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Context-dependent demographic and genetic effects of translocation from a captive breeding project

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Abstract

Translocations are a widespread approach to conserve threatened populations. Given the rapid decline and genetic deterioration of many natural populations, translocations are expected to become even more common in the future. The success of translocations is, however, dependent on multiple context-dependent factors, such as demographic and genetic status, habitat quality and animal behaviour. The Scandinavian arctic fox (*Vulpes lagopus*) exists in a small, fragmented population that is demographically vulnerable and exposed to inbreeding depression. In the early 2000 s, releases of arctic foxes from the Norwegian Captive Breeding Programme were initiated with the purpose of reintroducing populations to formerly inhabited areas and promoting connectivity. Since 2008/2009, 61 foxes have been released in Junkeren, Norway to re-establish an unoccupied area. We used a combination of field observations and microsatellite genotyping from the release site and two neighbouring subpopulations to investigate (i) the probability of establishment and reproduction for released foxes at the release site and in neighbouring subpopulations, and (ii) the impact on litter size and genetic composition in the recipient populations. Results showed that 18% of the released foxes were established at the release site, or in neighbouring subpopulations and 11.5% reproduced successfully. The extent of post-release dispersal into neighbouring subpopulations was also relatively high (11.5%). During the study period, the number of litters more than doubled in the subpopulations with released foxes contributing 29.5% to this increase, but no clear effect of immigration on litter size was found. There was a slight increase in genetic variation in one of the subpopulations, and a significant decline in genetic divergence between subpopulations. We conclude that despite extensive releases, demographic and genetic effects were highly context-dependent. This study highlights the challenges of reinforcement programmes in small populations and reintroductions to unoccupied sites, especially for highly mobile species in a fragmented landscape.

Introduction

According to the 'small population paradigm' (Caughley, 1994), the dynamics of small populations are influenced by an interplay between demographic and genetic factors (Gilpin & Soulé, 1986; Caughley, 1994). For instance, demographic Allee effects, where individual fitness is reduced by a small population size (Allee & Bowen, 1932), can reduce population growth and recovery. Difficulties in finding an unrelated mate lowers the probability of reproduction and may increase the probability of emigration to other local populations, especially if the species is highly mobile (Deredec & Courchamp, 2007). Further, the 'extinction vortex model' (Gilpin & Soulé, 1986) predicts that genetic drift and inbreeding will be powerful processes in a small population (Lynch, Conery, & Burger, 1995). If inbreeding increases the expression of harmful recessive alleles, this will reduce individual fitness (i.e. cause inbreeding depression; Shields, 1987). Inbreeding depression can drive a continued population decline, making the vortex spin towards extinction. Empirical evidence of an extinction vortex has been recorded in natural populations of Iberian lynx (*Lynx pardinus*; Palomares *et al*., 2012), southern dunlins (*Calidris alpina schinzii*; Blomqvist, Pauliny, & Larsson, 2010) and the Glanville fritillary butterfly (*Melitaea cinxia*; Saccheri *et al*., 1998).

Immigration (i.e. appearance of an individual from another population) and gene flow (i.e. immigrant reproduction) from unrelated individuals (Slarkin, 1985) can reverse negative impacts and rescue an inbred and declining population both numerically (e.g. demographic support) and genetically (e.g. genetic rescue). Both theory and empirical data suggest that interbreeding between resident and immigrant individuals may produce outbred offspring with high fitness (i.e. heterosis; (Darwin, 1877)). This can increase population evolutionary potential (Hedrick & Garcia-Dorado, 2016) and contribute to faster population growth (Åkesson *et al*., 2016; Hasselgren *et al*., 2018).

Conservation translocations are expected to be increasingly used in the future to prevent population declines (Swan, Lloyd, & Moehrenschlager, 2018). Translocation of individuals, between populations or release of captive-bred individuals into the wild, can bring positive effects on both population size and genetic variation (Slough, 1994; Smith & Clark, 1994; Servheen, Kasworm, & Thier, 1995; Madsen, Ujvari, & Olsson, 2004; Johnson *et al*., 2010), but that is not always the case (White *et al*., 2020). A successful translocation can be defined by a specific population size, or IUCN red list classification (Seddon, 2015). Robert *et al*. (2015) however argued that reaching a stable population size at carrying capacity is a component that should be included in evaluations of translocation success. In general, successful establishment of released individuals depends on the release strategy and the number of individuals released, but also factors such as social structure, life history traits, behaviour and personality (Griffith *et al*., 1989; Miller *et al*., 1999; Bremner-Harrison, Prodohl, & Elwood, 2004; Armstrong & Seddon, 2008; Mihoub *et al*., 2011; Sinn *et al*., 2014; Milligan *et al*., 2018). Numerous challenges have however been encountered during translocations; for instance, there may be difficulties in making the released individuals establish at the release site (e.g. immigrant settlement in a territory or at a den), especially in an unoccupied or almost unoccupied area (Cook, 2004; Oro *et al*., 2011). Post-release dispersal from the release site to another population can also lower the chances of establishment at the release site (Mihoub *et al*., 2011). For highly mobile species, translocations must therefore be evaluated over a sufficiently large geographic scale (Deredec & Courchamp, 2007; Robinson *et al*., 2020). If establishment occurs, the next obstacles are connected to survival and reproductive success (Clark, Huber, & Servheen, 2002). Additionally, habitat factors, food abundance and predation risk can influence the success of a translocation (Armstrong & Seddon, 2008). Despite numerous translocation case studies, there is little research covering the entire process, from release to establishment to genetic and demographic effects.

Morris *et al*. (2021) pointed out that translocation strategies should be improved based on experiences drawn from different species, environments and contexts. Given this, it is of scientific and applied value to learn from specific conservation translocations (e.g. Griffith *et al*., 1989; Miller *et al*., 1999; Bremner-Harrison, Prodohl, & Elwood, 2004; Armstrong & Seddon, 2008; Mihoub *et al*., 2011; Sinn *et al*., 2014; Hasselgren *et al*., 2018; Milligan *et al*., 2018; Lotsander *et al*., 2021). One example of captive-bred individuals released to re-establish unoccupied areas and promote connectivity is the Scandinavian arctic fox (*Vulpes lagopus*) (Landa *et al*., 2017). The arctic fox went through a severe bottleneck due to extensive hunting in the late 19th century (Lönnberg, 1927; Tannerfeldt, 1997). Ever since 1928 in Sweden and 1930 in Norway, when hunting was banned and the arctic fox was legally protected, the population has been struggling to recover (Haglund & Nilsson, 1977; Angerbjörn *et al*., 2013). The slow recovery is connected to irregular Norwegian lemming (*Lemmus lemmus*) cycles that cause food scarcity, and the expansion of red fox (*Vulpes vulpes*) (Hersteinsson & MacDonald, 1992; Angerbjörn *et al*., 2013; Elmhagen, Berteaux *et al*., 2017) that causes competition. Another contributing factor is the extremely small population size, that along with geographic fragmentation (Herfindal *et al*., 2010) cause Allee effects as well as accelerated inbreeding and genetic drift (Norén *et al*., 2017). During the bottleneck, the arctic fox population lost 25–50% of their genetic variation, and with substantially reduced immigration from Russia, no gene flow has been able to counteract this decrease (Nyström, Angerbjörn, & Dalén, 2006; Larsson *et al*., 2019). Within one Swedish subpopulation (Helags), increased inbreeding, followed by inbreeding depression has been observed (Norén *et al*., 2016; Hasselgren *et al*., 2018).

