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REVIEW

The Swedish Arctic Fox Project: 40 years of research in ecology and conservation

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Abstract

The scientific community widely recognizes the value of long-term studies, especially those with individual-level resolution; however, maintaining a consecutive data series is associated with multiple challenges connected to funding, national and international research strategies, and staff. The Swedish Arctic Fox Project was established in 1985, with the primary aim of identifying factors halting recovery from a demographic decline initially driven by intensive fur harvesting in the early 1900s. Research in The Swedish Arctic Fox Project has, over the past 4 decades, been centered around 4 themes: species interactions, life history and population dynamics, behavioral ecology, and conservation genetics. Monitoring on both individual and population levels has generated a unique data set, offering an unprecedented opportunity to follow population recovery and individual fitness. Key contributions of general value include interspecific competition in a climate change context, life-history strategies in a fluctuating environment, and small population processes such as inbreeding depression and genetic rescue. Furthermore, there has been a strong link between research output and practical conservation, enabling a scientifically informed foundation for design, evaluation, and

refinement of highly efficient conservation actions, as well as guidelines and recommendations. The Swedish Arctic Fox Project constitutes an important yet rare example of long-term studies with deliverables for general science, applied conservation, and science-policy work, and highlights the role of the arctic fox as an informative model system.

KEYWORDS

arctic fox, behavioral ecology, conservation genetics, informed conservation actions, long-term research, model system, population dynamics, species interactions

Long-term studies of natural populations are of significant value for research in ecology and conservation (Clutton-Brock and Sheldon 2010, Murray and Krebs 2024). Traditionally, many long data series have focused on temporal changes in distribution and abundance at the population level (e.g., Krebs 2011, Henttonen et al. 2017, Ehrich et al. 2020). However, temporal individual-based studies of wildlife populations have made important contributions to the general understanding of community dynamics, population processes, life-history biology, and population genetics and have informed practical conservation. Examples of such influential long-term data sets with individual resolution are the Isle Royale grey wolf (*Canis lupus*; Nelson et al. 2011), the Soay sheep (*Ovis aries*; Clutton-Brock and Pemberton 2004), and the Isle of Rum red deer (*Cervus elaphus*; Pemberton et al. 2023). Although generally attributed great value, maintenance of long-term data sets is often challenged by uncertain funding opportunities and usually builds on consecutive short-term grants centered around specific research goals rather than continued monitoring (Sheldon et al. 2022).

The Swedish arctic fox (*Vulpes lagopus*) is another example of a mammal population that has been studied over multiple decades. Long-term monitoring of this population is important because the population is of conservation concern, and it can also function as a model system for ecological and evolutionary research on cyclic population dynamics (Elmhagen et al. 2011, Angerbjörn et al. 2013, Meijer et al. 2013).

As a representative of an arctic species at the edge of its southern distribution limit, long-term research on the population and its surrounding ecosystem can provide early knowledge on global change (Elmhagen et al. 2017), whilst monitoring during and following a pronounced population bottleneck has allowed research on key processes operating in small populations (Nyström et al. 2006, Norén et al. 2016). In conservation biology long-term data are invaluable for evaluating possible threats to populations. However, Caughley (1994) pointed out in the declining population paradigm that population declines caused by external factors often require specific studies, with limited general value. In The Swedish Arctic Fox Project, our goal has been to focus on science-based studies, sometimes with a conservation perspective but always with a general scientific basis.

The Swedish arctic fox was legally protected in 1928 following a severe demographic decline likely primarily driven by fur harvesting (Hersteinsson et al. 1989). The Swedish population is a part of a transnational metapopulation in Fennoscandia also including tundra ecosystems in Norway, Finland, and the Kola Peninsula, with similar processes operating throughout its distribution (Hersteinsson et al. 1989, Angerbjörn et al. 2013, Tirronen et al. 2021). Despite protection for many decades, the population did not recover and was on the verge of extinction in the 1990s, with only 40–60 individuals remaining in Sweden, Norway, and Finland (Angerbjörn et al. 2013). The Swedish Arctic Fox Project was established in 1985 in Vindelfjällen nature reserve with research focusing primarily on species interactions and population dynamics. With time, the project extended the study area to cover a large part of the arctic fox distribution in Sweden. Data collection through yearly summer monitoring has been the backbone of the project since the start, combining population- and individual-level perspectives. A highly valuable component is the individual ear-tagging program, initiated in 1989 when the population size was low. The

ear-tagging program is still active, allowing collection of long-term fitness data along with genetic sampling over consecutive generations. Based on this unique data set, detailed studies of life history, behavior, and population genetics were initiated.

Given the uncertainty regarding the lack of recovery despite legal protection, a strong emphasis on conservation strategies has influenced the research. Food scarcity driven by irregular small-rodent cycles in combination with increased spatial overlap with expanding red foxes (*Vulpes vulpes*) were suggested as key threats during the 1980s and 1990s (Hersteinsson et al. 1989, Kaikusalo and Angerbjörn 1995), and from the early 2000s management authorities have conducted conservation actions in the form of supplementary feeding and red fox control (Angerbjörn et al. 2013). Through close collaborations between The Swedish Arctic Fox Project and responsible authorities and research institutes both on national and international levels (Finland and Norway), the effects of these actions have been continuously evaluated and refined (Angerbjörn et al. 2013). Today, the arctic fox population in Sweden, Norway, and Finland has increased to 526 individuals (Wallén et al. 2025) in response to scientifically informed conservation actions and more regular prey conditions. However, recent research within the project has identified additional threats and challenges for the population, such as golden eagle (*Aquila chrysaetos*) predation, inbreeding depression, and pathogen outbreaks (e.g., Meijer et al. 2011, Norén et al. 2016, Hasselgren et al. 2024, Wallén et al. 2024).

The long-term study of the Swedish arctic fox has generated important scientific insights of both general and applied value. Although excellent colleagues in Norway and other countries have provided high-quality studies with strong relevance for arctic fox conservation (e.g., Ims et al. 2017, Landa et al. 2022, Hemphill et al. 2024), we chose to focus this paper on the Swedish perspective. Furthermore, the aim is not to provide a detailed account of the transnational conservation strategies and their impact on population development. In this paper, we subsequently summarize the first 40 years of Swedish arctic fox research, divided into 4 central themes: species interactions, life-history and population dynamics, behavioral ecology, and conservation genetics. The goals are to give an overview of the scientific contributions of this long-term project focused on the Swedish arctic fox population and outline future directions for arctic fox research.

STUDY AREA

Arctic fox habitat in Sweden covers the treeless mountain tundra (62°32′ N, 12°33′ E – 68°22′ N, 19°22′ E) with a total size of approximately 32,000 km^2. The Swedish tundra region is characterized by both high latitude and altitude, with forested valleys intersecting the tundra, causing natural fragmentation (Angerbjörn et al. 2013). This ecosystem is characterized by subarctic climate with short, cool summers and long, cold winters. Snow cover typically lasts from October until May or June. Land cover is characterized by dry heath, grass heath, dry fen, rocks, and fern (Stoessel et al. 2019). Three main vegetation areas dominate above the treeline: wetland areas (graminoids, water sedge [*Carex aquatilis*]), mesic areas (graminoids, shrubs, willows [*Salix* spp.], mosses [*Bryophyta* spp.], saxifrages [*Saxifraga* spp.], cinquefoils [*Potentilla* spp.], buttercups [*Ranunculus* spp.]), and dry heath areas (bilberry [*Vaccinium myrtillus*], crowberry [*Empetrum nigrum*], and lichens [*Lichenes* spp.]; Le Vaillant et al. 2018).

Microtine rodents, and especially the Norwegian lemming (*Lemmus lemmus*), are key prey species for the arctic fox. Additional relatively abundant microtine rodents are grey-sided vole (*Craseomys rufocanus*) and field vole (*Microtus agrestis*). Other arctic fox prey species include ptarmigan (rock [*Lagopus muta*] and willow [*L. lagopus*] ptarmigan) and other birds (Passeriformes, Anseriformes, Charadriiformes), mountain hare (*Lepus timidus*), and reindeer (*Rangifer tarandus*; Stoessel et al. 2019, Wilkinson et al. 2023). Besides the arctic fox, other predator species include mammals like mustelids (stoat [*Mustela erminea*], least weasel [*Mustela nivalis*]), wolverine (*Gulo gulo*), and the recently expanded red fox, and birds like golden eagle, white-tailed eagle (*Haliaeetus albicilla*), rough-legged buzzard (*Buteo lagopus*), gyrfalcon (*Falco rusticolus*), kestrel (*Falco tinnunculus*), long-tailed skua (*Stercorarius longiccaudus*), and raven (*Corvus corax*; Stoessel et al. 2019, Wilkinson et al. 2024).

