Translocation Evaluation Report
SEFALO+

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Introduction

Population fragmentation and declines in population size constitute an increasing threat to species across the world. These processes are often caused by human activities in the form of habitat degradation, changes in land use and, more recently, global warming. One of the most serious consequences of these processes from a conservation perspective is that the intrinsic rate of population growth can be reduced when population sizes are small (Courchamp et al. 1999a). The underlying reasons for this process, know as the Allee effect, can either be genetic or demographic. Genetic threats to populations include inbreeding depression and loss of genetic variation through genetic drift (Hedrick and Kalinowski 2000). Demographic threats are comprised of both stochastic processes leading to, for example, unequal sex ratios and loss of intra-specific cooperation (Courchamp et al. 1999a). Both the genetic and demographic components of the Allee effect may lead to local extinction of isolated subpopulations, and may in the end result in the whole population becoming extinct.

One potential solution to the problem of reduced growth in small populations is to augment isolated populations with individuals from other populations (Hedrick 2001; Tallmon et al. 2004). Changing the demographic properties of a population does however require the movement of quite large numbers of individuals. Offsetting the negative effects of inbreeding depression, on the other hand, can be accomplished using only a small number of individuals (Tallmon et al. 2004).

In addition to augmenting small existing populations, it is also possible to reintroduce a species in areas where it has already become locally extinct. Local extinctions may cause a non-linear increase in extinction risk for the population as a whole (Hanski 1998), both through an increase in inbreeding depression and through a loss of metapopulation dynamics. Local reintroductions can therefore alleviate the threat to the population as a whole, both from a genetic and demographic perspective.

The purpose of this report is to give an overview of translocation as a tool in conservation programs, and to evaluate whether this could serve as an appropriate conservation action in the management of the Scandinavian arctic fox. The term translocation is defined as the deliberate movement of individuals from one location to another (Moritz 1999), and comprises both augmentation of threatened populations and reintroduction into areas where the species has become extinct (IUCN 1987).

The genetic perspective
The purpose of translocation is often to obtain a genetic rescue effect (Tallmon et al. 2004), where the introduction of new genes to the population results in increased population fitness through heterosis. The basis for this is that inbreeding causes an increase in homozygosity of deleterious recessive alleles, leading to inbreeding depression in the population (Hedrick and Kalinowski 2000). Mating between genetically divergent individuals will lead to more heterozygous offspring, thus alleviating the effects of inbreeding depression. It should also be pointed out that immigrants to populations displaying inbreeding avoidance may provide a boost to the population from a purely demographic perspective (Liberg et al. 2005). Genetic rescue has been demonstrated in a number of studies, ranging from plants (Erickson and Fenster 2006) to

mammals (Hogg et al. 2006). Augmentation of populations through translocation thus has the potential of being a powerful tool for conservation biologists.

There is, however, a flip side to the coin. Introduction of genetically different individuals can also have an opposite effect to genetic rescue since it can cause a reduction in population fitness due to outbreeding depression. Such outbreeding depression can result from disruption of coadapted gene complexes or epistatic interactions (Edmands 2007). Local adaptations may also be lost if maladaptive genes introduced by immigrants become fixed in the population since genetic drift may be a stronger force than selection in small populations (Hedrick and Kalinowski 2000). In some cases, translocation could also lead to a simultaneous heterosis and outbreeding depression. Whether the end result is an increase or decrease in the population's fitness then depends on which force is the strongest. It should however be noted that the relative importance of these to processes may change over time. Indeed, several studies have shown that an initial fitness increase in the F_1 generation is reversed by outbreeding depression in later generations (Armbruster et al. 1999; Marshall and Spalton 2000; Marr et al. 2002).

The demographic perspective

In addition to genetic problems, small populations may suffer from a range of other problems associated with low density (Courchamp et al. 1999a). Small populations may go through stochastic fluctuations in sex-ratio, which can reduce population growth. Small populations may also face a loss of intra-specific cooperative interactions (also termed facilitation). Such problems include difficulties in encountering mates, decreased juvenile survival due to low colony sizes and loss of efficient anti-predator strategies (Courchamp et al. 1999a). These types of phenomena can even cause population growth to become negative if the population is below a certain critical threshold. Alleviating such problems through translocation may be difficult from a conservation perspective, since impractically large numbers of individuals may be required to reach the critical threshold. However, translocation of only a few individuals can, as noted above, have significant effects on the genetic health of a population, which in turn may induce population growth sufficient to reach the demographic threshold.

Deciding whether to translocate

In order to decide on, and successfully carry out, a translocation program, three key questions need to be answered. The first question is whether the translocation is likely to have the desired positive effect. To answer this, it needs to be established if the population suffers from a decreased population growth due to its small size. The second question is whether a translocation could have any negative effects, such as a loss of local adaptations, disruption of epistasis or exposure to novel diseases. It is, however, quite possible that a translocation could have both positive and negative effects, and in that case it is important to evaluate if the action will have a net benefit or not. If it is found that a translocation is likely to have a positive effect, the third question is how it should be carried out in practice.