To conserve the Scandinavian arctic fox population, various conservation efforts have been implemented in Scandinavia (Angerbjörn *et al*., 2013). Even though conservation actions have partly been coordinated across Norway and Sweden (Elmhagen, Eide *et al*., 2017), there are some important differences in management strategies. Swedish authorities have focused on supplemental feeding and red fox removal in the natural habitat (Angerbjörn *et al*., 2013), whereas Norwegian authorities developed a captive breeding programme to secure connectivity and increase genetic diversity of extant populations, and reintroduce the arctic fox to formerly inhabited areas (Landa *et al*., 2017). Between 2005 and 2017, 422 juveniles were released in four extirpated areas and in three numerically small subpopulations in Norway (Landa *et al*., 2017). In the winter of 2008/2009, the first release was conducted in Junkeren, Norway (Fig. 1) and since then, a total of 61 foxes have been released to the area (Appendix 1). The primary purpose was to re-introduce an arctic fox population to an unoccupied area (Junkeren, Norway), but given the proximity to other subpopulations (Saltfjellet and Vindelfjällen-Arjeplogsfjällen), the translocation was expected to bring positive effects to these areas as well. The aim of this study was to use this arctic fox translocation to investigate the outcomes and challenges of this conservation action. More specifically, we investigated (*i*) the number of released foxes that established and reproduced in the release site (Junkeren) as well as the adjacent Norwegian (Saltfjellet) and Swedish (Vindelfjällen-Arjeplogfjällen) subpopulations, (*ii*) the extent of gene flow, and (*iii*) the effect of the released foxes on demography and genetic variation in the adjacent subpopulations. We expected that the releases would lead to demographic support at the release site as well

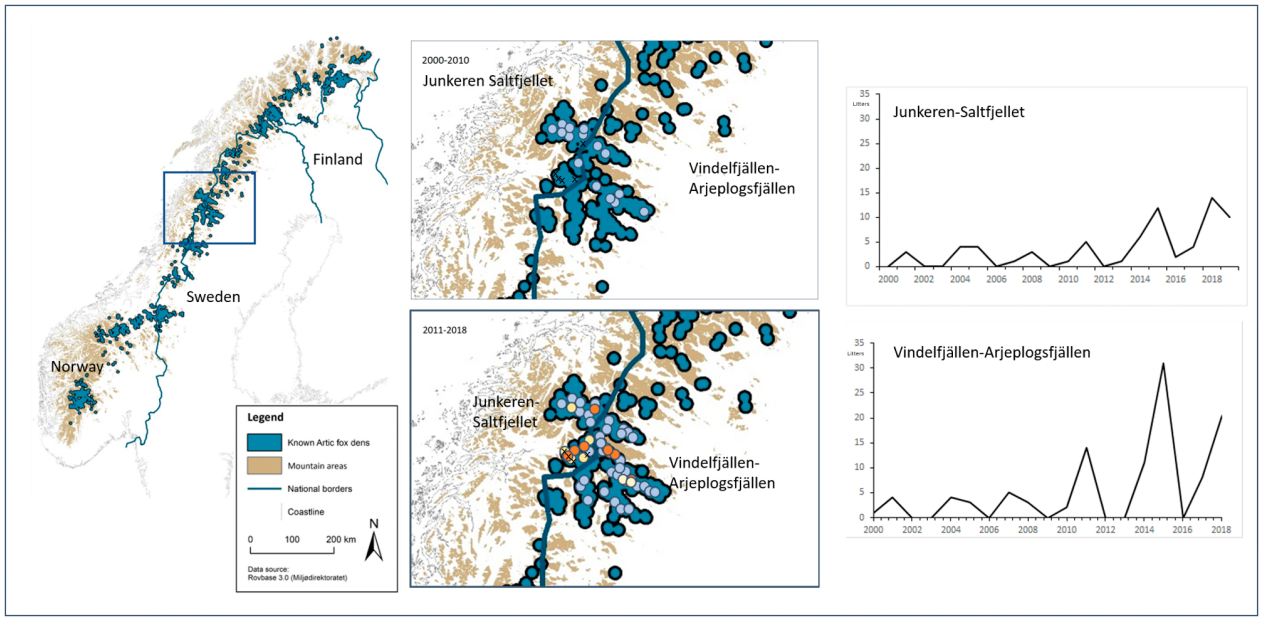

Figure 1 Map of the study area with blue dots representing dens were resident arctic foxes reproduced; orange dots: dens where released foxes reproduced and; yellow dots: dens where offspring of released foxes reproduced. Cross represent release sites. Population size is shown as the number of documented litters in each of the two areas.

as gene flow into adjacent populations through post-release dispersal. Given this, we expected that gene flow would increase litter size and genetic variation in the adjacent subpopulations (e.g. Hasselgren *et al.*, 2018).

Materials and methods

Study populations and conservation actions

The study covers a total of 17 years, where 2001–2010 represents the pre-translocation period and 2011–2017 represents the post-translocation period. The study area comprised the release site (Junkeren), and adjacent subpopulations located in the southern part of the northern core populations (Swedish Vindelfjällen-Arjeplogfjällen and Norwegian Junkeren-Saltfjellet; Fig. 1, Table 1). The Vindelfjällen-Arjeplogfjällen area is about 5500 km^2 and located on both sides of the border of Västerbotten and Norrbotten County (N 66° 9.00′, E 16° 6.00′) and the Junkeren-Saltfjellet area is about 3200 km^2 in Nordland County (N 66° 31.32′, E 15° 8.88′) (Fig. 1). Vindelfjällen-Arjeplogfjällen and Junkeren-Saltfjellet have been demographically connected in the past and are still partly geographically connected (Dalén *et al.*, 2006). However, due to low or absent reproductive success in Junkeren, Saltfjellet and Vindelfjällen-Arjeplogsfjällen have lost most connectivity and are today classified as different subpopulations (Herfindal *et al.*, 2010). Furthermore, Saltfjellet is separated from Junkeren by a forested valley, freeway and railroad.

