Biological Conservation 275 (2022) 109774

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Conservation of the endangered Arctic fox in Norway - are successful reintroductions enough?

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ARTICLE INFO

Keywords:
Translocation
Captive breeding
Survival
Reproduction
Small rodents
Community ecology
Metapopulation

ABSTRACT

Translocation of captive-bred animals has become a widespread conservation practice to counteract species extinctions. We analyse and discuss the apparent success and shortcomings of Arctic fox (*Vulpes lagopus*) reintroductions in alpine tundra areas of Norway. We followed the fate of 915 foxes between 2007 and 2020 and estimated the apparent survival and reproductive success of captive-bred and released Arctic foxes, compared to wild-born descendants. Relationship to abundance of small rodents, population size, and age were explored. Overall, apparent survival and probability of breeding were similar between captive-bred and wild-born foxes, positively linked to rodent abundance. For wild-born foxes, both breeding propensity and litter size declined with increasing fox population size. This could be a first sign of the limited capacity of single tundra patches to house self-subsistent populations. Thus, facilitating and maintaining connectivity among remnant and re-established Arctic fox populations, creating functional metapopulations, is essential for further improvement and long-term survival. Relying on the combined measures of supplementary feeding and red-fox (*Vulpes vulpes*) control, the Arctic fox captive-breeding and reintroduction programme has so far been highly successful. However, anthropogenic drivers facilitating red fox invasion into the Arctic fox habitat, along with climate driven irregularities and dampened small rodent cycles, could inhibit the establishment of a self-sustained population. A more holistic ecosystem approach and conservation measures to restore alpine fauna should be considered.

1. Introduction

The loss and degradation of natural habitats due to anthropogenic activities and climate change are the main factors driving local extinctions for many wildlife populations (Pimm et al., 2014; Rybicki et al., 2020). In response to this, translocations of captive-bred or wild-sourced animals have become a widespread practice, contributing to the re-establishment and conservation of diverse species (Hoffmann et al., 2015; Seddon et al., 2014; Sutherland et al., 2021). As such, conservation translocations involve the deliberate movement of organisms from one site to another, where the primary objective is to aid population-level recovery (Berger-Tal et al., 2020). The most common types of conservation translocations are reintroductions, where organisms are released within their historical range from which they have been extirpated, or reinforcements, where individuals are released into remnant populations to boost population size and improve population viability (IUCN, 2013).

Conservation translocations typically target remnant populations that are isolated, contain relatively few individuals or are locally extinct. Small subpopulation sizes and restricted connectivity within a metapopulation reduce gene flow and increase subpopulation vulnerability to genetic drift and inbreeding (Frankham et al., 2002; Jaenike, 1973). Loss of genetic variation and inbreeding may, in turn, reduce individual fitness, susceptibility to disease, and evolutionary potential (Altizer et al., 2003; England et al., 2003; Fernández et al., 2004; Frankham, 2005; Lacy, 1997; Spielman et al., 2004; Willi et al., 2006).

The remnant Arctic fox (*Vulpes lagopus*) population of the Fennoscandian mountain plateaus located in Norway, Sweden, and northern parts of Finland (Fig. 1) exhibits a typical metapopulation structure, and the isolated sub-populations have declined to critically low numbers (Herfindal et al., 2010). The population went through a major demographic and genetic bottleneck during the late 19th century as a

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https://doi.org/10.1016/j.biocon.2022.109774
Received 15 February 2022; Received in revised form 4 October 2022; Accepted 8 October 2022

result of excessive hunting associated with a lucrative fur trade (Linnell et al., 1999; Lönnberg, 1927; Nyström et al., 2006; Østbye et al., 1978). Despite their high reproductive potential, dispersal ability, and >85 years of protection (Sweden 1928, Norway 1930, and Finland 1938), the population failed to recover (Hersteinsson et al., 1989; Kaikusalo and Angerbjörn, 1995; Østbye et al., 1978) and numbered a mere 40–60 individuals at the turn of the 21st century (Angerbjörn et al., 2013).

While the historical fur hunting drove the near eradication of the Arctic fox in Scandinavia, complex environmental changes underpinned the species' failure to recover (Eide et al., 2017). Arctic fox reproduction and litter size are tightly linked to rodent cycles (Angerbjörn et al., 1991; Ims et al., 2017). As a result of climate change, winters have become more variable and led to dampened and interrupted rodent cycles (Ims et al., 2011; Kausrud et al., 2008), with detrimental effects on Arctic fox population growth. In addition to a warmer climate, anthropogenic activities have made the alpine tundra accessible to the superior boreal competitor, the red fox (Elmhagen et al., 2017). The red fox has benefited from increased resource availability and external subsidies at high altitudes (Elmhagen et al., 2015; Henden et al., 2014; Selås et al., 2010). This led to increased interspecific competition and intraguild predation on the remnant Arctic fox populations (Dalen et al., 2002; Henden et al., 2010; Rod-Eriksen et al., 2020; Rodnikova et al., 2011; Selås and Vik, 2007). As a result of a combined effect of these interacting drivers, the Arctic fox population disappeared from several mountain plateaus and the few remaining individuals were divided into three relatively isolated subpopulations (Dalén et al., 2006; Elmhagen et al., 2002; Nyström et al., 2006).

To save the Arctic fox from extinction (Linnell et al., 1999; Loison et al., 2001), red fox culling and supplementary feeding were started to mitigate threats associated with increased red fox competition and food resource decline in the core sub-populations (Angerbjörn et al., 2013; Direktoratet for Naturforvaltning, 2003; Elmhagen, 2008). To increase connectivity and facilitate gene flow, supplementary feeding and red fox culling were additionally implemented in stepping-stone areas in 2011 (Hemphill et al., 2020). In Norway, an ambitious captive breeding programme was initiated in 2005 (in its present form with large enclosures in natural Arctic fox habitat), rearing Arctic fox pups that were later released into the wild (Landa et al., 2017).

Many studies have demonstrated that translocation of wild-caught, rather than captive-bred individuals, represent a more effective strategy to supplement a threatened population or reintroduce a species back to a formerly inhabited area (Servheen et al., 1995; Slough, 1994; Smith and Clark, 1994; Stanley Price, 1989). Since the wild population of Arctic foxes initially comprised so few individuals, there were no suitable sources of wild Arctic foxes for translocation within Fennoscandia. The remaining remnant populations instead served as sources for