Fieldwork in The Swedish Arctic Fox Project has typically focused on 4–5 research areas providing high-quality habitat for the arctic fox (Figure 1). Research initiatives have generated a continuous data set from Vindelfjällen nature reserve (year 1985) geographically connected to Arjeplogsfjällen, and from Helagsfjällen (year 2000). For the northern subpopulations (year 1985), research initiatives have been periodic with temporally scattered projects. For Borgafjällen (year 2004), a close-to-continuous data set has been generated. This paper focuses on research conducted in the Swedish arctic fox population. When studies include additional regions (Norway, Finland, and the Kola Peninsula) in the broader metapopulation, we henceforth refer to it as the Fennoscandian population.

METHODS

The Swedish Arctic Fox Project has established an extensive protocol for fieldwork mainly carried out during the summer season in large parts of the distribution range. The field protocol, developed since 1985, integrates den surveys, animal tagging, genetic sampling, prey monitoring, and behavioral observation, yielding detailed demographic and ecological data (e.g., survival rates, litter sizes, population trends; Figure 2). Fieldwork is assisted by volunteer fieldworkers (~30 per year) and conducted primarily during July, when known fox dens are visited systematically and standardized surveys of prey abundance and habitat are conducted. The majority of the dens in our study area are long-lasting structures, excavated in glaciofluvial sand ridges with fine sorted sand. Such dens with many entrances are used over multiple generations, more than 100 years and probably even longer (Dalerum et al. 2002).

In the early years of the project, around 20–30 dens were inspected annually, whereas today, in collaboration with the County Administrative Boards, up to 80% of the 500 known dens in Sweden are surveyed each summer. The remaining dens are low-priority sites, such as collapsed, long-abandoned, or red fox dens. The percentage of active breeding arctic fox dens varied between 0 and 19% during the project period. Volunteer fieldworkers can access the majority of dens through hiking during summer. In remote areas, helicopter transport may be used. During the winter season (February–May), fieldwork is limited by harsh weather conditions, long periods of darkness, and a reduced chance of observing foxes. Winter and spring monitoring has therefore mainly been accomplished using remote cameras and collection of scat samples for genetic analyses; however, specific teams monitor the tundra community in selected areas through systematic wildlife triangle (3 × 4 km) snow-tracking (Stoessel et al. 2019, Wilkinson et al. 2024).

Den monitoring and ear-tagging

When a den is active, the number of adult arctic foxes and cubs, and the identity of already tagged adults, is recorded (Figure 2). In research-intensive areas, cubs, and occasionally adults, are captured at active dens using baited live traps (models 206, 207, and 208; Tomahawk Live Trap, Hazelhurst, WI, USA) and fitted with unique colored ear-tags for individual identification. Foxes are handled while conscious in a handling bag, and crews note information about sex and color morph, collect genetic samples (skin biopsy, hair), and record standard measurements (body mass, hind-foot length) for each captured individual. Thereafter, ear-tagged foxes can be identified by their tag colors both from a distance and on wildlife cameras. Immigrants from the Norwegian captive breeding program are identified via observations of ear tags or genetic analysis. For survival estimates, the den is sometimes revisited roughly 40 days after first discovery to count surviving cubs; juvenile summer survival is calculated as cubs in late summer/cubs at first visit and standardized to compensate for differences in visiting interval. In specific areas, we fit trapped adults with collars (1990–2008: very high frequency [VHF], Televilt, Lindesberg, Sweden; 2018 onwards: global positioning system [GPS], Milsar, Nicosia, Cyprus or Telonics, Mesa, AZ, USA) to collect data on home range and dispersal.

FIGURE 1 Arctic fox distribution (red) in Sweden (yellow), Norway, and Finland, with Swedish study areas circled and labeled by the year when research was initiated.

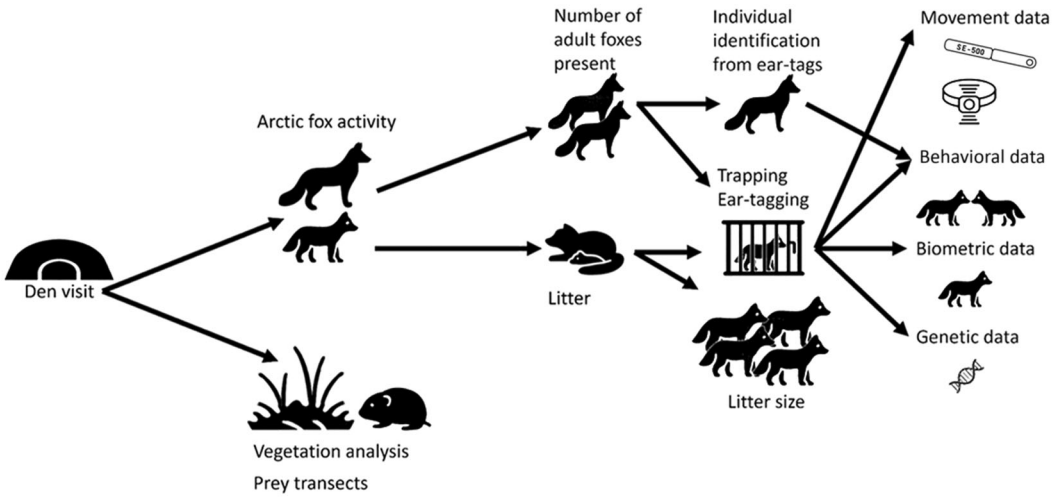

FIGURE 2 Schematic overview of fieldwork protocol in The Swedish Arctic Fox Project. Analysis of global positioning system (GPS) collar data is currently underway and not covered in this paper.

Behavioral observations

Whenever dens are occupied, detailed behavioral observations are made. Under specific permits, fieldworkers typically camp 150–200 m from active dens and record fox activity continuously when visibility and workload allow. During focused behavioral observations, fieldworkers document adult and cub behavior through a 5-minute screening approach for up to 48 hours per den. These observations capture parental attendance, cub play behavior, social grouping, among other behaviors. Motion-triggered camera traps used for behavioral study purposes are also placed at dens to gather round-the-clock data on fox activity within the defined study period. In addition, standardized human-approach trials have been conducted where an observer approaches a fox at set distances and records the response (vigilance, flight) at each step (Choi et al. 2019). These disturbance trials quantify fox tolerance to humans and inform management guidelines, such as recommending a ≥300-m minimum approach distance for the public (Larm et al. 2020). To assess variation in personality, the behavior of all trapped cubs is systematically scored during trapping and handling for ear-tagging, building on an approach originally developed for the kit fox (*Vulpes macrotis*; Bremner-Harrison et al. 2018).

Genetic and non-invasive sampling

Genetic analysis was integrated in the early 2000s, but sample collection started even earlier (1980s). Samples collected during ear-tagging are genotyped, and data are used to calculate population genetic estimates, identify population structure and gene flow, and construct pedigree to assess processes of inbreeding and genetic rescue (Dalén et al. 2006, Norén et al. 2016, Hasselgren et al. 2018). Since the early 2020 s, detailed explorations of conservation genetic processes have been accomplished through whole-genome sequencing (Hasselgren et al. 2021, 2024).

Besides tissue and hair samples collected from ear-tagging, fieldwork teams also collect other samples for DNA analysis, such as scat and hair from dens or feeding stations. Opportunistic collection of urine from dens, feeding stations, and snow tracks has also been implemented. Genetic analysis of non-invasive material can identify species (red or arctic fox; Dalén et al. 2004*b*) and generate individual genetic profiles through genotyping. Meijer et al. (2008) exemplified this approach by analyzing 98 arctic fox droppings collected during the winter of 2006.

The genetic profiles from scats were matched to profiles of known tagged foxes (2001–2005), and subsequent data were used to estimate population parameters. This approach can detect foxes that are otherwise unseen and improves estimates of population size even when population densities are low. Analysis of scat samples can also provide material for diet analysis (Elmhagen et al. 2000, Wilkinson et al. 2023).

