compared to ‘coastal’ fox populations (Fig. 6). This may reflect a higher gene flow among populations of ‘lemming’ foxes than between the two ecotypes or between ‘coastal’ fox populations. The ecological causes for such a pattern could be that arctic foxes from the lemming ecotype have a higher frequency of long distance migrations (Angerbjörn *et al.* 2004a), and that migrants from one type of habitat to the other have lower fitness compared to resident arctic foxes (Vibe 1967). However, as indicated in Paper II, the similarity in the mtDNA between Scandinavia and the other ‘lemming’ populations seems to be a consequence of recent genetic drift, suggesting that Scandinavia may not belong to the ‘lemming’ group in terms of genetic partitioning.

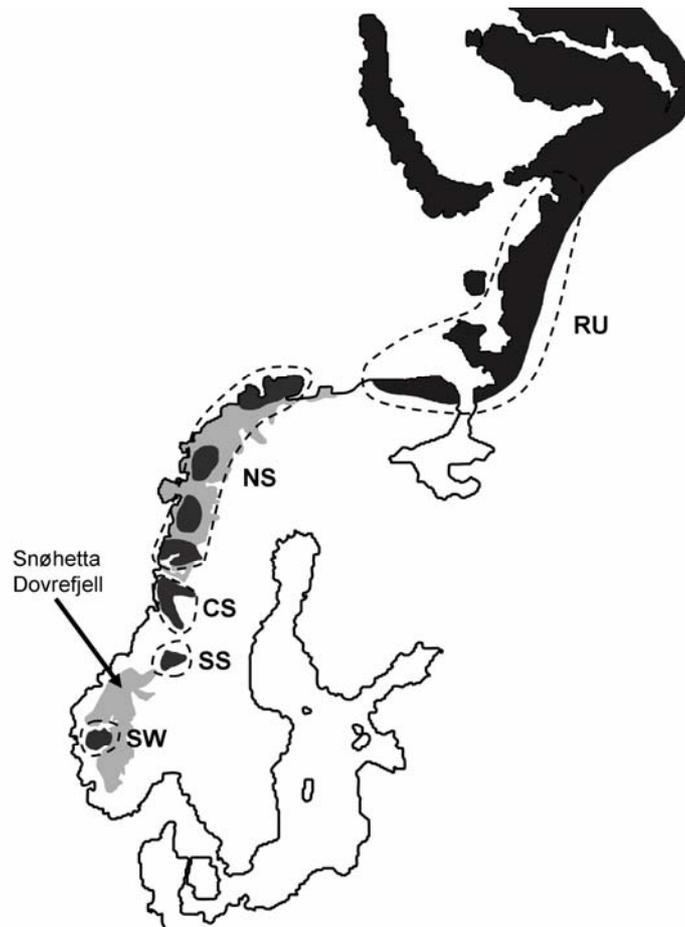


Figure 7. Map over the mountain tundra regions in mainland Europe. Dark grey areas show the current distribution of arctic foxes. Light grey areas illustrate mountain tundra no longer inhabited by arctic foxes. The five populations Russia (RU, $n = 21$), North Scandinavia (NS, $n = 64$), Central Scandinavia (CS, $n = 32$), South Scandinavia (SS, $n = 17$) and Southwest Scandinavia (SW, $n = 11$) are encircled by dashed lines. The Snøhetta/Dovrefjell region, a possibly extinct population, is also shown.

Spatial – mesoscale

Even small geographical barriers may impede or prevent dispersal between different habitats. Furthermore, the higher mortality often associated with dispersal (Waser *et al.* 1994) implies that individuals should minimise the time they disperse, and consequently the distance travelled from their birth place. Genetic variation can therefore be asymmetrically distributed on a regional scale and even within populations. Historical records suggest that the arctic fox in Scandinavia was capable of long distance dispersal, even through forested areas (Pulliainen 1965, Paper II). Such dispersal in the arctic fox could either be positively density dependent (Murray 1967), or an

adaptation to spatial synchrony in lemming fluctuations (Tannerfeldt & Angerbjörn 1996). Since the population density in Scandinavia has decreased dramatically over the last century, the former hypothesis predicts that dispersal in Scandinavia should have decreased, whereas the latter implies that dispersal should still be high.

In Paper IV, we investigated the spatial distribution of microsatellite DNA variation in Scandinavia. The results showed that the genetic variation was distributed in four genetic clusters, suggesting that there are four genetically differentiated populations in Scandinavia (Fig. 7). The Kola Peninsula and northwest Russia together formed a large fifth population.