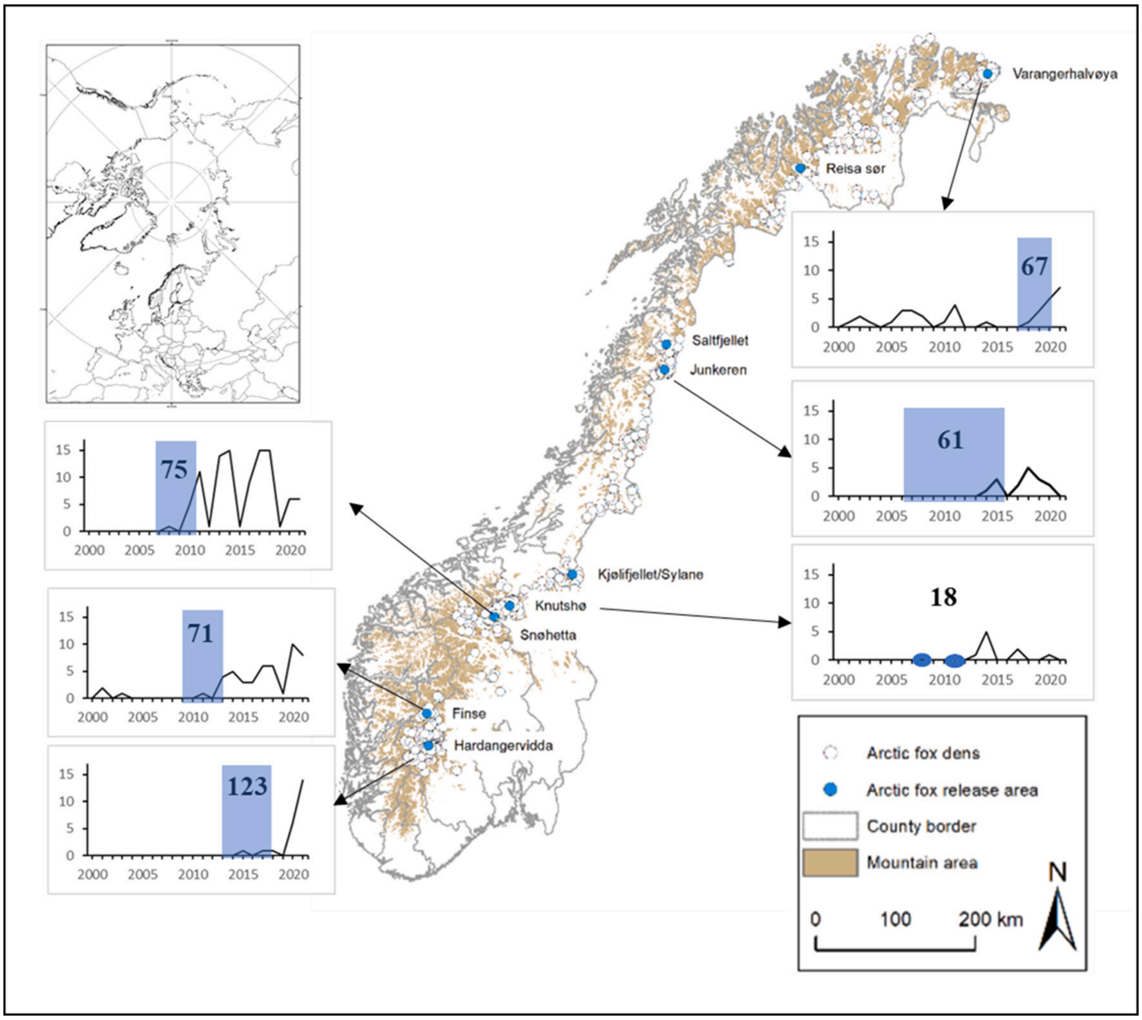

Fig. 1. Map of Norway (in grey on the small map) highlighting release sites of captive-bred Arctic foxes. Area shaded in blue on the diagrams' x-axis shows the release period (varying from single years to 3–8 years), and the total number of captive-bred foxes released during that period. Diagrams show the recorded number of Arctic fox litters per year for each release site, before and after release. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

founders that were included in the captive breeding programme, thereby also ensuring that the remaining genetic variability was preserved (Landa et al., 2017). Between 2006 and 2020, a total of 434 pups were released in nine different mountain plateaus in Norway (Fig. 1). The success of the Arctic fox captive breeding programme has thus become central in Norway's national conservation strategy of saving this endangered canid, together with supplemental feeding and red fox culling (Eide et al., 2017).

Translocations are logistically challenging and expensive, often inhibiting effective post-release monitoring which provide critical information to facilitate adaptive management and optimalisation of release strategies (Berger-Tal et al., 2020). In this study we evaluate post-release survival, establishment probability, and reproductive success of captive-bred Arctic foxes. We explore the impact of population size and rodent abundance, in order to assess possibilities for adaptive release strategies that could optimize post-release survival and reproductive success in the ongoing conservation programme. In spite of supplementary feeding in the release areas, rodent abundance and population density is still expected to impact breeding output and survival (Angerbjörn et al., 2013). We compare the survival and reproductive success of captive-born foxes to those of wild-born descendants of released foxes in order to evaluate potential variability between these groups. Several studies of population reinforcement have shown that captive-bred individuals generally had poorer performance compared with wild residents with respect to survival, behaviour, or breeding success, irrespective of animal species (Brittas et al., 1992; Hansen et al., 2000; Letty et al., 2007; Mccall et al., 1988; Poteaux et al., 1999; Sage et al., 2003). Therefore, we should expect that in general, wild-born foxes should perform better than captive-reared individuals. We discuss the conservation implications of our findings and other supportive actions in context of anthropogenic impact, management practice and climate driven changes that the Fennoscandian tundra habitat is currently exposed to.

2. Methods

2.1. Population monitoring and data collection

The Arctic fox population in Norway is monitored within the framework of a national monitoring programme, from which much of the data used herein are collected. The programme was established in 2003 and measures the activity at known den sites in both winter and summer, as well as collects faecal samples for DNA individual based monitoring (Ulvund et al., 2021). The monitoring programme, covering the whole range of the species in Norway, is run after a strict protocol standardized across Fennoscandia. During winter (March–April) all native den sites are visited. Those with winter activity are also visited during summer at the time of pup emergence to verify breeding and estimate litter size (July–August).

2.2. Captive breeding and release

The setup of the captive breeding programme and all details from how we built up the breeding stock, design of the outdoor housing, selection of the release sites, and description of release methods, is described in Landa et al. (2017). In this paper we present data from translocations conducted between 2007 and 2020 and follow the fate of the foxes in two selected study areas where the released individuals and the population is monitored intensively (see description below).

Our analyses focus on the foxes that were released in the southernmost Arctic fox subpopulations, Snøhetta/Knutshø and Finse/Hardangervidda (Fig. 1). The species had been extirpated from these areas (Eide et al., 2020) but was re-established by release of Arctic foxes during 2007–2013 and 2009–2016, respectively (Ulvund et al., 2020). The number of released Arctic foxes differed between years and study areas. Captive-bred Arctic foxes were born in May/June at the Sæterfjellet breeding station near Oppdal, Norway, and released during the following winter together with their siblings at historic den sites, or alternatively soft-released from the enclosure at the captive breeding station. In a few cases ($n = 15$), foxes escaped from the enclosure but were included as released, due to their contributions to local wild populations. In release areas, supplementary food was provided at feeding stations designed to feed Arctic foxes exclusively (Landa et al., 2017).

Before release, all captive-bred foxes were ear-tagged with a unique colour combination and marked with a passive integrated transponder (PIT) tag. Wild-born pups descending from released individuals were trapped at the den sites during summer (July/August) and marked with PIT-tags only. Ear tissue and hair samples were taken for DNA identification. Our total study sample consisted of 915 Arctic foxes monitored between 2007 and 2020, including released foxes ($n = 288$) and wild-born descendants ($n = 627$). Live and dead encounters (events) of individual foxes were obtained by seven different methods: (a) individual identification based on genotyping from faecal and hair samples collected during den controls in winter (Ulvund et al., 2021), (b) records of PIT-tags from readers set up at feeding stations based on Biomark (Biomark, Inc.) and Trovan systems (Trovan Ltd.; Landa et al., 2017; Thierry et al., 2020), identification of ear-tags from (c) wildlife camera traps or (d) opportunistic visual observations, (e) live captures of wild foxes, (f) recovery of carcasses of dead individuals and (g) parentage identification from tissue samples collected from offspring captured during summer marking on active dens. Counts of litter size were standardized through wildlife camera observations at each active den during pup emergence, and a maximum of 48 h manual observation prior to capture and marking of pups.