Prey and prey habitat use surveys

Prey abundance and prey habitat use have been recorded since the 1990s in parallel with fox counts. Snap-trapping transects with Krebs-lines (Krebs et al. 2003; typically 30–60 traps per grid or transect) are maintained for 48 hours to estimate small-rodent density. Catches (rodents/100 trap-nights) provide a standardized index of lemming and vole availability. Vegetation plots based on the Hult-Sernander-Du Rietz scale (Trass and Malmer 1973) are recorded along the rodent trap lines to analyze prey habitat use. In parallel, line-transect surveys are carried out to monitor birds, especially ptarmigan, grouse, and other large fox prey species. These prey and vegetation data help explain annual variation in small-rodent presence and associated variation in fox breeding success.

RESULTS

Species interactions

An understanding of factors halting arctic fox population recovery was lacking during the early stages of the project, but Hersteinsson et al. (1989) proposed that temporal resource availability and interactions with northwards expanding red foxes could be involved. A related concern in the late 1980s and 1990s was a rapid additional decline in arctic fox population size, which went from small to the brink of extinction around 2000, possibly due to a low availability of lemmings (Angerbjörn et al. 1995). Building on this, the relationship between the arctic fox and other species in the tundra community has been a central research focus within The Swedish Arctic Fox Project, with important implications for conservation management as we consider below.

Lemmings and voles

Small rodents are tundra keystone species and the primary prey of the Fennoscandian arctic fox (Elmhagen et al. 2000, 2002). In the mountain tundra, lemmings and voles generally display cyclic dynamics with high-abundance peaks every 3–5 years (Collett 1911, Elmhagen et al. 2011), which have a strong impact on the predator guild (Ims and Fuglei 2005). Angerbjörn et al. (2001) conducted a meta-analysis of population dynamics of lemmings in Fennoscandia and found that 4-year cycles were most common. However, small-rodent cycles have shown periodic disruptions in the twentieth century, with long periods without high-abundance peaks (Henttonen and Kaikusalo 1993), possibly as an indirect effect of climate change (Angerbjörn et al. 2001; Elmhagen et al. 2011, 2015).

The dynamics of small rodents is a key driver of multiple aspects of arctic fox biology (Krebs 2013). Elmhagen et al. (2000) found that although arctic foxes are generally opportunistic carnivores, they function ecologically as specialists on lemmings in inland Fennoscandia, with lemmings as dominant prey. The presence of alternative prey varied by year and region, suggesting opportunistic feeding when lemmings were scarce. A later genetic barcoding study in a Swedish subpopulation by Wilkinson et al. (2023) supported the finding of small rodents, and particularly lemmings, as the key prey for the arctic fox.

The relationship between arctic foxes and lemmings was explored in detail along the Siberian north coast during the 1990s (Angerbjörn et al. 1999). The study demonstrated that arctic foxes displayed a 1-year time lag in

numerical response to the Siberian lemming (*Lemmus sibiricus*), while litter sizes showed a direct, linear relationship. These strong temporal fluctuations in arctic fox numbers in high arctic ecosystems also have a profound effect on the abundance of arctic birds, where breeding in geese and waders follows the lemming cycle (Roselaar 1979, Summers 1985). There has been a discussion regarding the extent to which these phenomena can be attributed to functional responses or the delayed numerical response of arctic foxes, but a recent study from Angerbjörn et al. (2026) argues that it is the numerical response between arctic foxes and lemmings that generates a prey switch at low lemming abundance, thereby forcing arctic birds into the basic lemming cycle.

The spatial distribution of lemmings is expected to be a central parameter influencing the quality of arctic fox territories and subsequently a key factor predicting arctic fox distribution. Le Vaillant et al. (2018) found that lemmings were more habitat specific during the increase phase, with higher abundance in steeper areas facing north and east where snow typically accumulates because of the dominating southwesterly winds. In the peak phase, lemmings were less specific regarding landscape features and were more commonly found in more productive patches (Le Vaillant et al. 2018). The remote sensing method used in Le Vaillant et al. (2018) was further evaluated by Erlandsson et al. (2019), showing that readily available high-resolution orthophotos (typically collected by cadastral authorities) constitute a useful tool to assess primary productivity and vegetation properties at a scale relevant for individual small animals. An important consideration is that arctic fox reproductive success (measured as occupancy of breeding dens) is strongly correlated with lemming densities from the previous winter (Elmhagen et al. 2000). Connected to this, Vigués et al. (2022) investigated the distribution of lemming winter nests over different phases of the lemming cycle. Winter nests were primarily found in meadows and drier habitats and, to a lesser extent, in areas with risk of flooding. In agreement with Le Vaillant et al. (2018), associations between habitat characteristics and nest locations differed between phases of the lemming cycle.

Red foxes

In 1992, Hersteinsson and Macdonald put forth the hypothesis that throughout the circumpolar distribution of the arctic fox, its southern distribution limit should be determined by interspecific competition with the larger and physically dominant red fox. The red fox should consequently be able to exclude arctic foxes from resources, such as breeding dens and territories, and monopolize food resources such as ungulate carcasses. Hersteinsson and Macdonald (1992) also hypothesized that the northern distribution limit of the red fox should be determined by prey availability and ultimately by the harsh Arctic climate. Thus, a warming climate should favor the red fox, allowing it to expand to higher latitudes and altitudes. For the Fennoscandian mountain tundra, they specifically hypothesized that a warming climate should have allowed the red fox to start its expansion to higher altitudes in the late nineteenth century. Thus, in addition to overharvest, increased competition accompanied by intra-guild predation from red foxes should have been a contributing factor driving the arctic fox to decline in the early twentieth century (Selås and Vik 2006). Moreover, after the arctic fox was protected in 1928, red fox competition could be a sufficient reason why the population failed to recover (Hersteinsson and Macdonald 1992).

The hypotheses of Hersteinsson and Macdonald (1992) have inspired substantial research within The Swedish Arctic Fox Project. There is anecdotal evidence supporting red fox expansion in the late nineteenth and early twentieth century, as the red fox at the time was described as increasing in northern Sweden (Elmhagen et al. 2015). Early research in Vindelfjällen nature reserve confirmed that arctic and red foxes compete for similar resources (Elmhagen et al. 2000, 2002). Studies of fox diets showed that both species are opportunistic predators functioning as small-rodent specialists owing to the limited prey base in mountain tundra. Scat analyses showed significant between-year and between-den variation in the occurrence of different small-rodent species and alternative foods such as birds and reindeer carcasses (Elmhagen et al. 2000, 2002). Although arctic foxes generally consumed more lemmings, whilst red foxes consumed more voles and birds (Elmhagen et al. 2002), these differences were likely explained by a stronger association of red foxes with more productive habitats at lower altitudes

than by differences in fundamental food niche (Elmhagen et al. 2002, Stoessel et al. 2019). Based on long-term snow tracking data of foxes, wolverines, ptarmigan, and grouse, and records of lemmings from wildlife triangles, Wilkinson et al. (2024) showed that tundra red fox abundance was higher during years with high lemming abundance, suggesting that red foxes transitioned between habitats in response to food abundance. In winters before and after lemming peaks, red fox abundance was positively associated with ptarmigan abundance, which could indicate that red foxes monopolized habitats with a rich ptarmigan resource (Stoessel et al. 2019). In addition to prey, den sites constitute another resource over which competition occurs. Analyses of dens and den use in the mountain tundra showed that the arctic fox dens in this area were among the largest reported in the arctic, probably due to the lack of permafrost (Dalerum et al. 2002). Arctic foxes prefer to breed in dens with many openings, on average, 44, but ranging up to 140. Red foxes in the area had a similar preference for large arctic fox dens (Dalerum et al. 2002), but mostly do not use and maintain as many openings in these dens as arctic foxes do.

Early records of aggressive interactions between arctic and red foxes in Fennoscandia (Frafjord et al. 1989) highlighted the impact of interference competition. On the few occasions when arctic foxes did breed in the vicinity of red foxes, a high incidence of red fox predation on arctic fox cubs suggested that arctic foxes were more likely to breed successfully if they actively avoided establishment within red fox territories (Tannerfeldt et al. 2002). Although the predation rate is unknown, there are several records of red foxes killing both cubs and juveniles also in other populations (Frafjord et al. 1989, Pamperin et al. 2006).