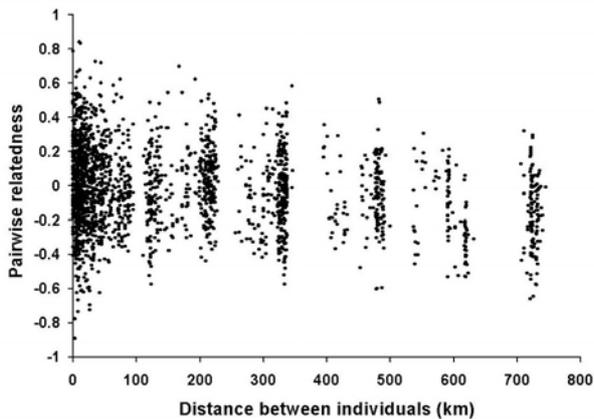


Figure 8. Pairwise relatedness (r in Queller & Goodnight 1989) and geographical distance between individuals within populations. There was no significant relationship between the two parameters ($p = 0.86$).

Within the populations, there was no relationship between pairwise relatedness and geographical distances among individuals (Paper IV, Fig. 8). This suggests that arctic foxes disperse for long distances within the populations, despite a high availability of empty territories close to natal dens. The results therefore supported the hypothesis that dispersal is an adaptation to the spatial synchrony in lemming fluctuations, rather than being density dependent.

Between the populations, however, population assignment tests showed that current dispersal is very low (Paper IV). Since the populations identified in the cluster analysis were composed of continuous mountain tundra and were separated by forested areas, this indicates that forested areas are significant barriers for dispersal. The relatively low F_{ST} values among the populations (Paper IV) could be due to that the populations are not in migration/drift equilibrium (Wright 1951). This observation, together with the historical accounts of long distance dispersal through forests, suggests that the current population subdivision may be a recent phenomenon. One possible explanation to this could be a recent altitudinal expansion of red foxes, reducing the amount of available high-quality arctic fox habitat (Elmhagen *et al.* 2002).

A comparison of the genetic variation in the Scandinavian populations showed that the average number of alleles and individual genetic variation (d^2) decreased from north to south (Paper IV). This, and the observation of a Russian genotype in northern Norway, supported an earlier hypothesis (Dalén *et al.* 2002, Paper I) of an ongoing gene flow from northwest Russia into Scandinavia. There are however some indications that the amount of gene flow may have decreased in connection with the demographic bottleneck in the beginning of the 20th century, since the genetic differentiation between northwest Russia and Scandinavia, as measured with F_{ST} statistics, seems to have doubled over the last 100 years (Paper II). Although the change in F_{ST} could equally well be attributed to recent genetic drift in Scandinavia, it is possible that the Kola Peninsula acts as an intermediate area in a stepping stone model (Kimura & Weiss 1964). A decrease in survival on the Kola Peninsula could then result in a lowered gene flow from Russia to Scandinavia.

Spatial – small scale

Interference competition among predators can force the inferior competitor to change its use of habitat (Palomares & Caro 1999), resulting in small-scale changes in a species' spatial niche. The threat from the dominant competitor may however change over time, for example between seasons. In such cases, the inferior competitor can be expected to change its distribution accordingly. On the mountain tundra in Scandinavia, arctic and red foxes are likely to have the same habitat preferences (*e.g.* Elmhagen *et al.* 2002). Being larger than arctic foxes, red foxes are dominant in direct interactions and may also kill arctic fox cubs if given opportunity (Frafjord *et al.* 1989, Tannerfeldt *et al.* 2002). This suggests that the cost for interactions with red foxes is higher in summer than in winter, since arctic foxes are not only outcompeted for resources during this period, but also risk losing their reproductive investment. We therefore predicted that arctic foxes should shift their spatial distribution in response to temporal variation in the threat

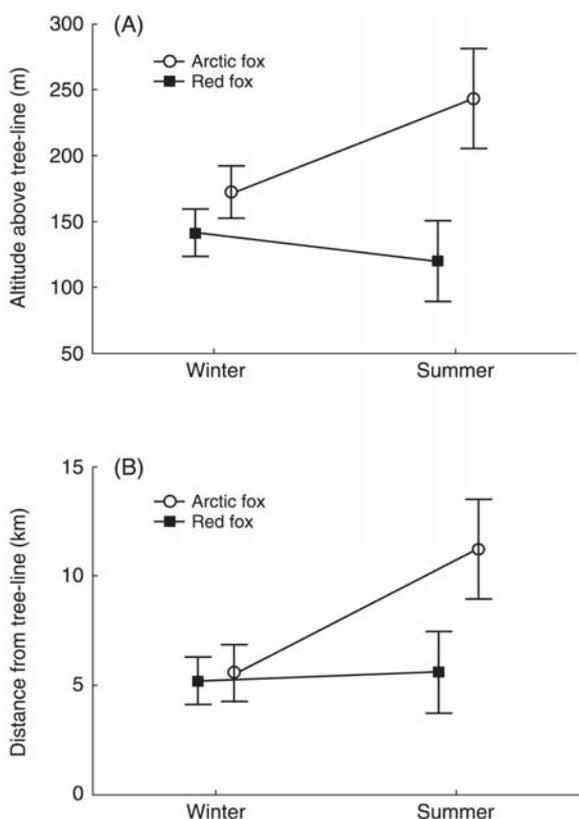


Figure 9. Mean relative altitude (A) and distance from tree-line (B) of arctic and red fox faecal samples in winter and summer. Faeces from red foxes were found at the same altitude and distance from tree-line during winter and summer, whereas arctic fox faeces were found at higher altitudes and farther from the tree-line during summer than winter.

from red foxes, causing the degree of spatial overlap between the species to vary between seasons (Paper VI).