2.2.1. Model approach

Encounter data was extracted from the full data set of 915 marked Arctic foxes, which included information on all recorded events for each individual fox. Event data were collected between October 2007 and October 2020 in the two study areas (Fig. 1). Encounter data were split into yearly encounters for each individual fox, where a positive identification of an individual was recorded for each year (1 = detection). All cases where an individual was not detected were coded as zero (0 = non-detection). We only included known individuals that had been marked as pups and where at least one of the parents was a known (previously marked) individual. Furthermore, we retained only post-release encounters of captive-bred foxes.

2.2.2. Survival analysis

We compared survival estimates of captive-bred foxes with estimates from wild-born foxes. Breeding of wild-born foxes was recorded first time in 2010. Thus, we restricted the data set to cover the time period 2010–2020, including a total of 254 captive-bred and 627 wild-born foxes, with 479 and 1066 encounters, respectively.

Yearly encounter data were fitted with Cormack-Jolly-Seber (CJS) live encounter models to estimate apparent survival (φ) adjusted for encounter probability (ρ), using package 'marked' (Laake et al., 2013) in R version 4.0.3 (R Core Team, 2020). As many Arctic fox individuals were only observed once during the study period, we expected some degree of overdispersion in the data. To correct for this, we calculated the *median* $\hat{c}$ in Program MARK v9.0 (White and Burnham, 1999) using a saturated model (fully time-dependent for apparent survival (φ) and recapture probability (ρ)). The model sets were then adjusted by the *median* $\hat{c}$ and ranked by QAIC. We considered the top ranked models with a ΔQAIC <2 as candidate models (Burnham and Anderson, 2002).

We investigated a separate set of models for captive-bred and wild-born foxes, where both sets included *rodent abundance* (number of rodents per 100 trap days), *population size* (from a population density model; (Ulvund et al., 2019)), *time* and *age class* as predictors for φ, and *rodent abundance* and *time* as predictors for ρ. Estimates of rodent abundance were available from the Norwegian Environmental

Monitoring Programme (TOV). These estimates are based on data from snap trapping of rodents in autumn along permanent transect lines in each mountain area (Framstad and Eide, 2021). *Population size* was included to adjust for yearly changes in populations within each mountain area. *Both rodent abundance* and *population size* were added as time-varying individual predictors fixed to the location (mountain area) and year for each fox. For the set of models for captive-bred foxes, we added time-since-release (*tsr*) as an age class for φ, to investigate survival during the first year after release, i.e., from the first mid-winter (time of release) to the next (sub-adult), and from the second mid-winter onwards (adult). For the set of models for wild-born foxes, we created three time-classes based on the time-since-marking (*tsm*) as wild-born foxes were not subject to captive-release. Here, the first age class covered the time from marking to the first mid-winter (juvenile), the second class covered the first mid-winter to the second mid-winter (sub-adult), similar to the first year after release for captive-bred foxes, and the third class covered subsequent years, i.e., from the second mid-winter onwards (adult). The age classes were specified in the design data lists for the respective model sets. As sampling effort varied between regions, mountain region was included as a latent non-focal covariate in all models.

2.2.3. *Reproductive success*

To investigate breeding success, i.e. the probability of successfully producing offspring, we retained only data on foxes which survived to minimum breeding age (10 months old). The data set consisted of breeding information on 293 unique foxes (134 captive-bred, 159 wild-born), for a total of 734 encounters from 2010 to 2020 within the study regions. To investigate if and under which circumstances Arctic foxes produced offspring, we built a model set with *breeding propensity*, i.e., the proportion of breeding events, as a binomial response variable in a generalized additive modelling (GAM) framework, using package *mgcv* in R version 4.0.3 (R Core Team, 2020). Foxes which were detected breeding in the wild after release (captive-bred) or birth (wild-born) were classified as breeders (1), and the rest were classified as non-breeders (0). We assigned breeding or non-breeding status to each fox and year of detection. We fitted the models with predictor variables which were common for both breeding and non-breeding foxes; their *origin* (captive-bred or wild-born), *sex* (male or female), *rodent abundance* and *population size* within the mountain area and year of detection. Fox *age* was included in all models using a smoothing function, with an upper limit for the degrees of freedom of $k = 8$. A total set of 25 models were ranked by AICc, where models within ΔAICc <2 were considered candidate models.

To investigate the number of offspring produced by successful breeders, and potential variation in reproductive output between captive-bred and wild-born foxes, we retained only breeding events from the data set on breeding propensity ($n = 209$). Reproductive success was here measured as the number of pups (*litter size*) in each recorded breeding event for each breeding fox. Number of pups in each litter ranged from 1 to 14. We used a generalized additive mixed modelling approach (GAMM) with a Poisson distribution function, using fox *origin* (captive-bred or wild-born), *rodent abundance* and *population size* as explanatory variables. Additionally, we separated between the first and subsequent recorded breeding events (1 = first breeding event, 0 = subsequent breeding event), as well-established foxes could potentially produce larger litters than first-time breeders. Furthermore, we included the *distance* (in kilometres) from the previous breeding event, or – in case of the first recorded breeding event – from the release (captive-bred) or birth (wild-born) site, to investigate if distance travelled could affect reproductive success. We used *den-year* as a random effect to account for fox pairs at a specific den site and year. Like the breeding propensity analysis, we used fox *age* as a regression smoothing factor in all models, with an upper limit for the degrees of freedom of $k = 4$. A total set of 32 models were ranked by AICc, where models within ΔAICc <2 were considered candidate models. In all statistical analyses, in cases with multiple candidate models and where the top ranked model was weighted <80 %, we selected to average the model predictors across candidate models and use the averaged model for predicting parameter estimates (Arnold, 2010).

3. Results

3.1. *Post-release survival of captive-bred versus wild-born foxes*

After correcting for overdispersion ($\hat{c} = 1.213$ [0.713, 1.714]), the top ranked survival model for captive-bred foxes ($n = 27$; Appendix A1) included the interaction term *tsr * rodent abundance * population size* for φ, and *rodent abundance* for ρ and was ranked ΔQAIC = 4.280 from the next ranked model, with a QAIC weight of 0.845. Mean estimated apparent survival probability (95 % C.I. in square brackets) during the first year after release (sub-adults) was 0.466 [0.329, 0.585], whereas the probability of survival after the first year of release (adults) was 0.757 [0.671, 0.824]. The mean estimated probability of recapture was 0.781 [0.694, 0.842].

After correcting for overdispersion ($\hat{c} = 1.505$ [1.153, 1.857]), the top ranked comparative model for wild-born foxes ($n = 27$; Appendix A2) included the interaction term *tsm * rodent abundance* for φ, and *time* for ρ, with a QAICω = 0.810. The model was ranked ΔQAIC = 2.980 from the next ranked model. Mean estimated apparent survival probability of wild-born juveniles was 0.375 [0.308, 0.439], whereas the survival probability of sub-adults was 0.681 [0.522, 0.804]. Survival probability for wild-born adult foxes was 0.736 [0.643, 0.806]. The mean estimated probability of recapture was 0.666 (95 % C.I. = [0.515, 0.787]).

Apparent survival of both released captive-bred and wild-born foxes was positively associated with increasing small rodent abundance (Fig. 2). The increase was steeper for sub-adult captive-bred and juvenile wild-born foxes, whereas sub-adult wild-born foxes declined slightly with increasing rodent abundance. Survival of captive-bred foxes, both sub-adults and adults, declined with increasing population size (not shown).