1a. Does the population suffer from inbreeding depression?

There are a number of different ways to assess if a population is suffering from inbreeding depression. The most straightforward is to use stud book data to calculate each individual's inbreeding coefficient and then compare that to different fitness estimates (Liberg et al. 2005; Bensch et al. 2006). If, as is often the case for wild populations, studbook data is unavailable, genetic analysis can provide an indirect way to measure the level of inbreeding in a population. This can be accomplished through a general assessment of the genetic variability of the population, and more accurately by testing for heterozygosity fitness correlations (Hansson and Westerberg 2002). Assessing whether individuals avoid mating with relatives may also give clues to whether inbreeding is a problem. Inbreeding depression can however in some cases be difficult to detect, for example if there is little variation in inbreeding coefficients among individuals due to that the whole population is heavily inbred (Hedrick and Kalinowski 2000).

1b. Are there any other demographic problems?

Apart from the rather obvious problem of skewed sex ratios, which is relatively straightforward to detect, demographic problems related to small population size are often dependent on the biology of the species in question. In-depth knowledge of a species' mating system, social and anti-predator behaviour, dispersal patterns, habitat preferences and other aspects of its biology is of importance to evaluate whether the population is below a critical demographic threshold (Courchamp et al. 1999b; Courchamp and Macdonald 2001; Gascoigne and Lipcius 2004).

2a. Is there a risk of outbreeding depression?

The risk of outbreeding depression depends on how differentiated the target population is from the putative source population. It should be noted, however, that outbreeding depression may occur even if both parental populations are adapted to the same environmental conditions, due to disruption of coadapted gene complexes (Frankham et al. 2002). One approach to assess the risk of outbreeding depression is through population genetic analyses, which can be used to estimate the degree of genetic variation among populations and the degree of shared history between the source and target populations. In addition, data on local adaptations such as litter size, feeding behaviour, timing of the mating period and parturition is often available from ecological studies. However, the degree of local adaptation can in some cases be overestimated due to difficulties in distinguishing phenotypic plasticity from true local adaptations (McKay and Latta 2002). On the other hand, some local adaptations may be cryptic and difficult to identify. Both these issues can potentially be resolved through quantitative genetic analyses of the source and target populations, for example through Q_{ST} statistics (McKay and Latta 2002).

2b. Is there a danger of exposure to novel diseases?

There is a risk that translocated individuals may introduce a novel disease or parasite into the endangered target population, having been exposed to the infection either in the source population or during captivity. Several guidelines have been published to deal with this problem (Cunningham 1996), including health screening of individuals (Mathews et al. 2006). Conversely, translocated individuals may also be susceptible to

diseases indigenous to the source population, which could add to the stress already induced by captivity and handling. In such cases, it may be necessary to vaccinate individuals brought in to the translocation program before they are released (Cabezas et al. 2006).

3. How should it be done in practice?
Before initiating a translocation program, it is important to establish its long-term objectives. This is because the long-term objective, for example whether to maximise the population size or maximise long-term persistence, affects how the translocation should be done in practice (Rout et al. 2007). Similarly, although translocation programs should always be designed so that their success can be evaluated, the optimal strategy for evaluation (*e.g.* using control populations) may often be in conflict with the goal of maximising conservation success.

In general, a translocation program requires the involvement of personnel from several disciplines and agencies, including biologists, government agencies, veterinarians, zoos and non-governmental organisations. In some cases, it may also be necessary with cooperation across national borders. One of the first steps in any translocation program is to identify a suitable source population (Edmands 2007). This can either be a captive or a wild population. Consideration may also need to be taken to avoid negative impacts on the source population when individuals are harvested from it, especially if the source population is small. Following this, it is important to determine the optimal way to release the individuals. This can be done through ecological modelling and population viability analysis, combined with genetic data on population structure, inbreeding and gene flow among populations. Such analyses can help to determine how many individuals should be translocated, as well as which and how many geographic locations to target (Armstrong and Davidson 2006; Rout et al. 2007; Seddon et al. 2007).

Depending on the ecology of the species in question, it also needs to be determined whether to translocate adults or juveniles (Robert et al. 2004), the optimal sex ratio of released individuals (Sigg et al. 2005), during which season they should be released (Sheller et al. 2006), whether to use "soft" or "hard" release (Bright and Morris 1994), and in cases of wild source populations, how much time should be spent in captivity prior to release (Molony et al. 2006). In cases where the source population is large and individuals can be readily caught, it may also be possible to select which individuals to translocate (Bremner-Harrison et al. 2004).