Although carnivores can be difficult to study directly, faeces deposited by them provide an alternative, more accessible, source of information. Since faeces contain genetic material originating from the defecator, DNA analysis of faeces can be used to indirectly investigate the spatial movements of animals (Kohn & Wayne 1997). We therefore developed a method to separate faeces from red and arctic foxes (Paper V). This method was subsequently applied on 119 faecal samples systematically collected in four Swedish mountain areas (Paper VI). Arctic fox genes, and presumably also the

arctic foxes themselves, were found on higher elevations and further from the tree-line during summer than during winter. Red foxes appeared to be sympatric with arctic foxes in winter, and remained at the same elevation and distance from the tree-line in summer (Fig. 9). It therefore seems that arctic foxes go through small-scale shifts in distribution, and that this is caused by interference competition from the red fox.

The realized niche of the arctic fox thus seems to be limited by the distribution of the red fox, supporting the hypothesis by Hersteinsson & Macdonald (1992). The results from Paper VI further suggests that the southern distribution of the arctic fox mainly is determined by the summer distribution of red foxes. Future studies exploring the distribution of arctic foxes in response to climate change may thus do well to focus on the summer rather than winter distribution.

Conservation aspects

Distribution in Scandinavia

Analyses on faecal samples and data from reproductions show that the arctic fox no longer is continuously distributed on the mountain tundra in Scandinavia (Paper IV, Fig. 7). Instead, the arctic fox mainly persists in seven mountain areas. Regional extinctions seem to have taken place in Snøhetta/Dovrefjell and northern Finland. In Snøhetta/Dovrefjell, no reproductions have been documented since 1995 (Linnell *et al.* 1999). In northern Finland, there have been no confirmed reproductions since 1996 (Kaikusalo *et al.* 2000) and despite analysing 71 faecal samples with presumed arctic fox origin, we have been unable to confirm the presence of arctic foxes (Paper IV). However, the observation of an arctic fox in northern Finland in May 2005 (Matti Mela *pers. comm.*) offers hope for a future reestablishment.

An important finding in this thesis is that the arctic foxes on the Kola Peninsula genetically belong to Russia and that there are

four genetically distinct populations within Scandinavia (Paper **IV**, Fig. 7). Fennoscandia does therefore not constitute a biogeographical unit for arctic foxes, and consequently not a single unit for conservation. Instead of there being one large Fennoscandian population, there are four populations in Scandinavia alone. This has consequences both for the risk of extinction in Scandinavia, and how management should be directed in the future.

Threats

A recent survey (Elmhagen *et al.* 2004) reported a ‘best case’ estimate of 120 adults in Scandinavia. Assuming that the number of reproductions during the period 2000-2004 (Paper **IV**) reflects differences in population size among the populations, this would mean that there were approximately 10 adult arctic foxes in Southwest Scandinavia, 20 in South Scandinavia, 40 in Central Scandinavia and 50 in North Scandinavia. The small population size in each of the populations and the high degree of isolation between them suggests that the risk of extinction through demographic and genetic stochasticity is higher than previously thought (Paper **IV**).

The decrease of individual genetic variation observed in the Vindelfjällen nature reserve (Paper **III**, Fig. 4) suggests an ongoing genetic drift and/or inbreeding. Vindelfjällen is a part of the North Scandinavian population, which is the largest and most variable of the four populations. Genetic drift and inbreeding can therefore be expected to be even higher in the other three populations. In Paper **III**, we also showed that fitness was associated with individual genetic variation, and that this was likely to be caused by inbreeding depression (Fig. 5). In small populations with strong genetic drift, the deleterious alleles causing inbreeding depression may become fixed in the population despite selection to the opposite (Hedrick & Kalinowski 2000). This may decrease the population size further, which will be followed by even stronger genetic drift, which in turn may lead to fixation of even more deleterious alleles. In theory, this could lead

to a ‘mutational meltdown’ and ultimately extinction (Lynch *et al.* 1995).

Arctic foxes seem to avoid close inbreeding. Despite the small population sizes in Scandinavia, we have never observed a mating between full siblings (*unpublished data*). Although this is positive from an inbreeding perspective, it might make finding suitable partners difficult. This could lead to an Allee effect (Courchamp *et al.* 1999), which could further increase the risk of local extinctions (Loison *et al.* 2001).