3.2. *Reproductive success*

The top ranked model ($n = 25$; Appendix A3) for breeding propensity included the interaction terms *origin* rodent abundance*, *origin * population size*, and *sex*, and was ranked ΔAICc = 1.443 from the next ranked model, with a ΔAICc weight of 0.451. The two next ranked models were within ΔAICc <2 and included the interaction term *origin * sex* and the additive term *origin + rodent abundance*, respectively. Cumulative AICc weight of the three candidate models was 0.845. Of the 293 unique foxes of breeding age included in the analysis, 109 (37.2 %) had become breeders after captive release or birth in the wild. From the averaged candidate models (Appendix A5), the mean predicted probability of breeding was non-significantly lower for captive-bred ($\bar{x} = 0.42$ [0.21, 0.64]) than wild-born foxes ($\bar{x} = 0.66$ [0.48, 0.84]), and similar between females ($\bar{x} = 0.57$ [0.38, 0.76]) and males ($\bar{x} = 0.51$ [0.32, 0.72]; Fig. 3a).

The predicted probability of breeding increased with increasing rodent abundance for both captive-bred and wild-born foxes (Fig. 3b). Breeding propensity for wild-born foxes declined with increasing fox population size, whereas captive-bred foxes showed a tendency towards a non-significant increase in breeding propensity with increasing population size (Fig. 3c). Breeding success was strongly determined by fox age, peaking at 4–5 years of age.

The top ranked model ($n = 25$; Appendix A4) for *litter size* as a measure of reproductive output was ΔAICc = 0.241 from the next ranked model, with an ΔAICc weight of 0.143. The model included the interaction term *origin * population size* and *rodent abundance*. The lower-ranked candidate models within ΔAICc <2 included variants of additive or interactive effects of the aforementioned terms, or the addition of

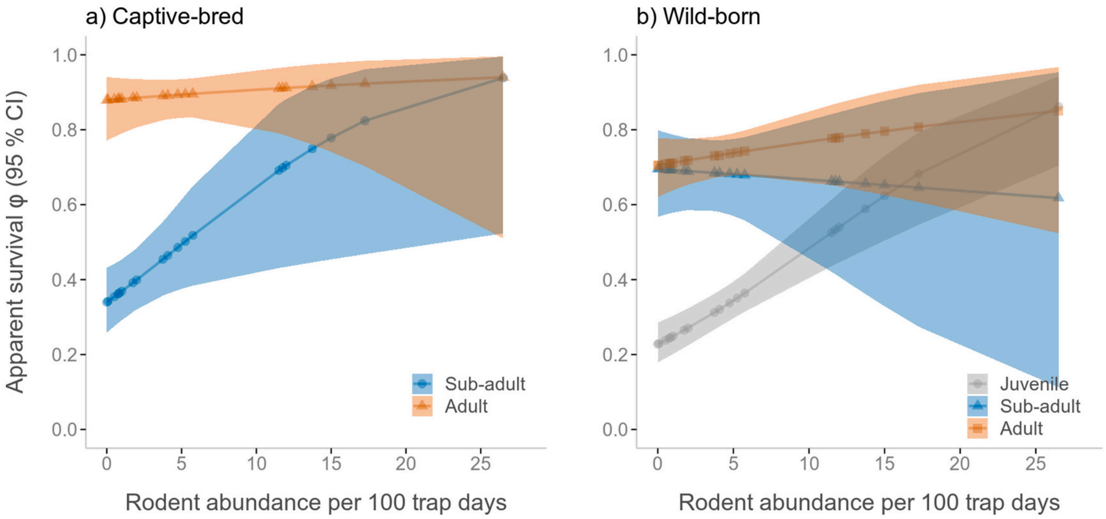

Fig. 2. a) Predicted apparent post-release survival of captive-bred Arctic foxes by age class in relation to rodent abundance (number of rodents trapped per 100 trap days), compared to b) predicted apparent survival of wild-born foxes by age class. The sub-adult age class represent foxes during their first year after release (first winter for wild-born foxes), whereas the adult age class is from the second winter onwards. Juvenile wild-born foxes represent the time-period from birth until the first winter. Shapes represent rodent abundance sampling points, whereas solid lines are the predicted apparent survival. Shaded areas represent 95 % confidence limits. Predictions were made using the median value of *population size*.

distance to release/birth location or previous breeding site. Of 209 successful breeding events, 54 % resulted in less than five pups, whereas 7 % resulted in >9 pups. From the averaged candidate models (Appendix A6), we found a non-significant tendency towards overall larger litters among captive-bred ($\bar{x} = 5.40$ [3.22, 7.58]) than wild-born ($\bar{x} = 4.23$ [2.41, 6.05]) foxes (Fig. 4a). Predicted litter sizes increased non-significantly with increasing rodent abundance (Fig. 4b), whereas litter sizes increased with increasing population size for captive-bred foxes and declined for wild-born foxes (Fig. 4c). Predicted litter sizes increased non-significantly with increasing distance from release or birth site (Fig. 4d). Litter size peaked at 3–4 years of age for both captive-bred and wild-born foxes, with a predicted average litter size of 6 pups at age 3.

4. Discussion

4.1. *Survival and breeding success of captive-bred versus wild-born Arctic foxes*

Our results demonstrate high survival rates and successful breeding among the released foxes and their descendants. Importantly, the survival of captive-bred Arctic foxes (subadults 47 % and adults 76 %) did not differ significantly compared to wild-born fox survival (subadults 68 %, adults 74 %). Juvenile mortality is highest during autumn, in our study 63 %, which is comparable to previous studies (Landa et al., 2017; Meijer et al., 2008; Nater et al., 2021; Tannerfeldt et al., 1994).

Captive-bred foxes are released in January–February and spend the preceding autumn in captivity, thereby protected from the high mortality rates that their wild-born conspecifics are subject to. The predicted probability of breeding was also similar between captive-bred and wild-born male and female foxes. ~~These results were somewhat unexpected.~~ Although captive-reared individuals used in translocation programmes may fare comparably well with wild individuals (Efrat et al., 2022), they have more frequently been found to have lower survival, breeding success, or suboptimal behaviour compared to wild residents or wild-caught individuals (Brittas et al., 1992; Hansen et al., 2000; Letty et al., 2007; Mccall et al., 1988; Poteaux et al., 1999; Sage et al., 2003). This is particularly true for mesocarnivores, who require both refined hunting abilities and anti-predator behaviour (Jule et al., 2008).

The overall similarities in survival and breeding success of captive-bred and wild-born foxes in our study suggests that rearing and release protocols are well designed and demonstrate that captive breeding programmes have good chances of success given an appropriate programme design. The rearing of foxes in large enclosures in a natural mountain habitat (Landa et al., 2017) were likely pivotal, and carefully planned release sessions further adds to the chances for establishment and breeding success.

4.2. *The importance of lemming cycles*

Survival and probability of breeding of both captive-bred and wild-born foxes were positively associated with abundance of small rodents. Small rodent abundance also had a positive effect on litter size. These results are in line with earlier studies demonstrating that the Arctic fox population in the Fennoscandian alpine areas is closely linked to abundance of rodents as an ecological factor, and especially lemmings (Angerbjörn et al., 1999; Elmhagen et al., 2000; Ims et al., 2017; Kaikusalo, 1982).

To mitigate the effects that low rodent availability could have on survival and reproductive success, a network of feeding stations were distributed across the mountain areas where foxes were released, often in close proximity to known den sites. Feeding stations were regularly (approximately every 1–2 months) filled with fresh dog pellets (Landa et al., 2017; Thierry et al., 2020). The maintenance and follow up of feeding stations has been continued within all release areas, also after the release years. However, the early releases (2007–2011) were likely also supported by a coincidental return of strong rodent peaks, compared to previous decades (Ehrich et al., 2019; Framstad and Eide, 2021).