Another step in the research program was to test if there was evidence for competitive exclusion of arctic foxes, and if so, how this might affect the arctic fox population (Tannerfeldt et al. 2002, Shirley et al. 2009). Spatio-temporal patterns in habitat use suggested that arctic and red foxes overlap in winter but less so in summer (Dalén et al. 2004*b*, Stoessel et al. 2019). Den use during summer showed that arctic foxes generally reared their litter in dens located outside the home ranges of known reproducing red foxes (i.e., avoiding overlap with red foxes during the breeding season). Simulations of arctic and red fox interactions in a spatially explicit population model confirmed that arctic fox avoidance of red fox territories during reproduction was sufficient to have a negative impact on arctic fox population trends (Shirley et al. 2009). Competitive exclusion could subsequently explain observed changes in arctic fox distribution over the last century. Although arctic fox dens were distributed throughout the mountain tundra, analyses of den use in the late 1900s showed that arctic fox reproduction had become restricted to high-altitude dens in the least productive parts of the species' former range, whilst red foxes occupied the more productive tundra in lower altitudes (Dalerum et al. 2002, Herfindal et al. 2010).

A review on interactions between arctic and red foxes in the circumpolar Arctic supported the hypothesis that red foxes are dominant over the arctic fox (Elmhagen et al. 2017). Red foxes can exclude arctic foxes from dens, habitat, and food resources, and they sometimes kill arctic foxes (e.g. Frafjord et al. 1989, Pamperin et al. 2006, but see Gallant et al. 2012). Where red foxes reach ecologically effective densities (e.g., in Fennoscandia), they can cause arctic fox decline and extirpation (e.g. Angerbjörn et al. 2013, Ims et al. 2017). However, in addition to climate change, red fox establishment and increase can also be driven by subsidies that can allow the red fox to establish north of its climate-imposed distribution limit (e.g. Killengreen et al. 2011), suggesting that synergies between subsidies and climate warming can speed up Arctic ecosystem change.

Golden eagles

Small rodents are important basal prey for the entire predator guild in the Fennoscandian tundra. Hence, intraguild predation pressure on fox cubs decreases when top predators such as golden eagles and wolverines rely on readily available lemmings. During lemming crashes, on the other hand, the pattern is reversed as generalist predators switch to alternative prey, including arctic fox cubs. Arctic foxes can be exposed to golden eagle predation (Tannerfeldt et al. 1994, Meijer et al. 2011), and the extent seems to be influenced by small-rodent abundance. Choi et al. (2019) recorded a high occurrence of golden eagle interactions with arctic foxes during one summer with an

early lemming crash, when both foxes and eagles were faced with food shortage. Juvenile arctic fox summer survival was remarkably low at the monitored dens, with only 51% of the cubs surviving until early August, and less than 10% in September. Further, no cubs from the monitored dens were observed as adults during the following years. Because starvation was excluded as a cause of mortality because of supplementary feeding, the low survival was attributed to a golden eagle prey switch following the lemming crash, but the juvenile survival was higher in dens where the parents showed a more bold behavior (Choi et al. 2019).

Apart from the small-rodent cycle, there are additional factors that can influence the vulnerability to golden eagle predation. Meijer et al. (2011) found that cubs with experienced parents (i.e., foxes that had raised a litter before) displayed higher summer survival compared to cubs with inexperienced parents and that there was a higher proportion of golden eagle attacks occurring on dens with inexperienced parents. Building on this, Erlandsson et al. (2017) suggested that differences in parental behavior between experienced and inexperienced parents influenced intra-guild predation and subsequent juvenile survival.

Life history and population dynamics

Arctic fox survival and reproduction across most of its geographic range are tightly linked to the cyclic population dynamics of small rodents, particularly lemmings. Using long-term data collected through The Swedish Arctic Fox Project, studies have examined temporal and spatial variation in vital rates, population development, and the impact of conservation measures.

Survival and reproduction

Common causes of arctic fox mortality are starvation and predation (Angerbjörn et al. 2004*a*). The importance of understanding the factors influencing juvenile survival was stressed in the 1990s, when Tannerfeldt et al. (1994) showed that juvenile summer survival was 79%, with starvation being the primary underlying mortality factor. Later studies have estimated juvenile summer survival between 51–96% (Meijer et al. 2011, Erlandsson et al. 2017, Larm et al. 2019). Many studies have highlighted the link between small-rodent prey and juvenile arctic fox survival in summer but have also revealed other external factors through indirect mechanisms. Arctic fox cubs are generally naïve regarding threats of predators and are much less vigilant than adults. Meijer et al. (2011) recorded average summer survival rates of 73%. For cubs with an inexperienced mother, survival was 42%, while cubs with an experienced mother displayed survival rates of 87% (Meijer et al. 2011). Erlandsson et al. (2017) explored whether litter attendance would have a positive effect on juvenile survival, and if first-time breeders were less efficient in protecting their juveniles. Based on a 7-year data set of litter attendance and juvenile summer survival, survival of cubs reared by first-time breeders decreased when small rodents were scarce. In contrast, juveniles reared by experienced females had a higher survival rate regardless of small-rodent abundance. In addition, survival rates were lower among litters that were left unattended for a longer time. Starvation was an unlikely explanation, as all litters were supplementarily fed and the trapped cubs were in good physical condition. Instead, the lower survival was attributed to a general increase in intra-guild predation due to prey switching primarily by eagles, which first-time breeding females were less able to cope with.

The most critical factor influencing the reproductive value of an individual (i.e., the expected reproductive contribution) is first-year survival, which can be even more challenging under cyclic prey conditions (Meijer et al. 2013). Tannerfeldt et al. (1994) documented first-year survival rates of 8.2% for arctic fox. In a later study, Meijer et al. (2008) used a combination of visual observation and genetic analysis of scats to assess survival rates after a small-rodent crash. Results were strikingly similar to Tannerfeldt et al. (1994) and showed that first-year survival was 8% (Meijer et al. 2008). A pronounced drop in survival was recorded during the first 6 months following

the rodent population crash with only 25% surviving (Meijer et al. 2008). During increasing small-rodent densities, however, first-year survival was considerably higher (32%). Estimates of adult survival range between 33–60% across studies (Tannerfeldt et al. 1994, Tannerfeldt and Angerbjörn 1998, Meijer et al. 2008). Tannerfeldt and Angerbjörn (1998) and Meijer et al. (2008) showed that adult survival was 59% during the year following a small-rodent crash, corresponding to the 50% second-year survival during a year of low small-rodent density estimated by Tannerfeldt et al. (1994).

Throughout most of the circumpolar range, arctic foxes act as opportunists in highly stochastic environments, showing extreme variation in reproductive output depending on prey abundance. The number of inhabited arctic fox dens and the number of litters born hence increase with lemming abundance (Elmhagen et al. 2000, 2011; Angerbjörn et al. 2013). Successful reproduction is largely restricted to lemming increase and peak years, and most breeding individuals are foxes born during previous peaks (Tannerfeldt and Angerbjörn 1996). This indicates a life-history strategy optimized for rapid reproduction during short windows of opportunity. Overall, population fluctuations appear to favor a risk-prone reproductive strategy, especially in high-quality animals (Tannerfeldt and Angerbjörn 1998). This includes arctic fox litter sizes of up to 18 cubs in Sweden during peak lemming years, which is among the highest recorded in Carnivora (Ewer 1973). In contrast, some arctic fox populations have more stable food resources, for example at bird cliffs and along coastlines. A comparison between arctic fox populations in fluctuating and stable environments showed that populations experiencing a more stable food supply between years tend to have significantly smaller average and maximum litter sizes, both at birth and at weaning (Angerbjörn et al. 2004*b*).

The link between small-rodent phase and reproduction was explored by Meijer et al. (2013). The study showed a higher weaning success (i.e., the proportion of established pairs in spring that produce a litter) during the peak phase of the small-rodent cycle compared to the increase and decrease phases. Meijer et al. (2013) found that litter sizes were similar in the increase (6.38 cubs) and peak (7.11 cubs) phases but significantly higher compared to the decrease phase (3.84 cubs). The study concluded a strong impact of food availability on arctic fox reproduction, and that females overproduce cubs during the increase phase. This suggests that arctic fox litter size is adjusted in relation to small-rodent phase and variation in offspring reproductive value (life history hypothesis), which is expected to be highest for cubs born at the increase phase (Meijer et al. 2013).