The Scandinavian arctic fox

Biology
The objective of this report is to evaluate the potential benefits and risks with translocation as a means to preserve the Scandinavian arctic fox. Such a translocation could be either be done among different regions within Scandinavia, or using an external population as a source. A translocation program also involves several practical questions regarding how, where and when to carry it out, all of which will be discussed below. The potential benefits and risks associated with translocation, as well as the practicalities

involved with such a project, depend on the ecology and population structure of the species in question.

The arctic fox is a small circumpolar carnivore that inhabits the arctic regions of North America and Eurasia as well as many arctic islands (Audet et al. 2002). The southern distributional limit of the arctic fox is constrained by competition from the red fox (*Vulpes vulpes*) (Hersteinsson and Macdonald 1992). The arctic fox is highly adapted to cold temperatures, and has several physiological and morphological adaptations to the harsh arctic environment (Scholander et al. 1950; Prestrud 1991; Fuglei and Oritsland 1999). It is a species with a broad food niche (Audet et al. 2002), but populations are often classified into two ecotypes: "lemming" foxes that mainly prey on lemmings (*Lemmus sp.* and *Dicrostonyx spp.*) and "coastal" foxes that mainly utilize marine resources, such as eggs, birds and carrion (Braestrup 1941). The disparity between these types of resources has led to a number of different life history adaptations, where lemming foxes undergo an enormous reproductive output during lemming peaks compared to coastal foxes (Tannerfeldt and Angerbjörn 1998).

The arctic fox colonised Scandinavia from Russia following the end of the last ice age (Dalén et al. 2007), and today inhabits the mountain tundra in Sweden, Norway and Finland. Arctic foxes used to be a common in this region, but due to heavy hunting at the end of the 19th century, the population was reduced from more than 10 000 individuals (Tannerfeldt 1997) to just a few hundred individuals (Lönnberg 1927). The arctic foxes have been unable to recover from this bottleneck (Haglund and Nilsson 1977), and today number about 100-200 individuals (Angerbjörn et al. 2007). A number of explanations for this non-recovery have been proposed. Inter-specific competition with red foxes seems to have resulted in a reduction in the amount of available habitat (Elmhagen et al. 2002; Tannerfeldt et al. 2002), and food availability is low due to irregularities in lemming fluctuations and decreased densities of large carnivores (Angerbjörn et al. 1991; Tannerfeldt et al. 1994). Problems directly associated with the small population size have also been proposed as a cause of the non-recovery (Linnell et al. 1999; Loison et al. 2001). Additional, and more recent threats to the population include human disturbance and changes in habitat (Hersteinsson et al. 1989), as well as introgression with escaped farm foxes (Norén et al. 2005; Norén 2007).

Are there small-population problems?
Genetic analyses on museum samples have shown that the bottleneck in the early 19th century, and the ensuing genetic drift over the last 100 years, have caused a significant loss of genetic variation (Nyström et al. 2006). In addition, gene flow from Russia has probably been reduced over the last 100 years (Nyström et al. 2006).

Historical records from the time before the bottleneck show that arctic foxes used to disperse to virtually all corners of the Scandinavian peninsula (Pulliainen 1965; Nyström et al. 2006), suggesting that there was once one single large population in Scandinavia. Today, however, the arctic fox is divided into four small populations (to avoid confusion, these are from here on referred to as "subpopulations"). These subpopulations stretch from Hardangervidda in the south to Finnmark in the north (Fig. 1). Both ear-tagging and genetic data show that there is little or no current gene flow among the subpopulations (Dalén et al. 2006). Genetic modelling suggests that the current population structure may be the result of a recent fragmentation of a once larger population (Dalén et al. 2006). It

is likely that this recent fragmentation was caused by an altitudinal shift in the red fox during the last 100 years (Elmhagen et al. 2002). Red foxes have taken over low-altitude mountain areas traditionally inhabited by arctic foxes, which probably prevents gene flow between more alpine regions.

Despite the severe bottleneck in the early 19th century, the subsequent small population size and the recent population fragmentation, genetic variation is still relatively high in the respective subpopulations (Dalén et al. 2006). One explanation for this is that, although reduced, gene flow has continued from Russia to Scandinavia. This will have helped maintain genetic diversity, at least up until the population became fragmented, as discussed above. Also, a contributing factor to the somewhat unexpectedly high genetic variation in Scandinavia is that it takes time for a population to reach migration/drift equilibrium (Wright 1951). A continued small population size and isolation of the current four subpopulations is therefore likely to result in a considerable loss of genetic variation in the immediate future (see, however, the discussion on selection below).