Across large parts of their distributional range, Arctic foxes live in an environment driven by the cyclic abundance of their main prey, lemmings and other small rodents. The cyclic dynamics of rodents also strongly affect many other species by trophic interactions, including ground-nesting birds such as ptarmigan (Bowler et al., 2020), geese (Nolet et al., 2013) and waders (Machin et al., 2019). According to the “alternative prey hypothesis”, the densities of ground-nesting birds and rodents are positively associated due to predator–prey dynamics and prey-switching (Bowler et al., 2020; Murdoch, 1969). The Arctic foxes in our study had access to ad libitum food. Variations in establishment and breeding success could therefore not be explained by food limitation

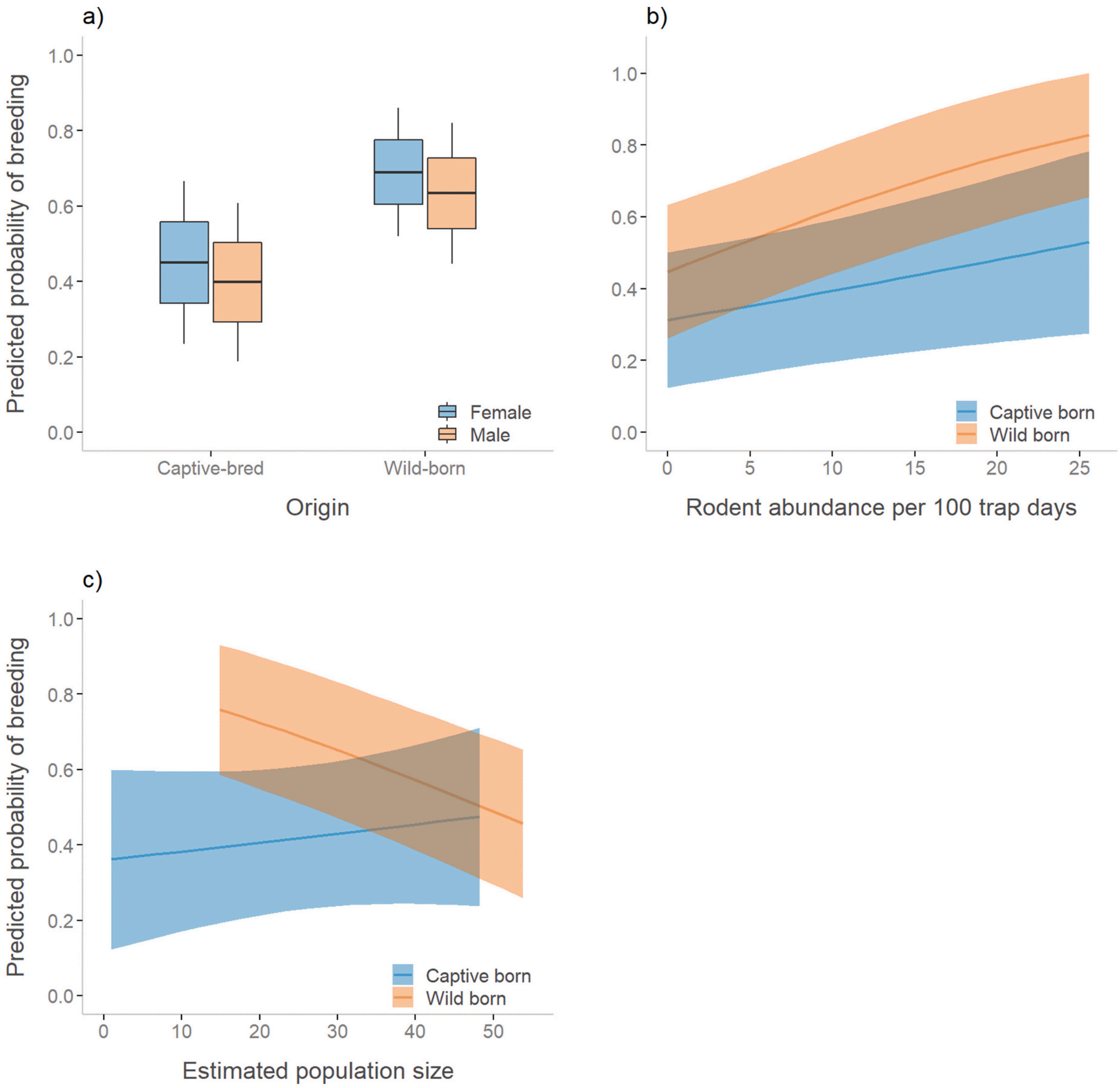

Fig. 3. The predicted probability of breeding for Arctic foxes depending on a) interactive effects of origin (captive-bred or wild-born) and sex (female or male), b) interactive effects of origin and rodent abundance, and c) interactive effects of origin and population size. Horizontal center lines in panel a) are the mean probabilities of breeding, whereas boxes represent SE and whiskers 95 % CI. Solid lines in panels b-c) are mean probabilities of breeding, whereas shaded areas represent 95 % Cl. Values are mean estimates from a prediction matrix based on model averaging the predictors of the candidate models.

alone. Angerbjörn et al. (2013) have earlier revealed that supplementary feeding could not decouple the strong link to the small rodent cycle, although the mechanisms remain unclear. Increased competition and predation pressure caused e.g., by prey switching during rodent declines (Bowler et al., 2020; Murdoch, 1969) could interact with other stressors. In snowshoe hare, the glucocorticoid levels have been found to vary depending on the phase of the cycle (Sheriff et al., 2011). During the decline phase, when the predators were most abundant, both baseline and stress-induced glucocorticoid levels were at the highest and the hares had lower reproduction and both offspring and adults were in poorer condition (Sheriff et al., 2009, 2011). For studies of wild Arctic foxes living in fluctuating systems, ecophysiological studies of rodent phase-effects on adrenocortical activity and indirect impacts of potential stressors might offer a better understanding of these complex interactions (Dantzer et al., 2014; Larm et al., 2021).

Our results reveal that timing of release into areas where rodents are in the increase phase clearly have the potential to increase subadult survival and trigger more first-time breeders during the following peak year. Occurrence of peak years vary to a large degree regionally (Ehrich et al., 2020; Framstad and Eide, 2021) and most years 2–4 potential release sites, based on foreseen rodent abundance, were identified as potentially suitable. We recommend that access to natural prey should always be considered when releasing animals into the wild. Although we have had access to monitoring data of small rodents in most release sites (Framstad and Eide, 2021), knowledge of regional prey densities is often not available.

Small rodent populations historically have a three- to five-year cyclic pattern of booming and collapsing (Angerbjörn et al., 1999; Ehrich et al., 2019). However, temporary irregularities of the cyclical lemming oscillations, as well as dampened peaks, have become more common in recent decades (Ims et al., 2011; Kausrud et al., 2008). Given foreseen climate change, rapid changes are expected in alpine and arctic tundra ecosystems (Ims et al., 2019). Indeed, changes in the small rodent cyclicity have been identified as one of the main threats to the future of the Arctic fox in Scandinavia (Henden et al., 2008), challenging future conservation of the species.