The arctic fox was listed as critically endangered (CR) but has recently been re-classified as endangered (EN) in both Sweden and Norway by SLU Swedish Species Information Centre and Norwegian Biodiversity Information Centre, respectively (ArtDatabanken, 2020; Artsdatabanken, 2021) in response to conservation actions (Angerbjörn *et al.*, 2013; Landa *et al.*, 2017). Since the early 2000 s, data collection, monitoring and other conservation actions were undertaken yearly in most parts of the Scandinavian range. During the EU-Life projects SEFALO and SEFALO+ (1998–2008), conservation actions and monitoring were expanded to the entire Fennoscandian range when Swedish, Norwegian and Finnish research institutes and authorities were united (Fig. 1). Trans-national conservation actions by supplemental feeding, red fox control and translocations were thereafter executed within the EU-Interreg funded projects Felles Fjellrev, Felles Fjellrev II, Felles Fjellrev Nord and Felles Fjellrev Nord II. Since 2017, a joint Swedish-Norwegian action plan became the foundation of conservation actions (Elmhagen, Eide *et al.*, 2017).

In Norway, the Norwegian Institute for Nature Research (NINA) initiated a captive breeding programme on behalf of the Norwegian Environmental Agency in 2000, with a functional breeding station established in 2005 (Landa *et al.*, 2017). The breeding stock includes genetic representation from most Scandinavian subpopulations where the number of breeding pairs in the facility have varied between five and nine (Landa *et al.*, 2017). Breeding pairs are matched to avoid inbreeding and to maximise genetic diversity. Replacement of the founder lineage occurs after a maximum of three generations in captivity to avoid artificial selection. Cubs have been released to the wild at 6–8 months of age, often along with their siblings (Landa *et al.*, 2017).

Table 1 Overview of the release site and adjacent sub-populations showing the number of known dens, number of litters reported during the study period (min–max), average observed heterozygosity (H_O) and allelic richness for 10 microsatellite loci (pre- and post-translocation) and data type available from each area

Area	Release site	Known dens	Yearly number of litters (2001–2017)	Average hetero-H_O	Average allelic richness	Ear-tagging	Faecal DNA sampling	Tissue DNA sampling
Junkeren	Yes	18	0–3			No	2008–2017	No
Saltfjell	No	37	0–9	Pre: 0.550 Post: 0.726	Pre: 4.34 Post: 5.04	No	2008–2017	No
Vindelfjällen-Arjeplogsfjällen	No	143	0–31	Pre: 0.641 Post: 0.676	Pre: 4.97 Post: 5.08	2001–2017	2008–2017	2001–2017

Field data collection

Data were collected by monitoring dens, ear-tagging juveniles and adults, recording and identifying adults from their ear-tags, counting the number of litters and assessing litter size, and collecting genetic samples. A released fox observed at a den site during the spring or summer inventories (April–August) was recorded as an established individual. Both reproducing and non-reproducing arctic foxes are usually relatively stationary at dens, especially when supplementary feeding is provided. Therefore, a released fox visually recorded with cubs, or with genetically determined parentage to a litter was recorded as a reproducing fox. Litter size was determined by visual/remote camera counts of cubs at the dens. Visual counts of litter size were determined during the three first weeks in July during den visits of at least 24 hours. Development in population size was measured as the number of recorded litters in each area.

Identification of released individuals was done through a combination of visual observations of ear-tagged foxes and genetic analyses (Table 1). Captive-born and released foxes in Norway were ear-tagged and a small piece of ear tissue and hair were collected for DNA analysis prior to release. In Sweden, the majority of wild-born cubs were ear-tagged and genetically sampled during summer inventories, which enabled individual identification from a distance, or from a remote camera. In addition to visual observations, we used genetic analysis of faeces and tissue to establish the extent of immigration (defined as the appearance of an individual from another population) and gene flow (defined as the immigrant reproductive success) from released foxes. In Saltfjellet, Norway, no wild arctic foxes were ear-tagged. Faecal samples were systematically collected through the National Monitoring Programme (Ulvund *et al.*, 2019). Since both released and resident ear-tagged foxes had known genetic profiles, we were able to identify both immigrants and their F1 offspring (Hasselgren *et al.*, 2018). Tissue samples from Vindelfjällen-Arjeplogsfjällen (collected between 2000 and 2017; n = 251) together with faecal samples (collected between 2008 and 2017; n = 122) were used for genetic analyses (Table 1). From Junkeren-Saltfjellet, we only used faecal samples (collected between 2008 and 2018; n = 872) (Table 1). We also included tissue samples of released foxes (n = 61), collected prior to release.

This study was highly dependent on sufficiently high detection rates of released foxes. Detection of released foxes was accomplished through direct identification of ear-tagged foxes (described in Lotsander *et al.*, 2021) in combination with genetic analysis of scats collected at known den sites (described in Meijer *et al.*, 2008). In addition, remote cameras were placed at the majority of active dens within the study area, and ear-tagged foxes were identified with remote camera photos. We also monitored the closest arctic fox subpopulations outside the study area (located 140–160 km away) through remote cameras and/or genetic analyses of scats throughout the study period. Out of 251 ear-tagged individuals (2001–2017), 26% were re-observed as adults. This detection rate, however, needs to be put in the perspective of juvenile mortality reaching 90% at low prey density (Meijer *et al.*, 2008). Among the released foxes, 32% (range 20–50%) were re-observed through visual observations, remote cameras or DNA within 12 months of release. Among the re-observations, 61% (range 22–100%) were identified through DNA analyses (Landa et al. unpublished).

In Sweden, all procedures involving live animals were approved by the Swedish Environmental Protection Agency and the Swedish Board of Agriculture in accordance with trapping and ethical permits (412-7884-07, NV-01959-14, NV-02547-17, A130-07, A131-07, A36-11, A18-14, A19-14, A10-2017) and following the current Swedish legislation. The scientific research done inside Vindelfjällen nature reserve was approved by the Västerbotten county administrative board (521–3191-2014). In Norway, collection of tissue samples in the breeding station and translocation were approved by the Norwegian Environmental Agency and Mattilsynet (VSID 1746).

Genetic analyses

DNA was extracted from a total of 1306 tissue and faecal samples using either QIAGEN's DNeasy tissue kit, QIAGEN's stool kit or the PowerMaxTM Soil DNA Isolation Kit (MO BIO Laboratories, Carlsbad, California, USA) in accordance with the manufacturers' instructions or as described by Taggart *et al.* (1992). Negative controls were included in all extractions to address possible contamination. All extractions and pre-polymerase chain reaction (PCR) preparations were made in an isolated DNA laboratory free

from PCR products. After extraction, the DNA samples were amplified and scored for genetic variation with 10–12 polymorphic microsatellites (Hasselgren *et al*., 2018). DNA was amplified with a Veriti® 96-Well Thermal Cycler (Applied Biosystems).