Gene flow from northwest Russia into Scandinavia may be an important factor to maintain genetic variation in Scandinavia. Even though several lines of evidence suggest that there is an ongoing gene flow from northwest Russia into Scandinavia (Papers **I**, **II** and **IV**), the rate remains unknown although it is likely to be small (Paper **IV**). Gene flow from northwest Russia will primarily only be to the North Scandinavian population, suggesting that the connectivity between North Scandinavia and the other populations is an important factor determining the amount of genetic drift and inbreeding in the populations. Additional local extinctions as the ones in Snøhetta/Dovre fjell and northern Finland could further disrupt this connectivity, and might lead to a non-linear increase in extinction risk in Scandinavia as a whole (Hanski 1998).

Another threat has recently emerged in the form of hybridisation with escaped farm foxes. Norén *et al.* (2005) showed that escaped farm foxes occur on the mountain tundra in Hardangervidda (Southwest Scandinavia). Recent genetic analyses (Norén *et al. unpublished*) suggest that hybridisation may have taken place between wild and farm foxes in Hardangervidda. It is thus possible that the some of the observed inconsistencies in genetic variation and differentiation in Southwest Scandinavia are due to such hybridisation (Paper **IV**). More research is needed to resolve this, but hybridisation between farm and wild foxes is a potential threat since it might introduce additional deleterious alleles into a population already suffering from inbreeding depression.

Directions for management

The four populations in Scandinavia should be considered as separate management units (Moritz 1994). The current conservation actions in Scandinavia are mainly focused on supplementary feeding and red fox control. Dispersal between the populations seems to be very low (Paper IV), and it is thus unlikely that actions in one of the populations will have any demographic spin-off effects in any of the other populations. Since the persistence of all populations is important to preserve the connectivity within Scandinavia, actions need to be taken in all populations to be effective. The threat from interspecific competition with red foxes (Tannerfeldt *et al.* 2002) seems to be especially high during summer (Paper VI). This suggests that the efficiency of red fox control is largely determined by the success in excluding red foxes from arctic fox habitats during the arctic fox's reproductive season.

Inbreeding depression, loss of genetic variation through genetic drift and the Allee effect are potentially large threats to the persistence of the arctic fox in Scandinavia. One possible action to increase viability is genetic restoration through translocation, both through augmentation of existing populations or reintroduction to regions where the arctic fox is currently extinct (Moritz 1999). There are several examples where translocation has restored fitness in populations suffering from inbreeding (*reviewed in* Hedrick 2001). The results presented in Paper III suggest that this could have a positive effect also in the Scandinavian arctic fox.

There is however a risk that translocation can lead to outbreeding depression through loss of local adaptations or disruption of coadapted gene complexes (Templeton 1986). The choice of source population is therefore an important issue, and it has been suggested that translocations should not take place between too genetically different populations (IUCN 1987). However, genetic differentiation in neutral loci might reflect recent fragmentation, without there being any important adaptive differences between the populations (Hedrick 2001). Moritz (1999) suggests that a possible strategy to avoid

outbreeding depression might be to translocate individuals between populations that have historically exchanged genes. The results in Paper IV suggested that the observed fragmentation within Scandinavia could be a recent phenomenon. Furthermore, there seems to have been a historically higher connection between Scandinavia and north-west Russia (Paper II). It therefore seems that translocation of individuals within Scandinavia, or from Russia to Scandinavia, is a viable option in the management of the Scandinavian arctic fox.

There are however always going to be risks involved with translocations. Even when there is no differentiation in neutral gene frequencies, there might be adaptive differences between geographical regions (Hedrick 2001), and individuals that are translocated may introduce novel diseases. The risk of a translocation must therefore be weighed against its potential benefits. For translocations within Scandinavia, the risks are likely to be small since it is unlikely that there are adaptive differences between these populations and the possibility of introducing new diseases is minimal. Translocation from Russia might be a more risky course of action, but then again, the pay-off could be higher.

An arctic perspective

The Arctic differs from more temperate regions in several ways that might affect arctic species, both in a temporal and a spatial perspective. It is likely that typical arctic habitats have been more extensive during Ice Ages than during interglacials. This suggests that the reversed response to glacial cycles, as proposed for the arctic fox (Paper I), may be a general phenomenon among cold adapted species. Indeed, both reindeer (*Rangifer tarandus*; Flagstad & Røed 2003) and collared lemmings (*Dicrostonyx torquatus*; Fedorov & Goropashnaya 1999) display genetic signatures of expansions in population size similar to that observed in the arctic fox (115 000 and 140 000 BP respectively). Similarly, rock ptarmigan (*Lagopus mutus*) in

Beringia and the Nearctic may have diverged from a common ancestor around this time (Holder *et al.* 1999). Furthermore, range contractions during the Pleistocene-Holocene boundary have been suggested for both arctic and alpine species (*e.g.* Ehrich *et al.* 2000, Pérez *et al.* 2002), where the latter may have contracted from a wide glacial distribution to elevational isolation in different mountain ranges. Long-term refugia for cold adapted species may thus include both high-latitude and high-altitude regions. Such refugia, if they have provided enough suitable habitat during warm periods and were not glaciated during cold periods, could be expected to display particularly high levels of genetic variation. Post-interglacial expansions of cold adapted species may prove difficult to study using phylogeography in a conventional sense, since these species currently are in a contraction phase. However, retrieval of DNA from fossil material using ancient DNA techniques (*e.g.* Wayne *et al.* 1999) could provide a solution to this problem.