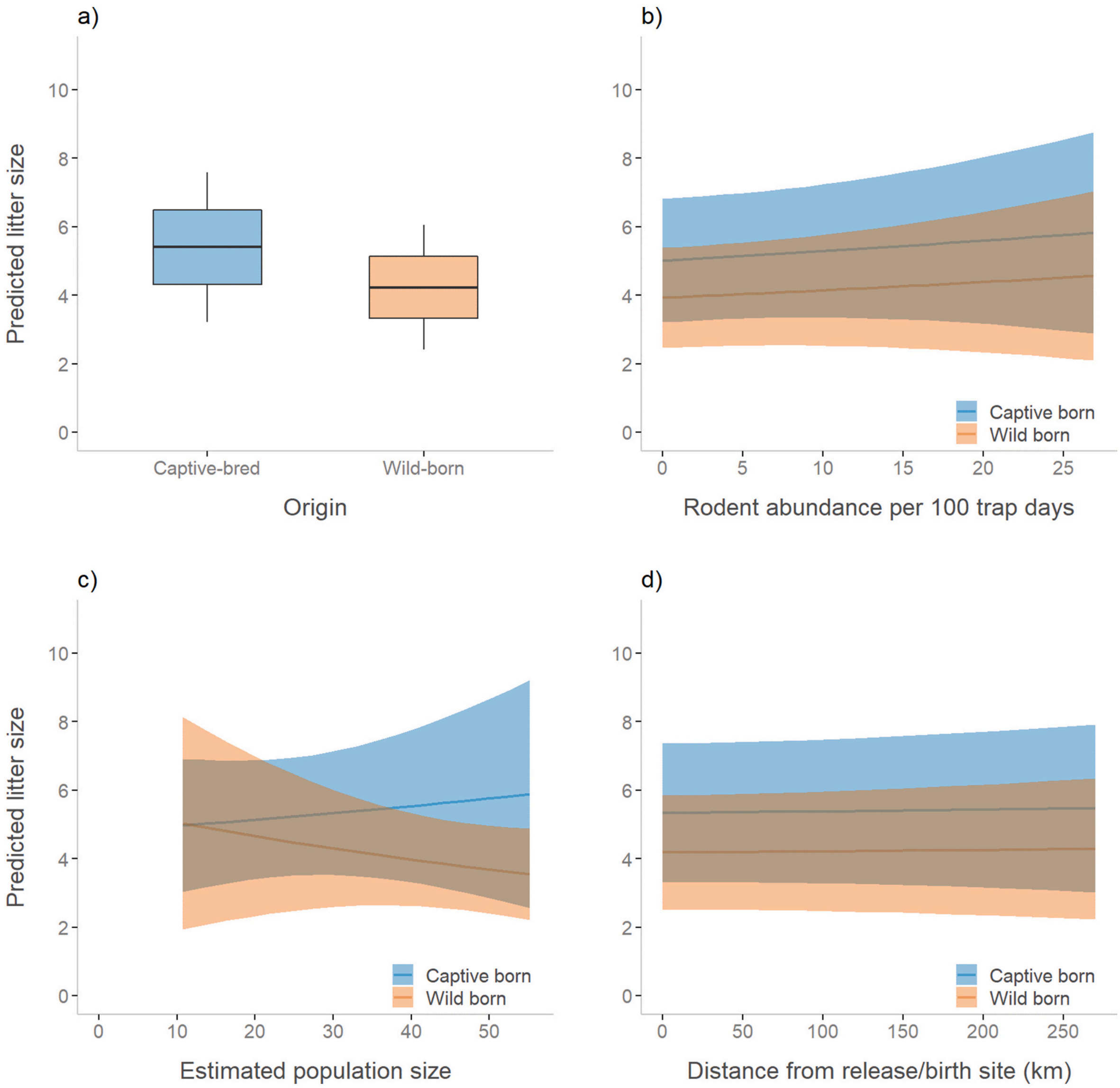

Fig. 4. Predicted litter size of Arctic foxes in relation to a) fox origin (captive-bred or wild-born), b) additive effects of origin and rodent abundance, c) interactive effects of origin and population size, and d) distance from release/birth site (km). Horizontal center lines in panel a) are the mean predicted litter size, whereas boxes represent one SE and whiskers 95 % Cl. Solid lines in panels b-d) are the mean predicted litter size, whereas shaded areas represent 95 % Cl. Values are mean estimates from a prediction matrix based on model averaging the predictors of the candidate models.

4.3. Density dependent effects and importance of metapopulation structure

Fennoscandian Arctic foxes inhabit artic and alpine tundra habitats where their distribution is restrained to patches of habitats embedded in forested areas (Herfindal et al., 2010). Our results showed that Arctic fox breeding propensity and litter size decreased with increasing population density for wild-born foxes, whereas a positive tendency were found among captive-bred individuals. The positive tendency among captive-bred foxes is likely explained by the fact that releases were primarily carried out in extinct populations (Landa et al., 2017), which could lead to a rapid release from Allee effects (Courchamp et al., 1999). Furthermore, during the short release period, female age distribution is skewed against young age classes since released individuals are sub-adults, and we observe that breeding propensity peaks at 4-5 yrs. of age as well as litter size peaking at 3-4 yrs. of age.

The observed negative density dependent effect for wild-born foxes is however more intriguing and a bit surprising, since the sub-populations are still quite small. These results could be a sign of the limited capacity of single tundra patches to housing self-subsistent populations that would be numerous enough to avoid loss of genetic variation (genetic drift and inbreeding) and negative impacts of environmental and demographic stochasticity (Chandler et al., 2015; Henden et al., 2008; Loison et al., 2001). The fragmented nature of the Fennoscandian alpine and arctic tundra implies that the Arctic fox, as well as other tundra species, should be managed as meta-populations (Hasselgren et al., 2018; Hemphill et al., 2020). Indeed, facilitating and maintaining connectivity among remnant and re-established Arctic fox populations are a key factor for further improvement and long-term survival (Chandler et al., 2015; Hemphill et al., 2020). Limited connectivity to surrounding populations is likely the fate of many endangered species living in increasingly fragmented habitats (IPBES 2020). Based on our study we recommend that conservation effort should always be targeted to several neighbouring habitat patches to optimize the effect of the actions.

4.4. Other supportive actions

The invading red fox is recognized as one of the main threats to the

Arctic fox (Elmhagen et al., 2017; Elmhagen et al., 2002; Shirley et al., 2009). Therefore, culling of red foxes was introduced early on as an action to assist Arctic fox population recovery. This has been a success in areas where populations occur in connectivity with other populations (Angerbjörn et al., 2013), but have failed in an isolated population (Ims et al., 2017), again pointing to the need for a metapopulation perspective in conservation management. However, culling one native species to protect another is controversial. Actions could alternatively be pointed directly to reduce the abundance of red foxes in typical Arctic fox habitats. Red fox invasion and establishment in the alpine and arctic tundra is positively affected and facilitated by anthropogenic activities and subsidies, and in some areas also vast abundance of ungulate carcasses (Henden et al., 2014). Actions targeted at reducing the amounts of subsidies could directly limit the occurrence of red foxes above the treeline. It is further recognized that large carnivores play an important role in shaping trophic structure (Malhi et al., 2016). Recent research reveals that both wolverine (*Gulo gulo*) and golden eagles (*Aquila chrysaetos*) have impact on the relationship between Arctic fox and red fox, favouring the Arctic fox (Rød-Eriksen, 2020). The Alpine tundra in Norway host extremely limited numbers of large carnivores, from political reasons, strictly controlled by management authorities (Gervasi et al., 2015; Saether et al., 2005). As a consequence, populations are currently far below functional densities. The Arctic fox has co-evolved with wolverines and golden eagles, which is probably why it is less prone to be victim of apex predation than the red fox (Rød-Eriksen, 2020). As such, restoring the populations of apex predators could possibly limit the abundance of red foxes in tundra habitat. There is clearly a need to explore if ecosystem-based management, e.g. allowing apex-predators and natural processes to re-establish, could be an alternative to costly and long term non-sustainable red fox control efforts.