Breeding success and juvenile survival are subsequently the most important and variable factors in arctic fox population dynamics, and several studies have concluded that the small-rodent cycles are highly influential. Even though time series analysis has confirmed a 4-year cyclicity in both arctic fox numbers and litter size in Sweden, there are geographical asynchronies with regular cycles being more common in the south (Angerbjörn et al. 1995). A meta-analysis identified periods of irregular lemming dynamics, more common in northern areas (Angerbjörn et al. 2001), suggesting subsequent impact on the arctic fox population.

Although the signal of small rodents is strong both regarding production of litters and litter size, there are additional factors influencing reproduction. Norén et al. (2016) and Hasselgren et al. (2018) recorded a decline in reproduction following increased inbreeding levels. Furthermore, Wallén et al. (2024) showed that outbreaks of sarcoptic mange were associated with demographic consequences apparent as a plateau in the number of produced litters and a lowered litter size. The link between adult survival and sarcoptic mange was not established in this study.

Population development and conservation actions

During the initial phase of The Swedish Arctic Fox Project, the arctic fox population was very small with few reproductions. In the late 1990s, the population was on the verge of extinction, with only 40–60 adults remaining in Sweden, Norway, and Finland (Angerbjörn et al. 2013). To mitigate this negative trend, efficient conservation actions were necessary. Experiments assessing the effects of supplemental feeding on mortality and cub growth (Angerbjörn et al. 1991, Tannerfeldt et al. 1994), as well as early attempts to control red foxes in Vindelfjällen nature reserve were conducted in collaboration with the County Administrative Board during the 1990s

(Tannerfeldt et al. 2002). During the 2000s, supplemental feeding and red fox control were performed as part of the EU/LIFE projects SEFALO (Swedish Finnish Alopex) and SEFALO+ (Saving the Endangered Fennoscandian Alopex), including also Finland and Norway. In short, active dens were provided commercial dog food deposited in specifically designed feeding stations or meat (e.g., reindeer carcasses or traffic-killed ungulates; Angerbjörn et al. 2013). Control of red foxes was accomplished during the winter season within arctic fox territories. The action was conducted by local authorities in Finland and Sweden (from 2000) and in parts of Norway (from 2005; Angerbjörn et al. 2013). The intensity and combination of actions varied between high and low across populations, with 3 populations functioning as control areas without actions (Angerbjörn et al. 2013).

The increasing number of reproducing arctic foxes, indicative of population development, in Sweden and Norway in 2001–2010 showed that intense conservation actions could reverse the population decline. The 2 key actions both had significant positive effects and resulted in a fourfold increase in total population size (Angerbjörn et al. 2013). Moreover, reproduction, despite the supplementary feeding, was highly dependent on small-rodent abundance, further emphasizing the key role of regular small-rodent cycles. Adding to this finding, Meijer et al. (2013) concluded that females provided with supplemental food produced larger litters compared to unfed females but that the effect of the small-rodent cycle remained despite the additional food. Building on these experiences, supplemental feeding and red fox control were integrated into the Swedish and, subsequently, the trilateral Swedish-Norwegian-Finnish action plan to be implemented by authorities.

In addition to supplementary feeding and red fox control, a captive breeding program was established on the Norwegian side of the border. Based on founders mainly captured in Norwegian subpopulations, the program releases first-generation offspring to the wild with the goal of providing demographic and genetic support for isolated subpopulations (Landa et al. 2017). Since 2006, approximately 500 arctic foxes have been released to the wild and some of these foxes have established in Sweden and Finland through post-release dispersal (Hasselgren et al. 2018, Wallén et al. 2023). The aim of this paper is, however, not to provide an extensive overview of transnational conservation strategies and their effects. A detailed account of the Norwegian captive-breeding programme and its effects can instead be found in Norwegian studies (Landa et al. 2017, 2022).

Besides the small-rodent cycle and intensive conservation actions, research from The Swedish Arctic Fox Project has suggested that there are additional internal and external factors that can influence population dynamics and development, at least on the local scale. Examples of such factors are golden eagle predation (Meijer et al. 2011, Choi et al. 2019), human presence (Larm et al. 2019), sarcoptic mange outbreaks (Wallén et al. 2024), and inbreeding (Norén et al. 2016, Godoy et al. 2018). These factors are taken into consideration in the current transnational action plan, guiding conservation strategies in Sweden, Norway, and Finland (Naturvårdsverket and Miljødirektoratet 2025).

Behavioral ecology

The Swedish Arctic Fox Project has explored behavior from different perspectives, including red fox interactions (Frafjord et al. 1989), social behavior (Kullberg and Angerbjörn 1992), parental behavior (Erlandsson et al. 2017), and personality (Choi et al. 2019). In particular, themes connected to social group formation, dispersal, and relationship with tourism have been investigated.

Mating system and social organization

The arctic fox generally breeds in pairs, but occasionally related females breed in the same den and show alloparental behaviors (Norén et al. 2012, Elmhagen et al. 2014). For example, up to 3 breeding females with a total of 27 cubs have been observed in the same den in Vindelfjällen (Elmhagen et al. 2014). Other types of group

formations constitute a breeding pair with non-breeding adults (Norén et al. 2012, Elmhagen et al. 2014). The non-breeding adults are often offspring of the breeding pair, usually yearlings (Norén et al. 2012, Elmhagen et al. 2014). Sufficient food resources are a prerequisite for group formation, and the proportion of groups can increase during supplemental feeding (Norén et al. 2012, Elmhagen et al. 2014).

Arctic fox social organization was explored in depth using genetic parentage and relatedness analysis to assess relationships within social groups in Sweden, Canada, Iceland, and Svalbard, with the aim of understanding how contrasting resource and predation levels influence mating system and group composition (Norén et al. 2012, Elmhagen et al. 2014). Social and genetic monogamy were the dominant strategies for all populations, and the occurrence of extra-pair paternity was low. Norén et al. (2012, 2017) introduced Hersteinsson's model, suggesting that group size was determined by a trade-off between the costs of increased resource consumption and the benefits of increased predator defense. Building on this, Erlandsson et al. (2022) explored the resource dispersion hypothesis and Hersteinsson's model using a 17-year data set. The resource dispersion hypothesis highlights that prey abundance is not evenly distributed (Macdonald 1983). Further, it stipulates that territorial individuals should configure their territory to encompass enough prey to provide sufficient food for the smallest group size (typically a pair) when prey is scarce. Following this rationale, a resident pair can tolerate joining adults at no cost whenever prey is more abundant than the minimum. For arctic foxes, this means that group size is expected to increase during lemming increase and peak years, while being limited to a single pair during lemming crash and low years. An important point of the resource dispersion hypothesis is that there is no need for cooperation or other beneficial aspects of group living to explain social groups, as long as prey availability is sufficient to eliminate the cost of increased group size. In contrast, Hersteinsson's model takes into account the potential benefits of group living. For arctic foxes, experiencing increased intraguild predation during a lemming crash, Hersteinsson's model predicts that a resident pair should accept joiners, despite limited food availability, as additional adults can increase vigilance against predators. Results showed that the group size increased during peak years but stayed disproportionately communal during crash years, lending support for Hersteinsson's model (Erlandsson et al. 2022).

Dispersal and habitat use

Early studies on natal dispersal based on a limited data set of ear-tagged juveniles documented that 50% of the dispersal events were shorter than 10 km and establishment in neighboring territories was common (Angerbjörn et al. 2004*a*). However, longer natal dispersal distances covered 80–220 km (Angerbjörn et al. 2004*a*). An analysis of Swedish and Icelandic data showed that natal dispersal typically occurs during the first or second year in life, with no apparent sex-specific differences (Angerbjörn et al. 2004*b*). Furthermore, an arctic fox territory is suggested to be 15–36 km^2 in inland Fennoscandia (Angerbjörn et al. 1997).

Arctic fox dispersal patterns have been explored with a more extensive data set consisting of genetic and demographic reobservations of Swedish and Norwegian arctic foxes of wild-born and captive-released ancestry between 2007–2023 (Bommerlund 2025). Results from this analysis showed that emigration to another habitat patch occurred in 12% of the foxes with both internal and external factors (e.g., wild vs captive origin, population size in the local patch, and distance to a patch with reproducing foxes) influencing dispersal patterns.