DNA storage, extraction and amplification were conducted in accordance with Hasselgren *et al*. (2018). The Swedish fragments were size-determined using LIZ-500 size standard (ThermoFisherScientific) on an ABI3730 capillary sequencer (Applied Biosystems, Macrogen Inc.). The Norwegian samples were run on an ABI3130xl capillary sequencer (Applied Biosystems, Macrogen Inc.). Fragments from the two laboratories were calibrated through a common analysis of 16 samples carried out at both NINA, Norway and Stockholm University, Sweden. A subset of faecal samples was size determined at least twice from separate PCRs to assess null alleles and genotyping errors. All samples displayed error rates that were within the expected range previously reported (<0.0002 for all loci; Meijer *et al*., 2008). To control for genotyping errors in the final data set, we used the software Microchecker 2.2.3 (Van Oosterhout *et al*., 2004) with a 99% confidence interval.

Data analysis

Released arctic foxes were detected and individual origin was genetically identified with GenAlEx 6.503 (Peakall & Smouse, 2006) by comparing genotyped samples from Vindelfjällen-Arjeplogfjällen (n = 373) and Junkeren-Saltfjellet (n = 456) to known genetic profiles from released foxes from the breeding programme (n = 61). The criterion for individual identification was a 100% match, where one homozygous locus was tolerated to minimise any effect of allelic dropout. As a measure of the genetic resolution for individual identification, we used probability of identity, calculated in GenAlEx.

We established the individual origin and relationship between individuals in three consecutive steps. First, pairwise relatedness values were calculated using a maximum likelihood method through ML-Relate (Kalinowski, Wagner, & Taper, 2006). To connect an individual to a litter, we used a threshold value of average $r > 0.35$, since the expected theoretical value for parent–offspring is 0.5. We also monitored for the range of relatedness within a litter using an individual r = 0.25 as the lowest acceptable value. Secondly, the individual parent–offspring relationships were tested against the alternative hypothesis of no relationship using 1000 simulations in ML-Relate (Kalinowski, Wagner, & Taper, 2006). Thirdly, we verified the relationships using the allelic exclusion principle (Norén *et al*., 2012).

To test for demographic effects of translocation, we used Linear Mixed Models (LMM), fit by maximum likelihood in R, to test if there were (i) differences in litter size before and after the translocation, and (ii) differences in litter size between foxes of immigrant ancestry (classified as originating from released foxes or from F1 offspring) and resident foxes (classified as offspring of two resident foxes). No cases of released foxes breeding with each other were recorded during the study period, but in a number of cases, we only identified one of the parents. We used litter size as the response variable and immigrant ancestry (immigrant vs. resident) or period (pre vs. post) as a binary fixed effect explanatory variable in two separate models (i and ii). For both models, we accounted for differences in prey population size, by using rodent phase (classified as 'low', 'increase' and 'peak') as a fixed effect explanatory variable following Meijer *et al*. (2013). Further, to test for differences in litter sizes arising from resident (resident * resident) and immigrant (immigrant * resident, or immigrant F1 * resident) parents, parental individual ID was used as a random variable to account for individuals producing multiple litters. Individual identity was verified with ear-tags or genotypes. In cases where we had verified identities for both parents, we ran the model separately for each parental ID. Because we lacked verified identities for both parents in several cases, we also ran the model using the den site as a random variable. To test for differences in litter size between the two periods, we only used the den site as a random variable because we did not have complete data on individual IDs extending back to 2001. We first ran the models for the full data set including subpopulation (Vindelfjällen-Arjeplogsfjällen and Junkeren-Saltfjellet) as a binary fixed effect explanatory variable. Thereafter, we ran the model separately for each subpopulation (Vindelfjällen-Arjeplogsfjällen and Junkeren-Saltfjellet). We ranked significant P-values, following Muff *et al*. (2021)., as moderate evidence (P = 0.05–0.01), strong evidence (P = 0.01–0.001), and very strong evidence ($P < 0.001$) for an effect.

To test for genetic effects of translocation, Hardy–Weinberg Equilibrium was calculated in GenAlEx (Peakall & Smouse, 2006) with a permutation test of 10 000 steps. Significance levels were corrected for multiple testing across loci using a Bonferroni correction (α = 0.005). Population average F_{IS} and allelic richness were calculated in FSTAT (Goudet, 1995) and unbiased heterozygosity was calculated in GenAlEx (Peakall & Smouse, 2006). We tested for differences in allelic richness and unbiased heterozygosity before and after translocation with Wilcoxon signed rank tests in R. Average individual heterozygosity was calculated manually as the proportion of genotyped heterozygous loci. We tested for differences before and after translocation with Kruskal–Wallis tests in R.

Genetic differences before and after translocation were estimated with a PCA and population pairwise F_{ST}, calculated in GenAlEx 6.503 (Peakall & Smouse, 2006). Significance testing for population pairwise F_{ST} used 999 permutations.

Results

Establishment and reproductive success

In total, 61 arctic foxes were released in Junkern, and four were established at the release site. Of these, three were documented to reproduce and in total, four litters were produced from the released foxes in the release site. Three litters were

Table 2 General information on the arctic fox individuals released from the Norwegian captive breeding programme that has been observed in Vindelfjällen-Arjeplogfjällen and Junkeren-Saltfjellet until 2019

Individual	Area	Sex	Year born	Year released	Release site	Year observed	Post-release dispersal	Cubs	Visual obs	DNA match
AF0093	Vindelfjällen-Arjeplogsfjällen	F	2010	2010	F-NNO-058	2011–12, 14–17	~ 85 km	Yes	Yes	Yes
AF0186	Saltfjell	M	2010	2010	F-NNO-052	2011	~ 20 km	Yes	Unknown	Yes
AF0193	Vindelfjällen-Arjeplogsfjällen	M	20190	2010	F-NNO-052	2011	~ 105 km	Yes	Yes	Yes
AF0169 /AF0171	Vindelfjällen-Arjeplogsfjällen	M/F	2010	2010	F-NNO-058	2011	~ 35 km	Yes	Yes	No
AF0204	Saltfjell	M	2011	2012	F-NNO-052	2012–15	~ 45 km	Yes	Yes	Yes
AF0240	Saltfjell	M	2011	2012	F-NNO-064	2012–15, 17–19	0 km	Yes	Yes	Yes
AF0342	Saltfjell	F	2014	2015	F-NNO-052	2018–19	~ 5 km	Yes	Unknown	Yes
AF0384	Vindelfjällen-Arjeplogsfjällen	M	2015	2016	F-NNO-050	2016–18	~ 20 km	Yes	Yes	Yes

sired by the same male (AF0240, Table 2). In the adjacent area, Saltfjellet, another three released foxes established, and one individual reproduced. In total, two litters from one individual (AF0204, Table 2) were recorded in Saltfjellet.