4.5. Successful reintroductions, but is it enough?

At the onset of the captive breeding project, the Arctic fox was critically endangered, and the entire Fennoscandian population consisted of extremely few individuals. Sixteen years later, Norway's Arctic fox population alone is estimated to number ca. 300 individuals (Ulvund et al., 2021), while the total Fennoscandian population numbers ca. 470 foxes (Wallén et al., 2021). In addition, genetic variation within populations as well as metapopulation connectivity has increased significantly during the last decade (Hasselgren et al., 2018; Hemphill et al., 2017). Indeed, the release of captive-bred foxes was instrumental in increasing population sizes and saving the species from local extinction, together with supplementary feeding and red fox culling contributing to the success. As a result of successful conservation actions, the Arctic fox was recently delisted from critically endangered (CN) to endangered (EN) in mainland Norway and Sweden (ArtDatabanken, 2020; Artsdatabanken, 2021).

Evaluating the success of reintroduction programmes is generally based on four criteria (Jule et al., 2008). Firstly, the first wild-born population need to successfully reproduce. The results presented in this study demonstrate that this has been achieved. Secondly, a population should successfully reproduce for three years, with recruitment exceeding the adult mortality rate. With the first foxes being released in 2006, successful reproduction and recruitment has occurred for 15 years in the re-established populations, despite inter-annual variations largely linked to environmental conditions. The third criterium states that an unsupported population should attain a minimum population size numbering 500 individuals. The last census shows that we are approaching this number. When considering the population as a whole, which spans the border region between Norway, Sweden and Finland, recent population estimates suggest that there are ca. 470 individuals (Wallén et al., 2021). More challenging, however, is the specification that the population should be self-sustaining. In this respect, the conservation and management of Arctic foxes in Norway and Sweden is extraordinary, given the excessive resources used to support the populations with supplementary feeding. While the feasibility of rearing and releasing foxes into the wild is well documented (Landa et al., 2017), population persistence in the absence of supplementary feeding is not and represents an important facet currently receiving research attention. Indeed, the population's ability to persist without supplementary feeding will ultimately determine whether this fourth and final criterium will be met or not.

5. Conclusion

The Arctic fox captive breeding programme has been highly successful and can serve as a baseline study for similar projects. However, some of the major challenges such as interrupted and damped lemming cycles and red fox invasion into high alpine areas suggest that a more holistic ecosystem approach is needed for the future conservation of this species.

Declaration of competing interest

All sources of funding are acknowledged in the manuscript and there are no direct financial benefits to any of the authors from eventual publications.

Data availability

Data will be made available on request.

Acknowledgments

We thank all field personnel, students and volunteers who were involved in the captive-breeding and release programme, the Norwegian Nature Inspectorate, several park rangers (fjellstyrer) and Statskog for den site monitoring and field assistance.

Funding

The Norwegian Captive Breeding Programme for Arctic Fox (19087015) and The Arctic Fox Monitoring Programme in Norway (contract 18087019) were funded by the Norwegian Environment Agency.

Ethical aspects

We carried out this study in accordance with the Norwegian animal welfare act and the regulation on the use of animals in research. Capture and marking of free-ranging arctic foxes was approved by the institutional animal welfare unit, the Norwegian Animal Research Authority, and the Norwegian Environmental Agency. Marking of Arctic foxes performed at Sæterfjellet captive breeding station is regarded part of the management procedures of the approved animal research facility (Unit number 150).

CRediT authorship contribution statement

AL, LRE, ØF, AMT, CJ, KRU and NEE conceived and designed the study on establishment success. AL, NEE, and ØF coordinated the long-term national programmes for captive-breeding and monitoring of Arctic fox in Norway. AL, NEE, ØF and KRU collected field data through these programmes, with the help of numerous mountain rangers and field personnel. LRE analysed the data with input from AL, NEE, ØF, AMT, CJ and KRU. AL drafted the manuscript except parts of methods and result which was drafted by LRE. All authors contributed critically to the drafts.

Appendix A. Model selection tables

Appendix A1

Model selection table for the live encounter survival model of captive-bred Arctic foxes, showing the top 20 models ($n = 27$). Model parameters are abbreviated, where Phi (φ) is the apparent survival, and p (ρ) is the recapture probability, *tsr* are the 2 age classes (sub-adult and adult) since release, *rod* is the rodent abundance (rodents per 100 trap days) and *pop* is the population size. Par is the number of parameters for each model.

Rank	Model	Par	QAIC	DeltaQAIC	QAICweight	neg2lnl
1	Phi(~tsr * rod * pop)p(~rod)	10	507.879	0	0.8452556	591.823
2	Phi(~tsr * rod * pop)p(~1)	9	512.159	4.280	0.0994457	599.441
3	Phi(~tsr * rod)p(~time)	14	513.727	5.848	0.0454125	589.212
4	Phi(~tsr * rod * pop)p(~time)	18	516.777	8.898	0.0098799	583.208
5	Phi(~tsr * pop)p(~1)	5	533.468	25.589	0.0000024	634.993
6	Phi(~tsr * rod)p(~rod)	6	534.491	26.612	0.0000014	633.809
7	Phi(~tsr * pop)p(~rod)	6	534.661	26.781	0.0000013	634.014
8	Phi(~tsr * rod)p(~1)	5	535.434	27.555	0.0000009	637.378
9	Phi(~tsr)p(~time)	12	538.070	30.191	0.0000002	623.593
10	Phi(~tsr * pop)p(~time)	14	539.033	31.154	0.0000002	619.909
11	Phi(~tsr)p(~rod)	4	552.053	44.174	0.0000000	659.964
12	Phi(~tsr)p(~1)	3	553.389	45.509	0.0000000	664.010
13	Phi(~rod)p(~time)	12	554.792	46.913	0.0000000	643.879
14	Phi(~time)p(~rod)	12	555.581	47.702	0.0000000	644.835
15	Phi(~time)p(~1)	11	557.691	49.812	0.0000000	649.821
16	Phi(~rod * pop)p(~time)	14	558.148	50.269	0.0000000	643.097
17	Phi(~time)p(~time)	20	561.103	53.224	0.0000000	632.125
18	Phi(~rod * pop)p(~1)	5	566.198	58.319	0.0000000	674.697
19	Phi(~rod * pop)p(~rod)	6	567.582	59.703	0.0000000	673.949
20	Phi(~1)p(~time)	11	572.337	64.457	0.0000000	667.587

Appendix A2

Model selection table for the live encounter survival models of wild-born Arctic foxes, showing the top 20 models (n = 27). Model parameters are abbreviated, where Phi (φ) is the apparent survival, and p (ρ) is the recapture probability, *tsm* are the 3 age classes (juvenile, sub-adult and adult) since marking, *rod* is the rodent abundance (rodents per 100 trap days) and *pop* is the population size. Par is the number of parameters for each model.