Given the natural fragmentation of the Fennoscandian mountain tundra (Elmhagen and Angerbjörn 2001, Moen et al. 2004), isolation of small subpopulations and ongoing expansion of the treeline, detailed understanding of dispersal behavior and connectivity is central for future conservation efforts. Moreover, dispersal is of relevance for pathogen transmission. Even though sarcoptic mange can occur throughout arctic fox distribution, it has so far only been recorded in Borgafjällen (Figure 1). Wallén et al. (2024) found that transmission of sarcoptic mange within that subpopulation could be driven by a limited number of foxes moving between multiple dens (i.e., super-spreaders). During a sarcoptic mange outbreak in one of the subpopulations, one arctic fox with visible signs of sarcoptic mange was recorded to visit 6 different den sites (Wallén et al. 2024).

Tourism

Global interest in nature-based tourism is increasing, and over the past decade, the arctic fox has emerged as a popular attraction for tourists. Larm (2024) explored the interactions between arctic foxes and tourists from both natural and social perspectives. The research was conducted in Helagsfjällen (Figure 1), an accessible and popular area for recreational activities. Some arctic fox dens in the area are located close to trails and mountain cabins, and the foxes inhabiting those dens experience a relatively high level of human disturbance compared to dens located farther away. By comparing how foxes at disturbed and undisturbed dens acted when a human approached, they found that arctic foxes at disturbed dens, who are more used to human activity, tolerated closer approaches before increasing their vigilance and before they hid or fled (Larm et al. 2020). The study provided a scientific basis for the recommended minimum approach distance of 300 m and confirmed that it is sufficient for most foxes not to flee or hide. However, there was individual variation, and many foxes became vigilant at distances >300 m. At both disturbed and undisturbed dens, the probability of hiding increased rapidly when approached within approximately 200 m.

One den in Helagsfjällen is regularly visited by guided arctic fox safari tours during the summer and was selected as a focus for behavioral studies. At that den, both juvenile and adult foxes increased their presence at the den when the level of noise and movement from the tour group increased during safari tours. The adult foxes also guarded the juveniles more; they were active during a larger portion of the time when there were juveniles at the den during a tour compared to the same time on days with no tour (Larm et al. 2021*a*). When compared to 2 undisturbed dens, foxes inhabiting the den visited by guided tours were more active during the day and less active during the night, while the foxes at the undisturbed dens both had activity peaks at dawn and dusk and lower activity during daytime. Daytime is also when the disturbance from tourism is highest. Combined, these findings suggest that the arctic foxes do not perceive humans as a threat when the recommended minimum approach distance is respected, but they are likely less comfortable leaving the den site and the juveniles when humans are present. Physiological changes, such as changes in stress hormone levels, can also be used to investigate responses of an animal to a disturbance. A successful validation of fecal glucocorticoid metabolites as an indicator of physiological stress in arctic foxes was conducted in close cooperation with the Norwegian Institute of Nature Research (Larm et al. 2021*b*). The validation was a first step towards physiological studies in arctic foxes that can complement the results from behavioral studies.

To investigate fitness consequences of disturbance from human activities on arctic foxes, juvenile summer survival was compared between dens disturbed by tourism and those undisturbed. Surprisingly, they found that survival was higher at disturbed dens than at undisturbed dens, but the effect was only found during years of declining small-rodent densities (Larm et al. 2019). During the decline phase, predation on arctic foxes is at its highest, as eagles and red foxes switch to alternative prey when small rodents become scarce (Elmhagen et al. 2000). The probable mechanism behind the increased survival at disturbed dens could be a human-induced predator refuge for the foxes near human activity.

Conservation genetics

In 2000, The Swedish Arctic Fox Project included genetic analyses as a tool to better understand the biology of the arctic fox. By integrating historical, modern, and non-invasive genetic data, this work facilitated studies on population history, gene flow, connectivity, inbreeding, genetic rescue, and introgression, providing important empirical data both for practical conservation and for the broader field.

Population history

An initial step was a broad-scale assessment of genetic diversity across the species' circumpolar range. Contrary to the genetic signatures of post-glacial expansion commonly found in temperate species, the results showed that the

arctic fox experienced a demographic expansion at the onset of the last glacial period (Dalén et al. 2005). This suggests that glacial cycles have had an inverse effect on arctic versus temperate taxa, where, for example, arctic foxes expanded during cold periods and contracted during warmer interglacials. Furthermore, genetic analyses revealed widespread and closely related mitochondrial haplotypes with minimal phylogeographic structure, suggesting extensive Holocene gene flow across much of the species' range, particularly among populations reliant on lemmings as a food source. The observed lack of strong genetic structuring is also consistent with the species' capacity for long-distance dispersal over sea ice. Iceland appeared as a genetic outlier, likely due to its isolation from other populations by year-round open ocean rather than sea ice.

The origin of the Fennoscandian arctic fox and the response to climate change have been addressed through ancient DNA analysis. During the glacial maximum, the arctic fox had a large distribution extending to central Europe while Fennoscandia was covered by ice. Analyses of samples from the Late Pleistocene collected in central Europe showed low overlap with the modern Fennoscandian population (Dalén et al. 2007). High genetic similarity with Russia, however, suggests that Fennoscandia was re-colonized from the east rather than the south at the end of the last ice age (Dalén et al. 2007), which in turn implies that arctic foxes in central Europe did not track the changing habitat northwards. This study suggests limited capacity for movement in response to climate change and constitutes an important example highlighting the value of ancient DNA analysis to make predictions for future climate change. A later study using complete mitochondrial genomes supports the lack of overlap with present Fennoscandia, suggesting that genetic material has likely been lost through local extinctions (Dalén et al. 2007, Larsson et al. 2019). Neither of the studies found support for a recolonization from Russia during the Pleistocene, highlighting the possibility of an unsampled source population, or more recent gene flow from Russia.

Genetic structure

Building on the conclusions from Dalén et al. (2005), large-scale patterns of divergence and gene flow across the circumpolar distribution were explored through microsatellite variation (Norén et al. 2011*a*). Overall, there was a low level of genetic divergence between most regions. Presence of sea ice enabling long-distance dispersal and gene flow was identified as the primary determinant of genetic structure. The role of sea ice was further supported in a follow-up study, where pulses of long-distance movement over the sea ice triggered by crashes in the small-rodent cycle influenced the temporal genetic structure (Norén et al. 2011*b*). Regions surrounded by year-round open water displayed higher levels of genetic distinctiveness (Norén et al. 2011*a*), and Fennoscandia distinguished itself as one of the divergent populations. Even though the lack of sea ice is likely a contributing factor, the genetic consequences following the demographic bottleneck (Nyström et al. 2006) were emphasized as yet another driver (Norén et al. 2011*a*).

Within Fennoscandia, microsatellite analysis documented a pattern of recent changes in genetic diversity and structure. Following a dramatic population decline in the early twentieth century due to overharvesting, the Fennoscandian arctic fox experienced a severe demographic bottleneck. Analyses of museum specimens collected prior to this bottleneck revealed that although genetic variation was lost, the decline in heterozygosity was less severe than expected (Nyström et al. 2006). Simulations indicated that the genetic diversity observed today could not be fully explained by survival alone, suggesting post-bottleneck gene flow from adjacent populations in northwest Russia (Nyström et al. 2006). The loss of genetic variation following the bottleneck was supported by more recent studies using modern genomic tools (Larsson et al. 2019, von Seth et al. 2025). Based on whole-genome sequence data, Cockerill et al. (2022) compared contemporary subpopulations in northern Sweden and Norway to Russia and demonstrated higher levels of recent inbreeding along with higher levels of deleterious mutations in the homozygous state in Sweden and Norway, suggesting ongoing genomic erosion. In addition, a clear separation from Russia was demonstrated, highlighting low connectivity between modern-day populations.