In Vindelfjällen-Arjeplogsfjällen, four released foxes were visually observed and, of these, three matched the genetic profile of released foxes and were thus confirmed to originate from the captive breeding project. Four released foxes were documented to reproduce and, in total, seven litters were related to the released foxes. Of these, four were produced by the same female (AF0093, Table 2). In addition, three litters were documented from her offspring the following year (F1 generation). In 2017, AF0093 and her offspring produced 100% of the litters (n = 3) in this area.

Out of 61 released foxes, 18% were established at the release site (n = 4 foxes), or in neighbouring subpopulations (n = 7 foxes), and 11.5% reproduced successfully. The number of litters documented in the subpopulations increased from 29 litters during 2001–2010 to 71 litters during 2011–2017 (Fig. 2). Of these, 21 litters (29.5%) were traced back to released arctic foxes or their offspring (Fig. 2).

Demography

There was strong evidence for a difference in litter size between arctic fox subpopulations (LMM: t = 2.454, P = 0.014, df = 1) using the full data set. However, there was no evidence for an effect of small rodent phase (LMM: t = −1.105, P = 0.480, df = 2) or period (LMM: t = −0.210, P = 0.834, df = 1). Differences in litter size between individuals with resident or immigrant ancestry in the full data set showed no effect of origin (LMM: t = −0.234, P = 0.814, df = 1), area (LMM: t = 0.396, P = 0.692, df = 1) or small rodent phase (LMM: t = −1.276, P = 0.104, df = 2).

When running the models separately for each subpopulation, we found significant, moderate support for a difference in average litter size before and after translocation in Saltfjellet (LMM: t = −2.290, P = 0.022, df = 1, n_{pre} = 14, n_{post} = 30), where litter size increased after translocation (pre 4.3 cubs, post 6.3 cubs). There was no evidence for an effect of small rodent phase on litter size before and after translocation (LMM: t = −1.093, P = 0.332, df = 2, n_{low} = 5, $n_{increase}$ = 13, n_{peak} = 26). Further, we observed no significant difference in litter size between resident and released individuals (including F1-generation offspring) (LMM: t = 1.611, P = 0.10, df = 1, $n_{immigrant}$ = 8, $n_{resident}$ = 17), but strong evidence for a relationship between small rodent phase and litter size (LMM: t = −3.079, P = 0.002, df = 1, n_{peak} = 13, $n_{increase}$ = 10, n_{low} = 2). Average litter size was 4.8 cubs at the low phase, 5.7 at the increase phase and 6.2 at the peak phase.

In Vindelfjällen-Arjeplogsfjällen, there was a trend towards a difference in litter size before and after translocation (LMM: t = 1.837, P = 0.066, df = 1, n_{pre} = 10, n_{post} = 36), where litter size decreased after translocation (pre 9.7 cubs, post 6.9 cubs). There was no evidence for an effect of small rodent phase on litter size before and after translocation (LMM: t = 0.209, P = 0.790, df = 2, n_{low} = 3, $n_{increase}$ = 14, n_{peak} = 29). There was no evidence of a difference in litter size between resident and released individuals (including F1-generation offspring) (LMM: t = −0.729, P = 0.466, df = 1, $n_{immigrant}$ = 11, $n_{resident}$ = 26), or small rodent phase (LMM: t = −1.088, P = 0.268, df = 1, n_{peak} = 26, $n_{increase}$ = 8, n_{low} = 3). Average litter size was 6 cubs at the low phase, 8.2 at the increase phase and 7.8 at the peak phase.

Genetic composition

In Saltfjellet, few or no deviations from Hardy–Weinberg Equilibrium were found, whereas most loci deviated significantly from equilibrium in Vindelfjällen-Arjeplogsfjällen both before and after translocation (Table 3). A similar pattern existed after Bonferroni correction. Average F_{IS} values changed from 0.050 to −0.022 in Vindelfjällen-Arjeplogsfjällen, and from −0.066 to 0.042 in Saltfjellet after translocation.

For Saltfjellet, there was a trend potentially indicating higher average individual heterozygosity across loci before release (H_I = 0.71) compared to after release (H_I = 0.6) (Kruskal-Wallis χ^2 = 3.693, df = 1, P = 0.055). However, there was very strong evidence of an increase in allelic richness (AR = 4.34–5.04; Wilcoxon signed rank test, P = 0.008) following translocation. Unbiased heterozygosity