One might ask if there are any principal differences between glacial responses of arctic and more temperate species, and what the evolutionary consequences of such differences might be. First, when temperate species contract southwards, they also diverge in a sense that there are several refugia, which are geographically separated from each other. When arctic species contract, on the other hand, they converge towards the pole. Second, the time spent in refugia is longer for temperate species than arctic species, since glacials last for longer time than interglacials. In general, the glacial cycles could therefore be expected to have caused less genetic divergence in arctic species compared to temperate species. Convergent contractions in arctic species may also have resulted in a higher degree of phylogeographic congruence among arctic species than has been observed for temperate species (Taberlet *et al.* 1998), allowing for a higher degree of long-term coevolution among species (Sullivan *et al.* 2000).

A common feature for many arctic predators are the strong fluctuations in

resource availability in time and space, for example the population fluctuations in small rodents, which in general are synchronous over large distances (Krebs *et al.* 2002). This may force arctic predators to disperse over long distances (Tannerfeldt & Angerbjörn 1996, Paetkau *et al.* 1999, Wiklund *et al.* 1999, Fuller *et al.* 2003). A generally high dispersal in arctic predators can be expected to lead to high levels of gene flow among geographic regions, which from an evolutionary perspective may counteract local adaptation.

In conclusion, the interactions that determine the distribution and abundance of genetic variation in arctic species may include large-scale changes in habitat availability caused by the glacial cycle. For predators, such as the arctic fox, dispersal is likely to be high due to fluctuations in resource availability, which may counteract genetic divergence and local adaptation. Furthermore, competition with more temperate species may affect the spatial distribution of arctic species both on large and small scales, and the presence of competitors in forests and low-altitude mountain areas may act as barriers to dispersal.

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Sammanfattning på svenska

Inledning

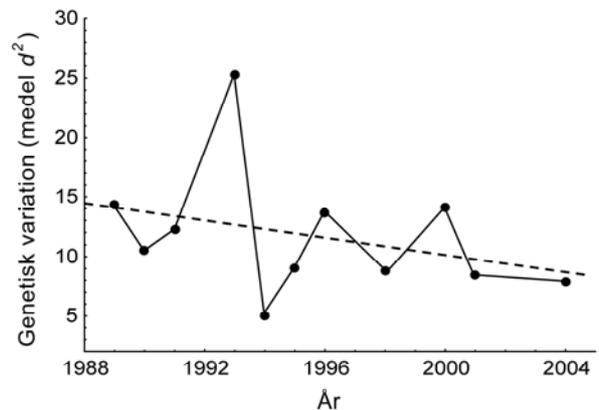
Både mängden och den geografiska utbredningen av genetisk variation i en organism styrs av hur dess gener rör sig genom tid och rum. I ett tidsmässigt perspektiv så uppstår ny genetisk variation genom mutation, medan den (om den är selektivt neutral) förloras genom en process som kallas slumpmässig drift genetisk drift. Den genetiska driften i sin tur, beror på populationsstorleken: ju mindre populationen är desto starkare är driften, och desto mer variation förloras. Förändringar i populationsstorlek påverkar alltså den genetiska variationen hos en organism. Sådana förändringar kan bero på allt från storskaliga processer som till exempel klimatförändringar i samband med istider, till konkurrens med andra arter och mänsklig påverkan.

Spatiala rörelser hos gener sker genom att individer som bär på dem flyttar sig. Sådana spatiala rörelser kan till exempel orsakas av att individer behöver söka nya födokällor eller partners, eller av att mängden tillgängligt habitat förändras. Individens spridning påverkas och styrs även av geografiska barriärer, vilka kan vara allt från hav och bergskedjor till små bäckar eller habitat av lägre kvalitet.

Den här avhandlingen handlar om hur genetisk variation hos fjällräv fördelar sig mellan geografiska regioner och vad detta beror på. För att ta reda på detta har ett antal prover analyserats med hjälp av DNA-teknik. Proverna bestod av vävnad, hår och spillning vilka samlats in från större delen av fjällrävens utbredningsområde.