Further analyses using microsatellite markers demonstrated that the Fennoscandian population remains highly fragmented (Dalén et al. 2006). Analyses revealed 4 genetically distinct subpopulations within Scandinavia (Sweden

and Norway), with the Kola Peninsula and other areas in Russia forming a fifth subpopulation. The 4 Scandinavian subpopulations corresponding to southwest, south-central, central, and northern regions were isolated from each other by forested areas that likely impede dispersal. Low levels of current gene flow among these subpopulations were of conservation concern, especially considering evidence of ongoing genetic drift and inbreeding. From a conservation perspective, the identification of 4 isolated subpopulations within Scandinavia suggested that the extinction risk was higher than previously estimated. As gene flow was insufficient to naturally counteract the effects of genetic drift and inbreeding, the work resulted in a recommendation of targeted conservation strategies for each population. It was also suggested that in addition to continued supplementary feeding and red fox control, management authorities should consider genetic restoration via translocations within Scandinavia, or from the genetically similar Russian population. Translocations have so far not been implemented within Sweden.

These questions were revisited almost 20 years later, when Bommerlund (2025) conducted a temporal analysis of single nucleotide polymorphism (SNP) data covering Sweden, Norway, and Finland between 2007–2023. Even though the sub-division into 4 genetic clusters remained (Dalén et al. 2006), the analysis by Bommerlund (2025) demonstrated increasing levels of gene flow and connectivity, reflecting a strong impact of releases from a captive breeding station in Norway (Landa et al. 2017).

Inbreeding and genetic rescue

Early genetic studies identified signs of inbreeding depression within some of the subpopulations in Sweden, with reduced individual microsatellite heterozygosity being associated with lower survival and reproduction. This finding supported the general hypothesis of associative overdominance, where reduced fitness results from genome-wide inbreeding rather than local effects of linked loci (Dalén 2005). Further, Geffen et al. (2011) documented high levels of kin encounter rates in Swedish subpopulations, supporting ongoing inbreeding.

Later on, the subpopulation in Helagsfjällen (Figure 1) became the focus of intensive studies to understand inbreeding and genetic rescue in detail. The subpopulation became functionally extinct in the 1980s but naturally re-established in 2001. Long-term individual and genetic monitoring enabled the construction of a near-complete microsatellite pedigree (Norén et al. 2016), revealing that the population was founded by just 7 individuals. In response to supplementary feeding, red fox control, and more regular prey conditions, the population increased rapidly. Inbreeding levels increased at the same time and within 9 years reached levels equivalent to half-sibling matings (Norén et al. 2016). Although foxes avoided mating with full siblings from the same litter, they did not appear to discriminate against other types of relatives (Godoy et al. 2018). The population exhibited phase-dependent inbreeding depression. In years of low rodent abundance, inbred individuals had lower juvenile survival, whereas in resource-rich years, inbred individuals were less likely to reproduce (Norén et al. 2016). These findings highlighted the urgent need for gene flow to restore genetic variation and population fitness.

In 2010 and 2011, gene flow occurred via 3 male foxes that immigrated to Helagsfjällen (Hasselgren et al. 2018). These individuals had been released as a conservation action into a Norwegian subpopulation by the Norwegian (https://www.nina.no/en/our-research/all-projects/arctic-fox-captive-breeding-programme) Arctic Fox Captive Breeding Programme and were first-generation offspring of arctic foxes captured in wild Norwegian subpopulations. Through post-release dispersal, these foxes moved approximately 120 km to Helagsfjällen. Two of the immigrants were brothers, and all 3 had mixed ancestry from multiple Norwegian subpopulations. Following their arrival, inbreeding levels dropped to levels equivalent to cousin matings, and population size increased. First-generation offspring of the immigrants had nearly double juvenile survival probability and 1.3 times higher breeding success compared to inbred native individuals (Hasselgren et al. 2018). This provided clear evidence of genetic rescue, demonstrating that even a few migrants can significantly improve fitness in an inbred population. However, no further gene flow was detected in subsequent years, raising concerns about the long-term sustainability of the rescue effect.

Later studies confirmed that the genetic rescue effect was short-lived. By the second generation, immigrant descendants no longer exhibited elevated fitness (Lotsander et al. 2021, Hasselgren et al. 2024). Inbreeding levels began to rise again, including within immigrant lineages (Lotsander et al. 2021). Whole-genome analyses revealed long runs of homozygosity in second- and third-generation immigrant descendants, indicative of inbreeding due to recent ancestors (Hasselgren et al. 2021). These findings underscore the transient nature of genetic rescue and the need for continuous or repeated gene flow to maintain fitness.

Further genomic analyses identified a higher proportion of putatively harmful loss-of-function mutations in immigrant descendants compared to native individuals. A greater burden of homozygous deleterious mutations was associated with reduced lifetime reproductive success and longevity, offering one of the first direct links between deleterious mutations and fitness in a wild population (Hasselgren et al. 2024). Sequencing the genomes of the immigrant individuals revealed low genome-wide inbreeding but high levels of harmful mutations. The immigrants likely introduced novel harmful mutations into Helagsfjällen (Hasselgren 2022). The mixed ancestry of the immigrants resulted in an accumulation of harmful mutations in their genomes, which were masked in the F1 generation but became increasingly expressed in later generations. A comparison was made with the less isolated subpopulation in Vindelfjällen–Arjeplogsfjällen (Figure 1), where another gene flow event was recorded. This subpopulation received gene flow from 4 captive-bred foxes released by the Norwegian Arctic Fox Captive Breeding Programme between 2011–2016 (Wallén et al. 2023), and the descendants of immigrants in this area did not carry an elevated burden of highly deleterious mutations (Hasselgren 2022). It also seemed like fewer novel harmful mutations were introduced, suggesting that population structure plays a critical role in the outcome of gene flow.

These studies showed that the consequences of gene flow depend on demographic history of both source and recipient populations, the number of migrants, and environmental conditions, among other considerations. Gene flow from unrelated individuals has the potential to result in long-term genetic rescue, but it has also been suggested that immigrants from large, outbred populations entering very small and inbred ones may introduce substantial deleterious variation. For highly isolated populations, such as the Helagsfjällen population, immigration from neighboring, genetically similar populations may thus be more beneficial than translocations from admixed or distantly related sources. Incorporating risk assessments of harmful variation in both source and recipient populations will subsequently be increasingly important when planning translocations. Ultimately, the establishment of regular gene flow and a functioning meta-population structure will be essential to preserve genetic diversity and long-term viability in the Fennoscandian arctic fox.

Farm fox introgression

In parallel to inbreeding depression and loss of genetic variation, introgression of genetic material from semi-domesticated foxes, used for fur farming, has been highlighted as another prevailing threat based on anecdotal observations. Norén et al. (2005) identified strong genetic divergence between farmed and wild arctic foxes and also identified a fixed mitochondrial haplotype (H9) in all farmed foxes. This paved the way for using genetic analysis as a screening tool to identify escaped or released farmed foxes and introgression in wild Swedish and Norwegian subpopulations. Through this approach, the farm-fox-specific haplotype was identified in 13.7% of all samples of which the majority of the samples were located in a specific subpopulation in southwestern Norway (Norén et al. 2009). To exclude a potential historical sub-structure, genetic analyses of historical samples (1897–1975) collected from this subpopulation suggested that introgression had occurred relatively recently.

Norén et al. (2009) recommended removal (trapping or lethal control) of farmed foxes and hybrids in the wild, and Norwegian management authorities removed the remaining population of farmed foxes and hybrids in 2009 (Norén et al. 2017). Norwegian researchers backtracked the introgression and concluded that deliberate releases of farmed foxes had occurred over an extended time period to attract tourists (Norén et al. 2017). Following the releases, the gene pool had been completely swamped, and the last record of a native arctic fox was from 2000.

According to historical records, it has been described that farmed arctic foxes have ancestry mainly from coastal areas where ecological conditions are highly divergent compared to Fennoscandia. Furthermore, they have been bred in captivity for about 100 years, increasing the genetic divergence through artificial selection and genetic drift. A recent study by Cockerill et al. (2025) used whole-genome sequences to confirm that the farmed population displayed a coastal origin, with the closest phylogenetic relationship to the Icelandic population. The study also identified signatures of the domestication process, apparent as elevated levels of inbreeding and lowered levels of genetic variation.

Genetic tools

An innovative aspect of early genetic work was the development and application of a DNA-based method for identifying arctic fox fecal samples, enabling these to be separated from those of sympatric red foxes and wolverines (Dalén et al. 2004*a*). This technique enabled non-invasive sampling, thus enhancing the ability to monitor the distribution and genetic status of the population without disturbing the animals, and became an important tool in later genetic studies (Meijer et al. 2008, Wilkinson et al. 2023). The species identification method was also used to examine seasonal patterns in habitat use, revealing that arctic foxes seem to shift their spatial distribution to higher elevations and farther away from the tree line during summer (Dalén et al. 2004*a*). This pattern is likely a response to increased predation risk and competition from red foxes during the breeding season.