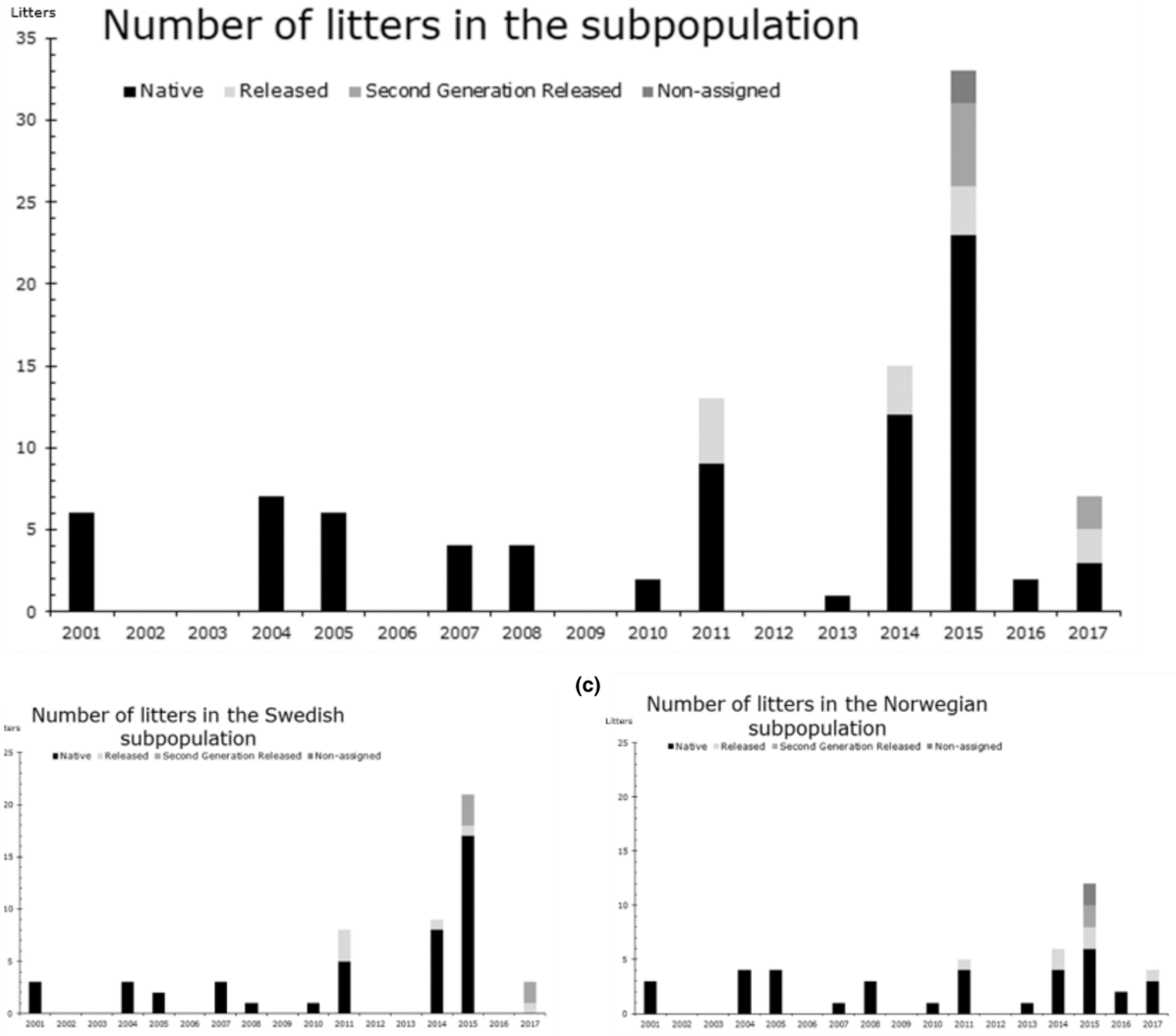

Figure 2 Number of litters in (a) the total sample between 2001 and 2017 by resident, released or second generation released; (b) Vindelfjällen-Arjeplogsfjällen, and; (c) Junkeren-Saltfjellet.

showed no difference between the two periods (uHe = 0.674–0.585; Wilcoxon signed rank test, $P = 0.313$).

In Vindelfjällen-Arjeplogsfjällen, average individual heterozygosity across loci showed no difference before ($H_I = 0.625$) or after ($H_I = 0.700$) translocation (Kruskal-Wallis $\chi^2 = 2.409$, $df = 1$, $P = 0.121$). The same holds for allelic richness (AR = 4.97–5.08; Wilcoxon signed rank test, $P = 0.742$) and unbiased heterozygosity (uHe = 0.671–0.623; Wilcoxon signed rank test, $P = 0.640$).

The PCA showed a change in genetic distance between Saltfjellet and Vindelfjällen-Arjeplogsfjällen with increased genetic overlap after translocation (Fig. 3). To verify that this was not just an effect of a single locus, all loci were excluded one by one, and independently of the locus removed, the PCA showed the same pattern (data not shown). This was supported by population pairwise differentiation between Saltfjellet and Vindelfjällen-Arjeplogsfjällen, where $F_{ST} = 0.03$ ($P = 0.01$) before translocation and $F_{ST} = 0.018$ ($P = 0.010$) after translocation.

Discussion

The aim of this study was to use an arctic fox translocation as case study to understand outcomes under natural conditions. We investigated establishment at the release site and in two neighbouring subpopulations, the extent of gene flow, and the influence of released foxes on litter size and genetic variation in Scandinavian arctic fox populations. Overall, we

Table 3 Observed (Ho) and expected (He) heterozygosity before and after translocation in the Arctic fox populations in Vindelfjällen-Arjeplogfjällen and Saltfjellet. Significant P-values show deviation from Hardy–Weinberg equilibrium

	Vindelfjällen Arjeplogsfjällen, pre-translocation			Vindelfjällen Arjeplogsfjällen, post-translocation			Saltfjellet pre-translocation			Saltfjellet, post-translocation		
Locus	H_O	H_E	*P*	H_O	H_E	*P*	H_O	H_E	*P*	H_O	H_E	*P*
3	0.748	0.756	0.122	0.741	0.840	0.000	0.750	0.815	0.293	0.835	0.785	0.924
9	0.541	0.665	0.011	0.677	0.553	0.002	0.800	0.645	0.148	0.352	0.371	0.082
140	0.636	0.693	0.000	0.596	0.579	0.121	0.905	0.780	0.479	0.667	0.652	0.627
173	0.555	0.525	0.081	0.557	0.575	0.779	0.476	0.455	0.660	0.582	0.569	0.906
250	0.477	0.620	0.008	0.708	0.669	0.000	0.714	0.648	0.628	0.615	0.637	0.171
377	0.427	0.459	0.000	0.658	0.598	0.015	0.350	0.449	0.139	0.385	0.510	0.001
606	0.591	0.524	0.303	0.842	0.746	0.008	NA	NA	NA	0.671	0.611	0.116
671	0.831	0.683	0.004	0.551	0.571	0.010	NA	NA	NA	0.468	0.528	0.167
758	0.766	0.730	0.000	0.726	0.682	0.224	0.684	0.659	0.548	0.618	0.662	0.507
771	0.838	0.778	0.000	0.708	0.742	0.000	0.714	0.617	0.509	0.626	0.700	0.093