The current small population size in Scandinavia suggests that inbreeding is likely to occur in the population. Experimental studies on captive farm foxes have shown that inbreeding causes inbreeding depression, expressed as reduced litter sizes and lowered juvenile survival (Nordrum 1994). Inbreeding depression could thus be a contributing factor to the non-recovery of the Scandinavian arctic fox. One indication that inbreeding may be detrimental is that monitoring data from the SEFALO+ project shows that despite the small number of individuals in each of the subpopulations, sibling and parent-offspring matings are very rare or non-existent (*unpublished data*). At present, there is not sufficient stud book data to directly estimate individual inbreeding coefficients for the wild populations. However, recent genetic analyses suggest that there is a correlation between individual heterozygosity and fitness (Dalén 2005). Individuals that survive and reproduce have significantly higher genetic variation than those that do not. The reason for this pattern may be that individual heterozygosity, as measured with microsatellites, is associated with the inbreeding coefficient (Hansson and Westerberg 2002). The observed heterozygosity-fitness correlation would thus be indicative of an ongoing inbreeding depression in the population. Alternatively, the observed pattern can be due to an ongoing selection against individuals with low genetic variation (Bensch et al. 2006). This could be due to a lowered survival of homozygous individuals, or due to that heterozygous individuals are favoured during pair-formation. This second scenario would also be symptomatic of problems associated with low genetic variation and/or inbreeding. Interestingly, this latter scenario would lead to genetic variation being maintained in the population, and could thus serve as an additional explanation to the unexpectedly high variation observed in the Scandinavian arctic fox.

It also seems likely that the arctic fox suffers from purely demographic problems associated with the small population size (Loison et al. 2001). The arctic fox's reluctance to mate with close relatives means that finding a suitable partner is difficult, and during some years even impossible (Linnell et al. 1999). Furthermore, the current low density in most areas means that active dens often are inhabited by only one adult pair during the breeding season (Angerbjörn et al. 2007). When at high density, for example prior to the bottleneck in Scandinavia, arctic fox dens were regularly inhabited by multiple pairs (Zeeterberg 1945). It is plausible that such multiple pairs could more easily fend off

intruding red foxes. An additional consequence of the current low density in Scandinavia could therefore be that red fox predation of arctic fox cubs is disproportionately high. A lowered population growth due to sex-ratio fluctuations within the subpopulations is also a possibility, although at present there is a lack of adult sex-ratio estimates.

In summary, the arctic fox in Scandinavia has lost a significant amount of genetic variation over the last 100 years, and a recent fragmentation of the population means that genetic drift proceeds at an even higher rate than before. An additional loss of genetic variation is therefore anticipated. Both genetic analyses and observations of inbreeding avoidance indicate that there is an ongoing inbreeding depression. Furthermore, there may be difficulties in finding suitable mates and a reduced capability to defend dens and cubs against red foxes. Taken together, these results suggest that the arctic fox's small population size in Scandinavia has a negative impact on its population growth. Translocation of arctic foxes, either between the subpopulations in Scandinavia or from Russia to Scandinavia, has the potential to solve these problems.

Potential negative effects of translocation
The division of the Scandinavian arctic fox into four isolated subpopulations is probably a recent phenomenon, going back only a few decades (Dalén et al. 2006). Genetic drift has led to moderate genetic distances (F_{ST} = 0.06-0.12) between populations composed of purely wild animals (Dalén et al. 2006; Norén 2007). Although moderate, these distances are unlikely to reflect any adaptive differences among the subpopulations given their recent ancestry and the historical records of long-distance dispersal in Scandinavia (Pulliainen 1965; Dalén et al. 2006; Nyström et al. 2006).

The Scandinavian arctic fox shares common ancestry with the population in northwestern Russia (including the Kola Peninsula), since they both originate from eastern Siberia (Dalén et al. 2007). The genetic distance between Scandinavia and northwestern Russia is moderate (F_{ST} = 0.06-0.09), but was lower (F_{ST} = 0.04) prior to the bottleneck in the 19th century (Dalén et al. 2006; Nyström et al. 2006; Geffen et al. 2007). Both the Scandinavian and the Russian populations belong to the lemming ecotype and therefore share many local adaptations. Both populations are mainly composed of individuals of the white colour morph, rely heavily on lemmings as a primary food source and have similar litter sizes (Tannerfeldt 1997). Furthermore, both populations display the same dispersal behaviour, with the long distance movements typical of the lemming ecotype (Eberhardt and Hanson 1978; Garrott and Eberhardt 1987). The timing of the mating period and parturition may however differ between Scandinavia and Russia due to the difference in latitude between the regions, although it is unknown whether this would reflect adaptive or phenotypically plastic differences.