Temporala processer

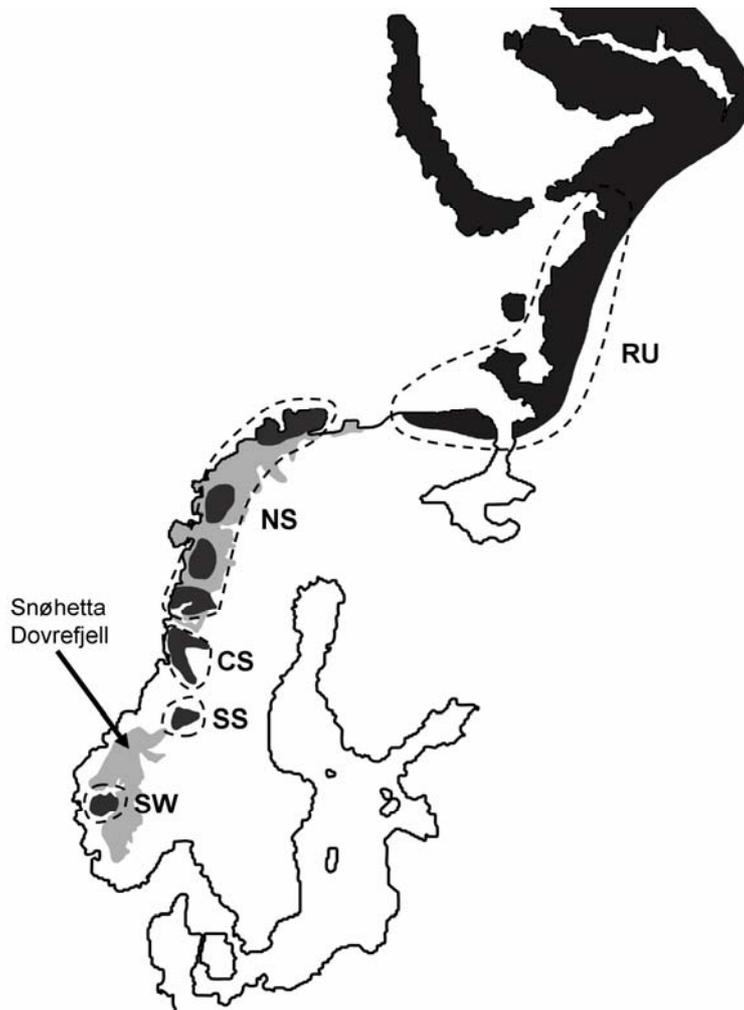
Istiderna som har kommit och gått under de senaste 2,4 miljoner åren anses ha haft en stor inverkan på arters utbredning och populationsstorlek. Arter som lever i tempererade miljöer har minskat i utbredning och populationsstorlek under istiderna, för att sedan återkolonisera mer nordliga bredd-



Figur 1. Medelvärden för genetisk variation på individnivå (d^2) hos fjällrävar födda mellan 1989 och 2004 i Vindelfjällens naturreservat.

grader under värmeperioder. Fjällräven är ju däremot en arktisk art som trivs när det är kallt, och vi ville därför undersöka hur den glaciala cykeln påverkat dess genetiska variation och populationsstorlek. Genom att analysera DNA hos fjällrävar från hela artens utbredningsområde fann vi tecken på att fjällräven expanderat kraftigt i populationsstorlek i samband med att den senaste istiden började för cirka 118 000 år sedan (Artikel I). Detta skulle kunna tyda på att fjällräven går igenom flaskhalsar under värmeperioder, och expanderar under istider.

I Skandinavien har fjällräven även gått igenom en mycket mer recent flaskhals. Detta skedde i början av 1900-talet, då fjällräven jagades så hårt att den minskade från uppskattningsvis 10 000 individer till några hundra stycken. I syfte att undersöka om, och hur mycket, genetisk variation som förlorats så analyserade vi DNA-prover från ben och tänder som samlats in från tiden strax innan flaskhalsen (Artikel II). Resultaten visade att en del genetisk variation mycket riktigt hade förlorats, men inte så mycket som man kunde förvänta sig. Detta var något överraskande, men det skulle kunna bero på att det kommit in ny genetisk variation till Skandinavien efter flaskhalsen. Det troligaste är att detta skett genom att fjällrävar vandrat in från nordvästra Ryssland.



Figur 2. Karta över fjällrävens nuvarande (mörkgrått) och historiska (ljusgrått) utbredning i Europa. De fem populationerna Nordvästra Ryssland (RU), Norra Skandinavien (NS), Centrala Skandinavien (CS), Södra Skandinavien (SS) och Sydvästra Skandinavien (SW) är inringade med streckade linjer.

Vi har även undersökt hur den genetiska variationen på individnivå förändras i en kort tidsskala. Detta har vi kunnat göra genom att analysera DNA-prover från fjällrävarna i Vindelfjällens naturreservat, vilka vi studerat under de senaste 16 åren (Artikel **III**). Vi fann här att den genetiska variationen varierar mycket från år till år, men att den sett över hela 16-årsperioden minskade något (Fig. 1).

Vi fann även att individer som överlevde och reproducerade sig hade en högre genetisk variation än de som inte gjorde det. Detta tyder på att det förkommer inavel i Skandinavien, och att denna påverkar överlevnaden negativt.