Rank	Model	Par	QAIC	DeltaQAIC	QAICweight	neg2lnl
1	Phi(~tsm * rod)p(~time)	16	1123.369	0	0.8100090	1642.368
2	Phi(~tsm * rod * pop)p(~time)	22	1126.349	2.980	0.1825360	1628.794
3	Phi(~tsm * rod)p(~rod)	8	1132.927	9.559	0.0068058	1680.830
4	Phi(~tsm * rod * pop)p(~rod)	14	1137.952	14.583	0.0005518	1670.334
5	Phi(~tsm * rod)p(~1)	7	1141.868	18.499	0.0000779	1697.294
6	Phi(~tsm * rod * pop)p(~1)	13	1145.358	21.989	0.0000136	1684.487
7	Phi(~tsm)p(~time)	13	1147.934	24.565	0.0000038	1688.365
8	Phi(~tsm * pop)p(~time)	16	1149.037	25.668	0.0000022	1680.995
9	Phi(~tsm)p(~rod)	5	1163.264	39.895	0.0000000	1735.512
10	Phi(~tsm * pop)p(~rod)	8	1164.284	40.915	0.0000000	1728.017
11	Phi(~tsm * pop)p(~1)	7	1168.666	45.297	0.0000000	1737.622
12	Phi(~tsm)p(~1)	4	1168.955	45.586	0.0000000	1747.087
13	Phi(~rod)p(~time)	12	1189.627	66.258	0.0000000	1754.116
14	Phi(~rod * pop)p(~time)	14	1191.115	67.746	0.0000000	1750.337
15	Phi(~time)p(~time)	20	1195.141	71.772	0.0000000	1738.337
16	Phi(~time)p(~rod)	12	1198.221	74.852	0.0000000	1767.050
17	Phi(~1)p(~time)	11	1199.327	75.958	0.0000000	1771.723
18	Phi(~pop)p(~time)	12	1200.404	77.035	0.0000000	1770.335
19	Phi(~time)p(~1)	11	1206.021	82.652	0.0000000	1781.797
20	Phi(~rod)p(~rod)	4	1209.392	86.023	0.0000000	1807.939

Appendix A3

Model selection table for the generalized additive binomial models (GAM) on breeding propensity of Arctic foxes, showing the top 20 models (n = 25). Model parameters are abbreviated, where *rod* is the rodent abundance (rodents per 100 trap days), *pop* is the population size, and *origin* is whether foxes are captive-bred or wild-born. df is the degrees of freedom, AICc is the AIC adjusted for small sample size, ΔAICc is the difference in AICc from the higher ranked model, and ΔAICc ω is the model weight. All models included fox *age* as a smoothing factor.

Rank	Model	df	AICc	ΔAICc	ΔAICc ω
1	breeding ~ rod * origin + pop * origin + sex	11.739	817.494	0.000	0.451
2	breeding ~ rod * origin + pop * origin + sex * origin	12.735	818.937	1.443	0.219
3	breeding ~ rod + origin + pop * origin + sex	10.690	819.386	1.892	0.175
4	breeding ~ rod + pop * origin + sex * origin	11.687	821.044	3.550	0.076
5	breeding ~ rod * sex + pop * origin	11.689	821.422	3.929	0.063
6	breeding ~ rod * origin + pop + sex	10.539	825.645	8.152	0.008

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Appendix A3 (*continued*)

Rank	Model	df	AICc	ΔAICc	ΔAICc ω
7	breeding ~ rod + sex + origin	8.593	828.668	11.175	0.002
8	breeding ~ rod * origin + sex	9.586	829.091	11.597	0.001
9	breeding ~ rod + sex * origin	9.592	829.927	12.433	0.001
10	breeding ~ rod + origin	7.584	830.023	12.529	0.001
11	breeding ~ rod * origin	8.568	830.519	13.025	0.001
12	breeding ~ rod	6.680	831.501	14.007	0.000
13	breeding ~ rod * pop	8.808	832.669	15.175	0.000
14	breeding ~ rod + pop	7.682	833.370	15.876	0.000
15	breeding ~ rod * origin * sex	12.548	833.822	16.328	0.000
16	breeding ~ pop * origin	8.755	833.899	16.405	0.000
17	breeding ~ pop + origin	7.680	837.803	20.309	0.000
18	breeding ~ sex + origin	7.715	838.625	21.131	0.000
19	breeding ~ sex	6.755	838.767	21.273	0.000
20	breeding ~ origin	6.710	839.147	21.653	0.000

Appendix A4

Model selection table for the generalized additive mixed models (GAMM) on reproductive output (litter size) of Arctic foxes, showing the top 20 models ($n = 25$). Model parameters are abbreviated, where *rod* is the rodent abundance (rodents per 100 trap days), *pop* is the population size, *origin* is whether foxes are captive-bred or wild-born, *distance* is the distance from previous breeding site (or place of release/birth), and *isFirstBreed* determines if this is the first breeding event or not. df is the degrees of freedom, AICc is the AIC adjusted for small sample size, ΔAICc is the difference in AICc from the higher ranked model, and ΔAICc ω is the model weight. All models included fox *age* as a smoothing factor.

Rank	Model	df	AICc	ΔAICc	ΔAICc ω
1	litter_size ~ origin * pop + rod	8	330.297	0.000	0.143
2	litter_size ~ origin * pop	7	330.538	0.241	0.126
3	litter_size ~ origin + rod	6	330.738	0.441	0.114
4	litter_size ~ origin + pop	6	331.322	1.024	0.085
5	litter_size ~ origin * pop + rod + distance	9	331.883	1.585	0.065
6	litter_size ~ origin + pop + rod	7	332.322	2.025	0.052
7	litter_size ~ origin * pop + rod + isFirstBreed	9	332.369	2.072	0.051
8	litter_size ~ origin * pop + origin * rod	9	332.479	2.182	0.048
9	litter_size ~ origin * pop + rod * distance	10	332.518	2.220	0.047
10	litter_size ~ origin * rod	7	332.536	2.239	0.047
11	litter_size ~ origin * distance	7	332.820	2.523	0.040
12	litter_size ~ origin * pop + rod + origin * distance	10	332.846	2.549	0.040
13	litter_size ~ origin * isFirstBreed	7	333.637	3.339	0.027
14	litter_size ~ origin * sex	7	333.848	3.551	0.024
15	litter_size ~ origin * pop + rod * isFirstBreed	10	334.023	3.725	0.022
16	litter_size ~ origin + pop + origin * rod	8	334.340	4.042	0.019
17	litter_size ~ origin * pop + rod + origin * isFirstBreed	10	334.428	4.130	0.018
18	litter_size ~ origin * pop + rod * isFirstBreed + distance	11	335.530	5.232	0.010
19	litter_size ~ origin + pop + rod * isFirstBreed	9	335.730	5.433	0.009
20	litter_size ~1	2	336.510	6.213	0.006

Appendix A5

Parameter estimates from model averaging of the three top-ranked candidate models (ΔAICc <2) for breeding propensity (Table A3). Values are shown on the logit scale.

Parameter	Estimate	SE	Adj. SE	*p*-value	Lower CI	Upper CI
(Intercept)	−0.963	0.214	0.214	< 0.001	−1.382	−0.543
Rodents	0.252	0.118	0.118	0.033	0.021	0.483
Origin (Wild born)	0.566	0.253	0.253	0.025	0.070	1.062
Sex (Male)	−0.244	0.214	0.214	0.256	−0.664	0.177
Pop.size	0.154	0.190	0.191	0.420	−0.220	0.528
Rodents * Origin (Wild born)	0.353	0.178	0.178	0.048	0.004	0.703
Pop.size * Origin (Wild born)	−0.717	0.232	0.233	0.002	−1.173	−0.261
Sex (Male) * Origin (Wild born)	−0.275	0.354	0.354	0.438	−0.970	0.419

Appendix A6

Parameter estimates from model averaging of the five top-ranked candidate models (ΔAICc <2) for reproductive output (Table A4).Values are shown on the log scale.

Parameter	Estimate	SE	Adj. SE	p-value	Lower CI	Upper CI
(Intercept)	1.721	0.081	0.081	0.000	1.562	1.880
Origin (Wild born)	−0.251	0.099	0.100	0.012	−0.446	−0.056
Pop.size	0.063	0.108	0.109	0.561	−0.150	0.276

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Appendix A6 (*continued*)

Parameter	Estimate	SE	Adj. SE	p-value	Lower CI	Upper CI
Rodents	0.056	0.047	0.047	0.232	−0.036	0.149
Pop.size * Origin (Wild born)	−0.247	0.122	0.123	0.044	−0.488	−0.006
Distance	0.001	0.001	0.001	0.381	−0.001	0.002

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