With the exception of occasional cases of sarcoptic mange, probably transmitted by contact with red foxes, no diseases are known to occur in any of the Scandinavian subpopulations. Conversely, several gastrointestinal parasites have been observed, although it is unclear whether these have any adverse effects on individual fitness (Aguirre et al. 2000). However, an unknown disease causing fatal necrotizing encephalitis has been observed in captive arctic foxes in Sweden (Berg et al. 2007). This disease, which has not been observed in the wild population, infected arctic foxes kept at different geographic locations, suggesting that it was transmitted via a vector not normally encountered by wild arctic foxes. Although less is known about disease in the

Russian Arctic, two diseases with major health concerns for humans are known to exist in Russian arctic foxes: arctic rabies and *Echinococcus multilocularis* (Bessonov 1998; Mork and Prestrud 2004). Both these diseases are absent in Scandinavia, although arctic rabies has been reported from the neighbouring Kola Peninsula (Selimov et al. 1990).

Translocation of arctic foxes could potentially be done either between Scandinavian subpopulations or from northwestern Russia to Scandinavia. In the former case, given that the fragmentation in Scandinavia seems to be a very recent phenomenon, it seems highly unlikely that the subpopulations have different local adaptations. Furthermore, there is no evidence for variance in disease or parasite prevalence among the subpopulations. Altogether, this strongly suggests that translocation between Scandinavian subpopulations would not lead to outbreeding depression or spread of disease. However, it should be noted that inbreeding may be strong in all subpopulations, and that translocation between subpopulations thus could have less positive effect than desired. Moreover, all subpopulations in Scandinavia are small and endangered. Removing individuals from one of the subpopulations for translocation purposes would therefore effectively reduce the size of the source subpopulation, and translocation within Scandinavia in general would obviously not have any net demographic benefit.

For translocations of arctic foxes originating from outside Scandinavia, northwestern Russia would be the obvious choice (*sensu* Moritz 1999), due to the low intra-population genetic divergence, as well as the shared ecology and ancestry among the populations. Other populations in geographical proximity to Scandinavia, for example Svalbard and Iceland, belong to the coastal ecotype, and would therefore be less suitable as source populations. However, even though no differences have been observed in local adaptation between the Russian and Scandinavian populations, it is possible that geographic separation during the Holocene has led to the evolution of locally coadapted gene complexes or other types of cryptic adaptations. On the other hand, gene flow occurs naturally among virtually all arctic fox populations throughout the Arctic including, at least up until recently, Scandinavia (Dalén et al. 2006; Geffen et al. 2007). Translocation from Russia would nonetheless involve greater risks to the target population compared to translocation among the Scandinavian subpopulations, including the risk of introducing diseases such as arctic rabies and *Echinococcus multilocularis*. However, the potential benefits may be greater in the form of a stronger genetic rescue effect. Translocation, regardless of whether from Russia or within Scandinavia, would also involve risks to the individual arctic foxes to be translocated, for example through stress during handling and exposure to disease while in captivity.

Further studies
There are a number of additional studies that could be done to further investigate whether the Scandinavian arctic fox suffers from problems related to its small population size, and if translocation would have any negative effects. Quantitative genetic analyses (McKay and Latta 2002) could help determine if there are any cryptic adaptive differences between the Russian and Scandinavian populations. However, this would require detailed ecological and behavioural data from the Russian population. Obtaining such data is not realistic given the problems of setting up large-scale field projects in Russia. A second approach would be to investigate if there is an ongoing inbreeding depression in Scandinavia by creating a stud book. This would require combining data from ear tagging

and genetic analyses. However, a large proportion of the observed breeders have not been ear tagged as juveniles and genetic samples from these individuals are not always available. Additional genetic markers would probably also need to be developed to obtain a high enough resolution (Norén 2007). Creating a stud book with high enough resolution to estimate inbreeding coefficients may therefore, if possible at all, require a considerable research effort. An alternative approach to address the question of inbreeding, also entailing the combination of ear tagging and genetic data, would be to investigate if the Scandinavian arctic foxes display inbreeding avoidance and if heterozygous individuals are favoured during pair formation. Such a study is currently underway (Geffen *et al.* in prep.). Finally, there is currently no data on whether the small population sizes in Scandinavia have led to skewed sex ratios in the adult populations. The problem with obtaining such estimates is that observational and genetic data is usually collected at dens, which mainly are occupied by breeders. Individuals not breeding, possibly due to the lack of partners, would thus fall outside the scope of a den-based survey. Unbiased samples could however be obtained from faeces collected along tracks and at scent stations, as well as from hair traps (Lynch et al. 2006).

All the areas of investigation discussed above would have high scientific value, and would increase the general knowledge of the population processes in the Scandinavian arctic fox. However, it seems unlikely that the outcome of any of the studies would have any substantial effect on the decision-making on whether to proceed with a translocation program.