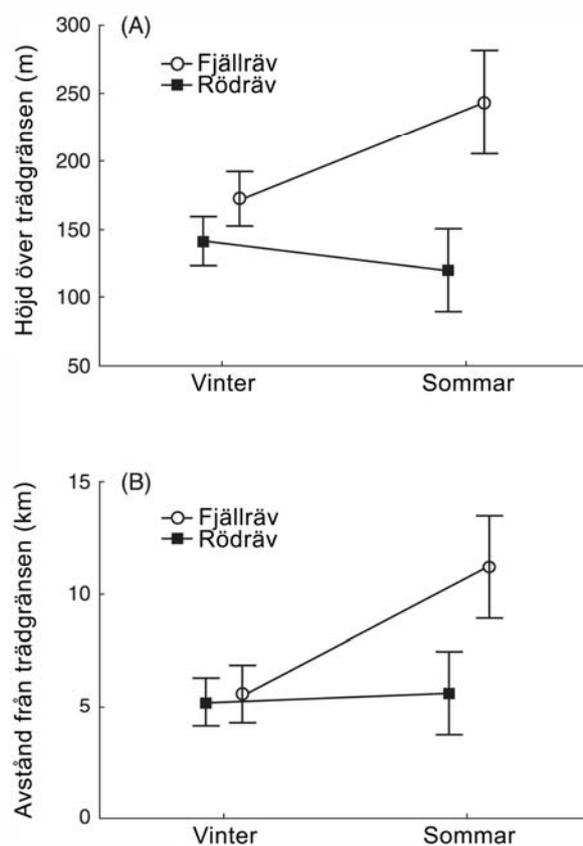
Spatiala processer

Fjällrävar är ovanligt bra på att förflytta sig över långa sträckor, och gör ofta så. Till exempel har man återfunnit märkta fjällrävar som gått mer än 100 mil över polarisarna. Sett i en stor skala, över hela Arktis, så fann vi inte heller några större genetiska skillnader mellan populationerna (Artikel **I**). Populationer som består av rävar som äter lämlar (Sibirien, Kanada, Alaska, Ost-Grönland och Skandinavien) är dock närmare släkt med varandra än sådana som lever i kustmiljöer (övriga Grönland, Island och Svalbard), vilket skulle kunna bero på att de förstnämnda sprider sig mer. Island tycks vara den mest isolerade populationen, vilket inte är så

konstigt med tanke på att havet runt Island är isfritt året runt.

Inom Skandinavien hade vi inte förväntat oss att hitta någon geografisk uppdelning mellan olika fjällområden, eftersom fjällrävarna är såpass bra på att sprida sig. Till exempel visar historiska data att långvandrande fjällrävar ibland återfanns så långt söderut som Falsterbo i Skåne. Det finns dock två hypoteser om varför fjällrävarna ger sig iväg på långvandringar. Den ena är att de gör detta för att hitta ett område där lämmelpopulationen är i uppgångsfas, och den andra är att de gör det för att slippa konkurrens från andra fjällrävar. Vi fann i Artikel IV att fjällrävarna i Skandinavien är uppdelade i fyra populationer (Fig. 2), men att spridningen inom dessa tycktes vara hög, trots att det numera finns gott om tomma revir i närheten av där de föds. Det verkar alltså som om fjällrävar sprider sig i jakt på lämmeltoppar. Däremot verkar det ovanligt att fjällrävarna flyttar sig mellan populationerna. Eftersom populationerna avgränsas av skogsland så kan man gissa att fjällrävarna numera drar sig för att ge sig ned i skogen, möjligen på grund av att det finns så mycket rödräv där. Resultaten visade även att fjällrävarna på Kolahalvön tillhör den ryska populationen. Flera olika analyser pekar dock på att det finns en viss grad av spridning från Ryssland in i Skandinavien, åtminstone till den nordligaste av de skandinaviska populationerna.

Konkurrens mellan arter kan resultera i att den ena arten förändrar sin utbredning. I Skandinavien finns ett konkurrensförhållande mellan fjällräv och rödräv, där den senare är dominant i direkta interaktioner. Dessutom dödar rödräven fjällrävsvalpar om den får tillfälle till det. På grund av det sistnämnda kan man tänka sig att hotet som rödrävarna utgör är större under sommaren än under vintern. Vi ville därför undersöka hur detta påverkar fjällrävens utbredning. Genom att analysera DNA från spillningsprover som samlats in i fjällen kunde vi identifiera från vilken art varje prov kom från (Artikel V). Genom att sedan jämföra detta med data på varifrån varje prov samlats in, kunde vi dra slutsatsen att på vintern så finns fjällrävarna



Figur 3. Medeltal för relativ höjd över havet (A) och avstånd från trädgränsen (B) för insamlade spillningsprover på fjället under sommaren och vintern. Spillning från rödräv fanns på samma höjd över havet och på samma avstånd från trädgränsen under sommar och vinter, medan spillning från fjällräv fanns på högre höjd och längre från trädgränsen under sommaren jämfört med vintern.

på samma höjd och på samma avstånd från trädgränsen som rödrävarna. Men under sommaren tycks fjällrävarna flytta högre upp i fjällen och längre bort från trädgränsen, medan rödrävarna stannar kvar i de lägre liggande, mer produktiva, habitaterna (Artikel VI, Fig. 3).