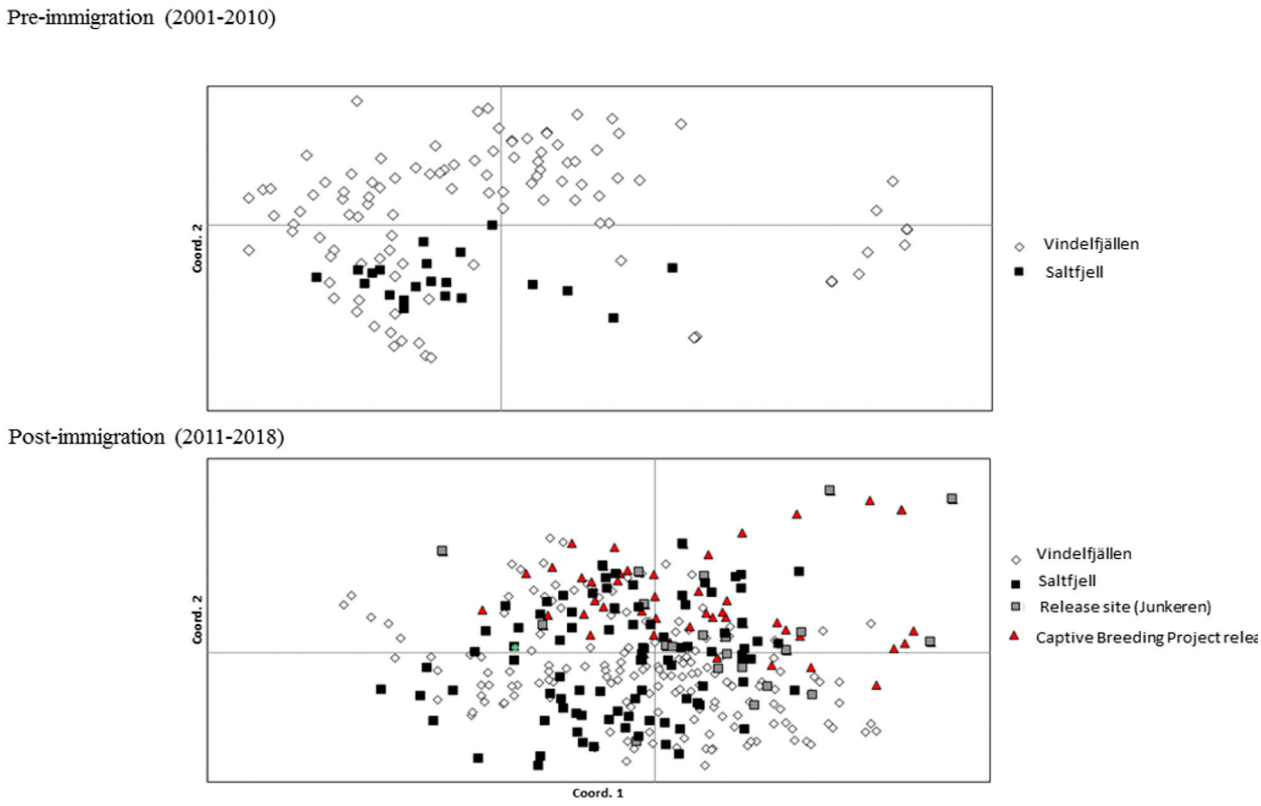

Figure 3 PCA (a) before and (b) after release with the 61 captive breeding foxes released in Junkeren shown as triangles.

found relatively low establishment (18% of the released foxes) and reproductive success (11.5% of the released foxes), but surprisingly high post-release dispersal.

In addition to reintroducing a population to a previously occupied habitat, another purpose of conservation translocations is to decrease inbreeding depression, which can occur through positive demographic effects (Åkesson *et al.*, 2016; Hasselgren *et al.*, 2018; Quinn, Alden, & Sacks, 2019). In contrast to our predictions, however, no unambiguous effect of gene flow from released foxes or their offspring was detected on reproductive success. The subpopulations went through an apparent increase in the number of litters (Fig. 2) and the released foxes contributed to 29.5% of the litters. However, the two subpopulations showed different patterns in litter size in response to translocation. Saltfjellet showed an increase in litter size, whereas Vindelfjällen-

Arjeplogsfjällen showed a close to significant decline in litter size following translocation.

Fluctuating resource conditions on the tundra can have a strong impact on arctic fox litter size (Tannerfeldt & Angerbjörn, 1998), and although we did not find any clear effect of small rodent phase on fox litter size, differences between the two subpopulations might be explained by subtle differences in the magnitude of small rodent fluctuations between the areas (e.g. Ehrich *et al*., 2020). Further, none of the areas showed a difference in litter size between released and resident foxes, which indicates that the reproductive capacity of released and resident foxes is comparable. This could either mean that heterosis did not occur when released and resident foxes bred, or that the benefits of outcrossing were stronger for another fitness metric besides litter size (e.g. Robinson *et al*., 2020).

Another purpose of conservation translocation is to increase the amount of genetic variation in genetically deteriorated populations (Robinson *et al*., 2020). In contrast to our predictions of increased genetic variation in response to gene flow, we found no unambiguous effects on genetic variation following immigration and reproduction. Saltfjellet showed a tendency for higher average individual heterozygosity across loci prior to the release and increased allelic richness after the release, whereas no such pattern was found for Vindelfjällen-Arjeplogsfjällen. In another Scandinavian arctic fox subpopulation (Helags), translocation decreased inbreeding by >40% and increased allelic richness shortly after immigration (Hasselgren *et al*., 2018; Lotsander *et al*., 2021). However, the expected impact of gene flow on genetic variation needs to be addressed in relation to standing genetic variation, since it is more likely to observe effects if the population exhibits low genetic variation before immigration. In the Helags subpopulation, average allelic richness was 3.69 prior to immigration (Hasselgren *et al*., 2018). For comparison, Saltfjellet displayed average allelic richness of 4.24 whereas Vindelfjällen-Arjeplogsfjällen displayed average allelic richness of 4.97 before releases (Table 1). Moreover, the change in average F_{IS} values suggests that the translocation did influence genetic variation. The average F_{IS} value in Vindelfjällen-Arjeplogsfjällen suggested that inbreeding levels decreased slightly, whereas the opposite pattern was found in Saltfjellet. It is possible that this is an outcome of the release strategy itself, where groups of siblings are released at the same den sites (Landa *et al*., 2017). To obtain a decrease in inbreeding, it is necessary for the released foxes to interbreed with unrelated individuals. In Vindelfjällen-Arjeplogsfjällen, the population was small but relatively stable before the immigration of released foxes, whereas the population in Saltfjellet was even smaller when translocation was initiated. Hence, inbreeding between related, released foxes could thus have occurred in Saltfjellet, whereas there was a higher chance of interbreeding between unrelated foxes in Vindelfjällen-Arjeplogsfjällen. Even though, we did not document inbreeding between released foxes in this study, we cannot exclude its occurrence. Further, the PCA confirms a change in genetic differentiation in response to immigration by released foxes. This was supported by the population pairwise F_{ST} values, which showed a decline in differentiation following the immigration of released foxes.

Despite extensive releases, we found an 11.5% reproductive success rate. Low reproductive success could potentially reflect an Allee effect, where lack of partners may increase the likelihood of post-release dispersal into another area rather than the establishment in an area with low abundance of unrelated conspecifics (Deredec & Courchamp, 2007). Furthermore, habitat quality and local prey dynamics need to be considered in this conclusion. Three other Norwegian mountain areas were re-established after just 4 years of release. One of them, the Snøhetta population, is today the largest arctic fox population in Norway (Landa *et al*., 2017; Ulvund *et al*., 2019). This suggests that habitat quality may be less optimal in Junkeren compared to other release sites. Moreover, translocation needs to be combined with actions in the natural habitat, for example supplementary feeding and red fox culling (Angerbjörn *et al*., 2013). This is, however, insufficient without regular lemming population peaks, which is a prerequisite for establishment and reproductive success (Angerbjörn *et al*., 2013). Findings from this study support the idea of individuals seeking out areas where conspecifics are present rather than remaining in unoccupied areas (Mihoub *et al*., 2011; Oro *et al*., 2011). However, it is difficult to distinguish between dispersal driven by differences in habitat quality, or a lack of conspecifics when statistical power is relatively limited.