Should arctic foxes be translocated?
The arctic fox in Scandinavia is likely to suffer from several problems associated with its small population size, which implies that translocation would have a positive effect. It is a bit more unclear whether such an approach would entail any negative effects for the population, especially in the case of translocating arctic foxes from Russia to Scandinavia. However, several of these concerns, especially those associated with disease, could be addressed through careful planning and execution of a putative translocation project. Such planning would also have the advantage of being able to draw on the experiences from a recent successful reintroduction program for the swift fox in the US (Ausband and Foresman 2007). Translocation within Scandinavia is very unlikely to have negative effects, and could decrease both the level of local inbreeding and facilitate breeding pair formation. Translocation from Russia has the potential for a stronger positive effect, but also involves greater risk. There is no data pointing towards that there are any meaningful adaptive differences between Scandinavia and Russia, although there is always a possibility of previously undetected local adaptations or epistatic interactions in Scandinavia that could lead to outbreeding depression.

In conclusion, all the data available at present suggest that a properly executed translocation program would have a positive net effect, regardless of whether the arctic foxes were translocated from Russia or within Scandinavia. However, the decision on whether to proceed with a translocation program depends on whether the current conservation actions, in the form of supplementary feeding and red fox control (Angerbjörn et al. 2007), are sufficient to build up and maintain a viable arctic fox population in Scandinavia.

Towards a translocation action plan

Objectives
A translocation action plan first of all needs to determine what the objective of the action is. For the Scandinavian arctic fox it seems reasonable that the overall objective should be to maximise the long-term persistence of the population. This would involve increasing the population size and genetic variability to a level where extinction from demographic stochasticity is unlikely and the population can maintain a long-term evolutionary potential. However, since it may take time for the population size to reach such a level, a more immediate and more easily evaluated objective could be to significantly increase the population growth. A wide variety of factors, discussed in more detail below, need to be taken under consideration in order to decide how, when, where and to what extent the translocations should be carried out. It would be advisable to develop a model that incorporates ecological, genetic and geographical data to help reach these decisions (Armstrong and Davidson 2006; Rout et al. 2007; Seddon et al. 2007).

Choice of source population
If a decision is made to use northwestern Russia as a source population, a more careful analysis needs to be done on how this could be carried out in practice, both in terms of exact geographic locations, infrastructure and permits. Translocation from Russia could be done as a short-term non-recurring action to increase the overall genetic variability of the Scandinavian population. Post-project implementation would thus not be necessary. Translocation within Scandinavia, which could be carried out regardless of whether translocation from Russia is done, would however probably need to be done over a longer time perspective to maintain connectivity among populations. This action may therefore need post-project implementation. To avoid negative demographic impacts in the Scandinavian source populations when individuals are brought into the translocation project, it could be possible to do reciprocal translocations, exchanging individuals between the subpopulations. There are five populations within Scandinavia that could potentially be used as sources for translocations, four wild populations (Fig. 1) and the Norwegian captive breeding population. At present, however, the Hardangervidda and captive populations are less suitable for this purpose due to introgression with farm foxes (Norén 2007), although it would be possible to use genetic analyses to select native individuals from these populations (Norén et al. 2005; Norén 2007).

Temporary captivity
Wild-caught individual arctic foxes brought into the translocation project will need to spend a certain amount of time in captivity prior to release. The time spent in captivity could range from a few hours during direct transport between geographic regions, up to several months. Although a minimal time spent in captivity may at first glance seem to be the desirable option, studies on other species have shown that an increased time in captivity may help reduce stress suffered on release and could allow the animals to build up important fat reserves (Molony et al. 2006). During captivity, it would also be advisable that pre-emptive treatment of gastrointestinal parasites is undertaken. Any Russian arctic foxes to be translocated would also need to be quarantined and screened

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for rabies and *Echinococcus multilocularis*, either through serological tests or genetic analysis (Dinkel et al. 1998; Ballard et al. 2001). Stringent steps would also need to be taken to avoid the unknown disease that earlier infected a Swedish captive population (Berg et al. 2007). A period of captivity could also represent an opportunity to train individual animals, especially if long periods of captivity have prevented them from acquiring essential learned behaviours (Seddon et al. 2007). Such training could include predator recognition (Griffin et al. 2000) and prey-catching techniques (Biggins et al. 1999).

Choice of release location
Individuals could conceivably be translocated into all of the Scandinavian subpopulations. However, when taking into account that there are four subpopulations and three different directions to choose from, there are actually 12 different options available. Adding the Russian population into the equation increases that number to 16. Modelling should preferably be used to assess the optimal course of action (Armstrong and Davidson 2006; Rout et al. 2007; Seddon et al. 2007). On a smaller geographical scale, the choice of release location within each of the subpopulations is also of importance. Geographical models could be employed for this purpose. These should include parameters such as historic den quality (Dalerum et al. 2002), resource availability (Elmhagen et al. 2000), proximity to resident arctic foxes and distance and altitude from the tree-line (Dalerum et al. 2002; Dalén et al. 2004).