Konsekvenser för bevarande

Fjällräven i Skandinavien är idag uppdelad i fyra populationer: Sydvästra Skandinavien (Hardangervidda), Södra Skandinavien (Helags/Sylarna), Centrala Skandinavien (Stekenjokk/Børgefjell), samt Norra Skandinavien (från Vindelfjällen i söder till Varangerhalvöya i norr). Fjällrävarna på Kolahalvön

tillhör inte Skandinavien, utan den ryska populationen (Fig. 2).

Den senaste uppskattningen av antalet fjällrävar i Skandinavien gjordes 2004 och angav att det i bästa fall då fanns cirka 120 fjällrävar. Om man antar att antalet reproduktioner under perioden 2000-2004 (Artikel **IV**) speglar skillnader i populationsstorlek mellan de olika populationerna, så fanns det 2004 cirka 10 vuxna rävar i sydvästra Norge, 20 st i Helags/Sylarna, 40 st i Stekenjokk/Børgefjell och 50 st i den stora nordliga populationen. Den låga populationsstorleken i varje enskild population, i kombination med graden av isolering mellan dem, innebär att utdöenderisken genom inavel och rena slumphändelser är större än man tidigare trott (Artikel **IV**).

Minskningen av genetisk variation i Vindelfjällens naturreservat under perioden 1989-2004 tyder på en pågående genetisk drift eller inavel (Fig. 1). Detta verkar även påverka fjällrävarnas överlevnad negativt, vilket tyder på att fjällrävarna i Skandinavien lider av inavelsdepression (Artikel **III**). I små populationer kan genetisk drift leda till att skadliga genvarianter fixeras i populationen trots selektion för det motsatta. Detta kan då leda till att populationen minskar ytterligare, vilket i sin tur skapar en ännu starkare genetisk drift med fixering av ännu skadligare genvarianter som följd. Denna process kallas 'mutational meltdown' och kan leda till att en population dör ut. Inflöde av gener från den ryska populationen, samt mellan de skandinaviska populationerna, kan tänkas vara en viktig faktor för att bevara mängden genetisk variation i Skandinavien. Flera analyser tyder på att det förkommer ett sådant inflöde av gener, åtminstone från Ryssland till den norra populationen, men graden tycks vara liten och har eventuellt minskat under de senaste 100 åren (Artiklar **I**, **II** och **IV**).

De fyra populationerna i Skandinavien bör behandlas som separata bevarandeenheter. De bevarandeåtgärder som i dagsläget pågår är utfodring och jakt på rödräv. Eftersom spridningen mellan populationerna tycks vara mycket liten (Artikel **IV**), så är det osannolikt att bevarandeåtgärder i en population har några positiva 'spin-off' effekter på de andra populationerna. Bevarandeåtgärder bör därför ske i alla populationerna. Den norra populationen måste här anses vara särskilt viktig eftersom det är möjligt att den upprätthåller en kontakt mellan Ryssland och övriga Skandinavien. Vad gäller jakten på rödräv, så tyder resultaten från Artikel **VI** på att närvaro av rödräv främst är ett hot under sommaren. Även om åtgärden sker vintertid bör syftet vara att hindra rödrävar från att etablera sig i goda fjällrävshabitat under våren och sommaren.

Inavelsdepression och genetisk drift är potentiellt stora hot mot fjällrävens fortsatta överlevnad i Skandinavien. En tänkbar åtgärd för att minska risken för utdöende i Skandinavien är att flytta fjällrävar, antingen mellan populationerna inom Skandinavien eller från Ryssland till Skandinavien. Sådana omflyttningar har hos flera andra arter visat sig ha en positiv effekt. De risker som finns med en sådan omflyttning kan till exempel vara att olika populationer har olika lokala anpassningar, speciellt om de varit isolerade från varandra en längre tid. Resultaten i denna avhandling tyder dock på att graden av isolering mellan de skandinaviska populationerna är ett nytt fenomen, samt att graden av genetisk differentiering mellan Skandinavien och Ryssland var mycket mindre för hundra år sedan jämfört med idag. Att flytta fjällrävar mellan populationerna kan därför vara en tänkbar, och kanske nödvändig, åtgärd för att säkra fjällrävens fortsatta överlevnad i Skandinavien.

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It is a pretty cool thing to be able to stand on the shoulders of giants and peek over the horizon. This thesis is the result of past efforts of so many people, I hardly know where to begin. The results are of course an extension of an immeasurable amount of previous scientific work, not least by researchers in arctic fox biology. I have had an enormous help by people more versed in genetics and DNA-methodology than me, many people have been great help and company at the department, and several persons have been kind enough to provide comments on manuscripts and other texts. I am immensely grateful to the field workers in the Swedish arctic fox project who have walked more than 17 000 km when collecting the samples analysed in this thesis. The genetic analyses and the travels to various places in the Arctic and other less cold places have cost a neat sum of money, and the organisations providing the funding deserve recognition (one of the faecal samples from the Kola Peninsula may well be one of the most expensive DNA samples ever analysed...)

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