Despite the relatively extensive use of translocations as a conservation tool, there is still a void in general guidelines for successful translocations. This study has demonstrated context-dependent effects in response to releases from a captive breeding project across sub-populations. Based on theoretical simulations, Robinson *et al*. (2020) recommended that evaluations of translocations should include a variety of demographic and genetic metrics to reliably detect effects, such as genetic rescue. Furthermore, this study highlights the broad importance of using detailed evaluation methods over large geographical scales and time spans to evaluate translocation success, especially for species where post-release dispersal is likely to occur (e.g. Mihoub *et al*., 2011). For populations that are distributed across large ranges, standardised trans-national monitoring protocols, along with detailed data on local ecological conditions, for example prey abundance, would be valuable. Modern technological advances, such as chip tagging or GPS collars, could also facilitate high-resolution information about survival, post-release dispersal and establishment. Finally, individual variation in personality (Bremner-Harrison, Prodohl, & Elwood, 2004; Sinn *et al*., 2014) or genetic composition (Hasselgren et al., unpublished) can also influence the released individuals' ability to survive and reproduce and should be considered to make informed management decisions on release strategies.

Conclusions

Even though translocations are among the earliest and most extensively used conservation actions, there are still numerous challenges to overcome (Greig, 1979; Griffith

et al., 1989; Morris *et al.*, 2021). This study illustrates the importance of context-dependent ecological factors influencing the success of conservation translocations. The outcomes of translocations are underpinned by multiple factors that can result in variable success. Despite ambitious releases, relatively low establishment at the release site and limited demographic and genetic effects were found in adjacent subpopulations. Furthermore, we documented a relatively high occurrence of post-release dispersal, where released individuals dispersed and established outside the release site. This adds to the prevailing view that captive breeding and translocations are a challenging conservation measure, especially when animals are highly mobile, environmental conditions are fluctuating and conservation actions extend over national borders.

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Authors contributions

JW, KN, AA, NE, AL and ØF conceived the ideas and designed methodology; JW, KN, AA, NE, AL and ØF collected the data; JW, KN and ØF analysed the data; JW and KN led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Appendix 1

The released arctic foxes from the Norwegian captive breeding programme in the Junkeren area

Individual	Year born	Date released	Release site	Sex	Colour
AF0064	2008	2008-09-30	F-NNO-052	F	White
AF0066	2008	2008-09-30	F-NNO-052	F	White
AF0068	2008	2008-09-30	F-NNO-052	M	White
AF0070	2008	2008-09-30	F-NNO-052	M	White
AF0074	2008	2008-09-30	F-NNO-052	M	White
AF0103	2009	2009-10-20	F-NNO-064	F	White
AF0105	2009	2009-10-20	F-NNO-064	M	White
AF0108	2009	2009-10-20	F-NNO-064	F	White
AF0109	2009	2009-10-20	F-NNO-064	F	White
AF0130	2010	2010-10-12	F-NNO-064	M	White
AF0131	2010	2010-12-10	F-NNO-064	M	White
AF0132	2010	2010-12-10	F-NNO-064	M	White
AF0133	2010	2010-12-10	F-NNO-064	F	White
AF0134	2010	2010-12-10	F-NNO-052	F	White
AF0135	2010	2010-12-10	F-NNO-052	F	White
AF0136	2010	2010-12-10	F-NNO-052	M	White
AF0137	2010	2010-12-10	F-NNO-064	F	White
AF0138	2010	2010-12-10	F-NNO-064	F	White
AF0185	2010	2010-12-10	F-NNO-052	M	White
AF0186	2010	2010-12-10	F-NNO-052	M	White
AF0193	2010	2010-12-10	F-NNO-052	M	White
AF0194	2010	2010-12-10	F-NNO-052	F	White
AF0093	2010	2010-12-10	F-NNO-058	F	White
AF0113	2010	2010-12-10	F-NNO-058	F	White
AF0167	2010	2010-12-10	F-NNO-058	M	White
AF0168	2010	2010-12-10	F-NNO-058	M	White
AF0169	2010	2010-12-10	F-NNO-058	M	White
AF0170	2010	2010-12-10	F-NNO-058	M	White
AF0171	2010	2010-12-10	F-NNO-058	F	White
AF0201	2011	2012-01-20	F-NNO-052	M	White
AF0202	2011	2012-01-20	F-NNO-052	M	Blue
AF0203	2011	2012-01-20	F-NNO-052	M	Blue
AF0204	2011	2012-01-20	F-NNO-052	M	Blue
AF0205	2011	2012-01-20	F-NNO-052	F	White
AF0206	2011	2012-01-20	F-NNO-052	F	White
AF0238	2011	2012-01-20	F-NNO-064	M	White
AF0239	2011	2012-01-20	F-NNO-064	F	White
AF0240	2011	2012-01-20	F-NNO-064	M	White
AF0241	2011	2012-01-20	F-NNO-064	F	White
AF0242	2011	2012-01-20	F-NNO-064	F	White
AF0243	2011	2012-01-20	F-NNO-064	M	White

Appendix 1 Continued.

Individual	Year born	Date released	Release site	Sex	Colour
AF0308	2013	2014-02-14	F-NNO-058	F	White
AF0309	2013	2014-02-14	F-NNO-058	F	White
AF0310	2013	2014-02-14	F-NNO-058	F	White
AF0311	2013	2014-02-14	F-NNO-058	M	White
AF0312	2013	2014-02-14	F-NNO-058	M	White
AF0297	2013	2014-02-14	F-NNO-052	F	White
AF0298	2013	2014-02-14	F-NNO-052	F	White
AF0330	2014	2015-02-24	F-NNO-058	M	White
AF0331	2014	2015-02-24	F-NNO-058	F	White
AF0336	2014	2015-02-24	F-NNO-058	M	White

Appendix 1 Continued.

Individual	Year born	Date released	Release site	Sex	Colour
AF0341	2014	2015-02-24	F-NNO-052	M	White
AF0342	2014	2015-02-24	F-NNO-052	F	Blue
AF0345	2014	2015-02-24	F-NNO-052	M	White
AF0353	2014	2015-02-24	F-NNO-052	F	White
AF0354	2014	2015-02-24	F-NNO-052	M	White
AF0383	2015	2016-01-04	F-NNO-050	F	White
AF0384	2015	2016-01-04	F-NNO-050	M	White
AF0385	2015	2016-01-04	F-NNO-050	F	White
AF0380	2015	2016-01-04	F-NNO-050	F	Blue
AF0381	2015	2016-01-04	F-NNO-050	M	Blue