There is also a possibility to reintroduce the arctic fox in regions where it is currently extinct. Although this may not have any immediate effects in terms of genetic rescue or relieving other Allee effects, such reintroductions may help increase the overall connectivity of the whole population. Such reintroductions could therefore be of crucial importance in maintaining a long-term viable population (Hanski 1998). Regions where the arctic fox recently has become extinct include northern Finland and Snøhetta/Dovrefjell in Norway (Dalén et al. 2006). Reintroductions into empty areas should preferably be done using individuals from different subpopulations to increase the chances of breeding pair formation and to maximise individual genetic variation. Such a reintroduction could also be used for an initial pilot study on the feasibility of translocating arctic foxes and to investigate the consequences of hybridisation between individuals from different populations. Additional conservation actions, such as red fox control and supplementary feeding, may however be necessary to prepare areas for reintroductions and to ensure a rapid initial population growth.

The release phase
When to release the arctic foxes may be an important factor in maximising individual survival. The time of season may affect food availability and thus overall success (Bremner-Harrison et al. 2004). For arctic foxes, a release in late spring would probably be the best strategy to ensure a high food abundance during the initial post-release period. On the other hand, increased territorial behaviour during this period (Hersteinsson and Macdonald 1982) could make settlement more difficult. The optimal time to obtain individuals from the source population, as well as the time spent in captivity, and the optimal age for release (see below) may however constrain when release is possible. Furthermore, since lemmings constitute the primary food resource for the arctic fox in

Scandinavia (Elmhagen et al. 2000), choosing the appropriate year to carry out translocations may also be of importance (Tannerfeldt and Angerbjörn 1996). Lemmings go through large-scale fluctuations in population density with a four-year cyclicity. Timing the releases to the increase phase of the lemming cycle would not only provide for an abundant food source, but would also set the stage for successful reproduction during the subsequent peak year.

Several empirical studies, including one on the arctic fox's closest relative the swift fox, recommend soft releases over hard releases since these increase survival and reduce dispersal distances (Bright and Morris 1994; Moehrenschlager and Macdonald 2003). For the arctic foxes, this could involve constructing a temporary fence around a suitable den. This would allow individuals to acclimatise to their surroundings and could reduce levels of post-release stress, although whether this is logistically and practically possible us unclear.

Which individuals to translocate

The minimum number of arctic foxes that need to be translocated to ensure a positive effect is obviously important to determine. Several studies have shown that even a small number of successful immigrants are sufficient to obtain a genetic rescue effect (*reviewed in* Tallmon et al. 2004). However, released arctic foxes need to survive and reproduce in order to be considered successful. The number of individuals to translocate therefore depends on their post-release survival rate and probability to form a breeding pair, which in turns depends on which type of individual is selected for translocation.

Genetic analysis on potential source animals could be applied to discover foxes with high heterozygosity, which could used to obtain a higher genetic rescue effect. Furthermore, studies on swift foxes demonstrate that variation in boldness is a predictor of post-release survival (Bremner-Harrison et al. 2004), opening up for the possibility to design behavioural tests to select suitable source individuals. Several studies suggest that juveniles are more suitable for translocation purposes, both from a genetic perspective (Robert et al. 2004) and because translocated juveniles disperse less than adults (Fritts et al. 1984; Moehrenschlager and Macdonald 2003). In addition, cub mortality is unusually high in the arctic fox (Tannerfeldt et al. 1994; Norén 2007), which suggests that harvesting cubs rather than adults for translocation purposes would have less of a negative impact on the source population. Finally, the sex of the individuals may also affect recruitment success. In the swift fox, translocated females had a lower survival rate, suggesting that a higher proportion of females should be used to balance the sex-ratio. Furthermore, if target populations are found to have skewed sex-ratios prior to translocation, the sex of the individuals to be translocated could be adjusted accordingly.

Evaluation

Evaluation is important not only to determine the overall success of a translocation project, but also to allow for a flexible and dynamic approach where procedures can be continually evaluated and changed. Although ecological, genetic and geographical modelling has already been discussed as a means to maximise the success of a translocation project, it should be pointed out that such modelling could also be used to develop a scheme to evaluate the efficiency of the different actions by generating predictions based on the different variables discussed above. Testing these predictions

could thus be used to estimate the relative importance of each variable. An evaluation would also need to take into account potential time lags in population fitness, since an initial genetic rescue effect may result in outbreeding depression in later generations (Edmands 2007; *but see* Willi et al. 2007). The target populations would therefore need to be monitored for several generations, using den surveys, ear tagging, radio tracking and genetic sampling.