Genetic analyses of fecal samples have also been informative for other purposes. Meijer et al. (2008) used microsatellite genotyping of fecal samples to estimate population size in the Helagsfjällen subpopulation through different estimators. Further, by combining visual observations of ear-tagged foxes with known genetic profiles and individual recaptures from fecal samples, they estimated juvenile and adult survival during a year of low prey abundance. Another example is a restriction-enzyme-based method developed to screen for the farm-fox-specific haplotype (H9; Norén et al. 2005). The tools developed by Dalén et al. (2004*b*), Norén et al. (2005), and Meijer et al. (2008) have been integrated in practical conservation for non-invasive monitoring of arctic and red foxes, estimates of local population size, and identification of escaped farm foxes.

The project has also used genetic analyses of fecal samples to investigate predator-prey relationships. In a study by Wilkinson et al. (2023), fecal samples were collected from fox dens over 2 consecutive summers. First, the approach by Dalén et al. (2004*b*) was used to determine whether the sample was deposited by a red or arctic fox. Secondly, short, standardized DNA fragments corresponding to small rodents, birds, and hare were amplified to assess the consumption of prey. In agreement with previous studies (Elmhagen et al. 2000, 2002; Wilkinson et al. 2023), small rodents were confirmed as the most common prey.

DISCUSSION

The aim of this review was to summarize the scientific contributions from a long-term study of the Swedish arctic fox, highlighting the role of long-term data to assess processes on both population and individual levels (Clutton-Brock and Pemberton 2004, Pemberton et al. 2023). Even though The Swedish Arctic Fox Project has been centered around a specific species, it has made important contributions to several fields, demonstrating the role of the arctic fox as an informative model system in ecology. Key contributions with relevance also for the broader scientific community include detailed assessments of predator-prey dynamics (Angerbjörn et al. 1999; Elmhagen et al. 2000, 2011), life-history strategies under fluctuating conditions (Tannerfeldt and Angerbjörn 1998, Angerbjörn et al. 2004*b*, Meijer et al. 2013), and the impact of boreal expansion in shaping species interactions (Tannerfeldt et al. 2002, Elmhagen et al. 2017). Further, genetic studies have made contributions to the general understanding of population responses to climate change (Dalén et al. 2005, 2007; Larsson et al. 2019), and to the field of conservation genomics by illustrating the relationship between inbreeding, genetic rescue, and introduction

of mutational load (Norén et al. 2016; Hasselgren et al. 2021, 2024). Even though, Sweden has been the main focus, strong collaborations with colleagues in Norway and Finland have played a central role in this research.

Several challenges have been tackled over the years and both creativity and persistence to continue have been instrumental. Personnel turnover challenges temporal consistency, specifically in keeping a competent and experienced volunteer team of fieldworkers and maintaining relationships with actors (i.e., academia, authorities, and non-governmental organizations) on a national and transnational level. However, funding insecurities have been the key challenge, especially in a context of changing priorities for natural resource management and national and international strategies for research funding. Despite this, contributions from multiple sources (e.g., research councils, non-governmental organizations, private donations, and the European Union) have facilitated 40 years of research spanning numerous scientific fields.

The Swedish Arctic Fox Project has served as a nurturing ground for the development of future generations of scientists and managers. Over the years, 12 doctoral students (Table S1), >70 master's and bachelor's students (Table S2), and >700 volunteer field workers have been associated with the project. Thanks to the knowledge generated by consistent research efforts by sequential generations of doctoral and master's students, data collection by fieldworkers and volunteers combined with long-term population monitoring and strong stakeholder involvement from authorities on local, national, and international scales, local communities, and Indigenous Peoples, the Fennoscandian arctic fox population, once on the verge of local extinction, is showing clear signs of recovery. While challenges remain, particularly in the face of climate-driven change altering tundra community dynamics and how threat processes impact the population, the scientific foundation for conservation is now considerably stronger with a very fruitful collaboration with Norwegian and Finnish scientists and authorities (Wallén et al. 2025).

The research conducted over the past 4 decades has not only made important contributions to science in general and arctic fox conservation in particular but has also inspired new perspectives for future studies. With the long-term data set as a basis, new tools provide promising opportunities to explore new questions. Habitat fragmentation and isolation constitute key threats to the long-term persistence of the Fennoscandian population, highlighting the need for in-depth studies of arctic fox dispersal. Ongoing collection of GPS telemetry data will provide detailed assessments of connectivity, identifying drivers of dispersal and subpopulations at high risk of extirpation. Furthermore, Norén et al. (2023) highlighted community processes in response to climate change and individual-level studies to investigate the link between behavior, genetics, and life history as important fields to explore, as well as assessing the role of individual factors in a larger community context. In particular, species interactions in the broader tundra community, the heritability and trans-generational effects of life-history variation, and the role of life-history traits and behavior in shaping population dynamics are intriguing aspects for future research. In addition, as an informative model system for conservation genetic processes, future studies should focus on the role of structural variants (larger mutations) for individual fitness, the genetic background underlying adaptation to tundra conditions, and the genomic consequences of fluctuating selection in response to prey cycles.

CONSERVATION IMPLICATIONS

The work of The Swedish Arctic Fox Project, balancing both research and practical conservation, exemplifies a broader shift from foundational ecology to applied conservation and science-policy integration. With consideration of the geographic distribution of the Fennoscandian arctic fox (Figure 1), both research and conservation strategies have often been performed with a transnational approach within a strong network of research institutes, authorities, and non-governmental organizations in Sweden, Norway, and Finland. These collaborations have been essential to frame the arctic fox not only as a species of conservation concern but as a symbol of ecological change in the subarctic ecosystem. By combining long-term ecological studies with experimental interventions and conservation policy, the project has contributed to a progressive change in how researchers approach endangered species in fluctuating environments, highlighting the importance of integrating basic ecological understanding and species-specific biology with practical management to reverse population declines.

A strong connection between research and management is sustained through continuous dialogue with authorities and active involvement in the development of action plans. This is exemplified by evaluations of supplementary feeding, red fox control, and releases from the captive breeding project (Angerbjörn et al. 2013; Wallén et al. 2023; Hasselgren et al. 2018, 2024), contributions to ongoing discussions about translocation strategies (Norén and Hasselgren 2024), and advancements toward a multi-faceted understanding of arctic fox biology in a conservation context. Research has also provided scientifically informed guidelines for authorities to minimize human disturbance (Larm et al. 2020). Moreover, by maintaining an active network between research and authorities, results can be integrated into practical conservation and used to refine ongoing actions. From a conservation perspective, the goal is to develop scientifically informed strategies that promote a stable and connected arctic fox population, without the need for continued conservation actions in the future. A way towards this goal is to establish adaptive management strategies where conservation actions are adapted in relation to the small-rodent cycle.

The arctic fox is classified as a climate change flagship species (Sillero-Zubiri and Angerbjörn 2009). Climate-related threats became evident in the Fennoscandian population at an early stage through red fox expansion, irregular small-rodent cycles, and habitat fragmentation, but similar challenges are likely to occur with time in other parts of its range, and in other species. The scientific foundation generated by The Swedish Arctic Fox Project is therefore expected to bring important implications for both research and management in other ecological systems.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

Swedish environmental law prohibits any activities that disturb protected species. Therefore, it is illegal to disturb and approach arctic foxes at den sites or in other situations. An exception can be made for research focused on improving the conservation status. All fieldwork and handling of animals is carried out under activity allowance (present version: 5.2.18-11440/19) and ethical permit (present version: A16-2022) from the Swedish Board of Agriculture. Specific approval for trapping and ear-tagging arctic foxes, despite being an endangered species, is given by the Swedish Environmental Protection Agency (present version: NV-25-003239). Specific permits and allowances were obtained from County Administrative Boards in Jämtland, Västerbotten, and Norrbotten considering work in nature reserves and county-specific regulations. Personnel are educated theoretically and practically following The Swedish Board of Agriculture's Regulations and General Advice on Laboratory Animals SJVFS 2019:9.

DATA AVAILABILITY STATEMENT

Data sharing not applicable to this article, as no datasets were generated or analyzed during the current study.

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