Concluding remarks

A translocation project for the Scandinavian arctic fox would bring together the two main conservation paradigms described by Caughley (1994), since it would provide a synthesis of the ecological causes for the non-recovery (the declining-population paradigm) and the problems directly associated with a small population size (the small-population paradigm). Taken together, all data currently available point towards that translocation would result in a positive effect for the Scandinavian arctic fox. The risks involved with this approach range from small to moderate depending on which populations are selected as sources, although these risks could be reduced if the project is carefully designed. A translocation project would therefore require a multi-disciplinary approach, and should include scientists with an assortment of expertise from the fields of biology, geography and veterinary medicine. This kind of project would also require the participation and support of the environmental protection agencies and relevant county administrative boards in Sweden, Norway and Finland, and possibly the corresponding authorities in Russia.

The arctic fox is known for its exceptional capability to survive in even the harshest environments, which makes it somewhat of a mystery why the Scandinavian population has failed to recover despite being a protected species since the early 19th century. This is even more surprising considering that the arctic fox has an extraordinary reproductive potential, with the largest litter size known to mammals. Indeed, this potential may also prove to be its salvation if the underlying mechanisms behind the non-recovery can be remedied. The arctic fox could then quickly return to its role as a keystone predator in the Scandinavian arctic ecosystem.

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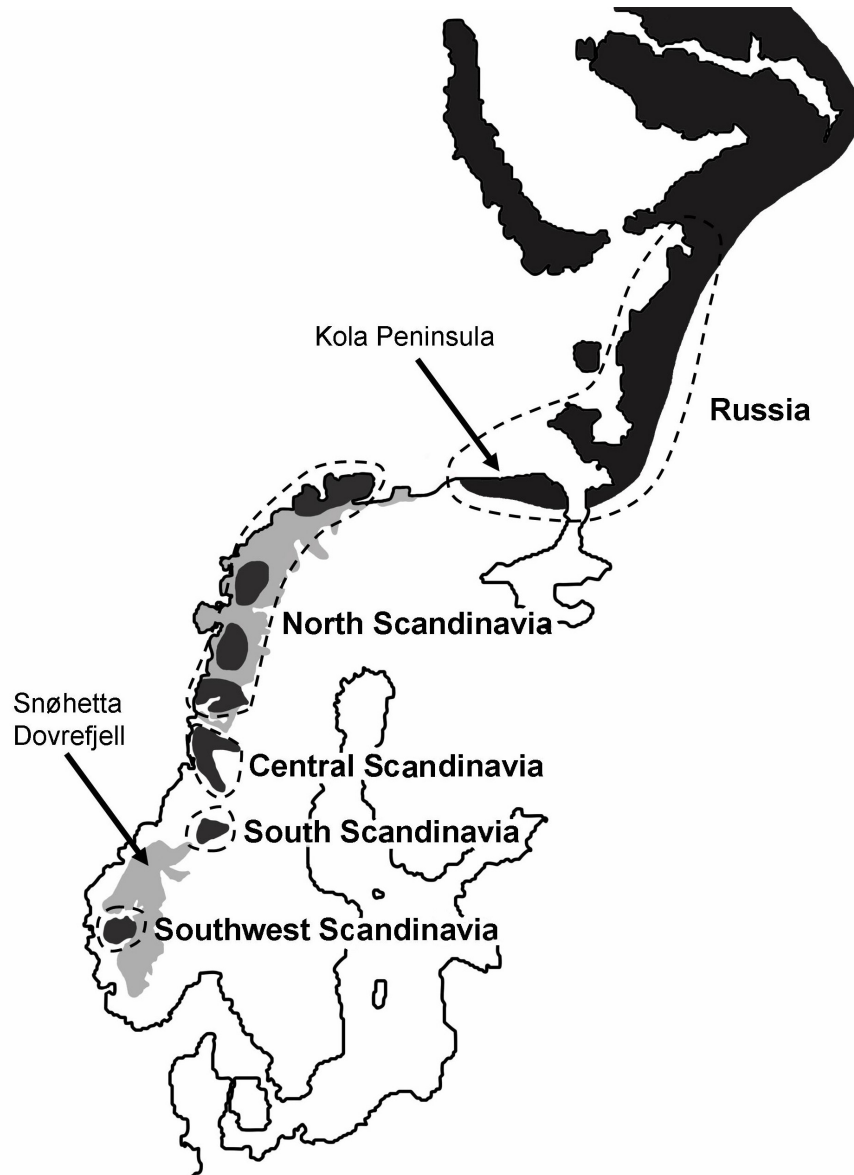
Figure 1.

Figure 1.
Map of the mountain tundra regions in northern Europe. Dark grey areas show the current distribution of arctic foxes. Light grey areas illustrate mountain tundra no longer inhabited by arctic foxes. Land areas in white illustrate the distribution of forest. The four Scandinavia populations and the population in northwestern Russia are encircled by dashed lines. The Snøhetta/Dovrefjell region, a possibly extinct population, and the Kola Peninsula are also shown.