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RESEARCH

Effects of habitat characteristics and spatiotemporal variation in prey on reproductive success in the Arctic fox (*Vulpes lagopus*)

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Abstract

Habitat characteristics such as resource availability and interspecific competition may have profound consequences for the reproductive success of territorial animals. As anthropogenic activities shift species distributions, resident specialist species may experience increased interspecific conflict with expanding generalist species. While this has been hypothesised to lead to reduced reproductive success for resident specialists in areas rich in common resources, few empirical examples of such scenarios have been demonstrated. We investigate the effects of habitat on reproductive success in the Fennoscandian Arctic fox (*Vulpes lagopus*), a tundra specialist that faces increased competition and intraguild predation from the expanding red fox (*Vulpes vulpes*). By pairing geospatial information with long-term Arctic fox den surveys from two Swedish populations and trapping indices of the Norwegian lemming (*Lemmus lemmus*), a common prey of the two fox species, we model spatiotemporal patterns of Arctic fox reproductive success. We find reduced Arctic fox reproductive success in dens located close to the boreal forest at all levels of prey availability in both populations, suggesting reduced reproductive success in the vicinity of red fox territories. Arctic fox reproductive success was higher in dens located in lemming-rich areas during the peak phase of the rodent cycle in one of the studied populations, but not in the low and increase phases. We propose that high-quality habitats may have a proportionally greater effect on Fennoscandian Arctic fox reproductive success at high prey availability, because interspecific conflict can be expected to be lower when common resources are more abundant. Under climate change-induced habitat loss and increased presence of boreal species in mountain tundra, managed refugia may be crucial for the conservation of species inhabiting the fringes of available habitat.

Keywords Range shift · Lemming cycle · Habitat quality · Interference competition · Optimal foraging

Introduction

Habitat quality is a central factor affecting the reproductive success of a breeding individual (Norris et al. 2004; Griffen and Norelli 2015; Acker et al. 2022). Therefore, the general assumption in spatial ecology is that animals occupy habitats that provide maximum fitness mediated by resource availability and predator avoidance (Fretwell 1969; Fretwell and Lucas 1969), thereby maximising rates of survival, growth, and reproduction (Brown 1969; Johnson 2007). However, in most ecosystems, productive habitats are also associated with costs since high resource abundance attracts competitors and potential predators (Schoener 1971; Nonacs and Dill 1990; Brown et al. 1999). Therefore, animals often face a trade-off between efficient energy intake and protection against predation (Dill 1987; Brown et al. 1999; Kozlowski et al. 2011). Apart from direct predation, predator and competitor presence can induce a stress response that can considerably reduce reproductive output (Peckarsky et al. 1993; Creel et al. 2007, 2009).

Habitat cost-benefit trade-offs are therefore particularly important for breeding animals since occupying poor-quality habitats may lead to low or even complete reproductive failure (Strasser and Heath 2013). Like the predictions of optimal foraging theory, breeding can still be successful in high-predation environments if it increases feeding rates in

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such a way that benefits outweigh predation risk or negative effects of e.g. stress responses (Gilliam and Fraser 1987; Brown 1999). Similarly, if food abundance and predation risk vary over time, a particular habitat can be more beneficial for reproduction during periods of high resource abundance and limited predation risk (Norén et al. 2012).

As human activities and climate change cause species distributions to shift (Guo et al. 2018), animals may face new patterns of competition and food abundance, which in turn may alter the implications of different habitats (Bøhn et al. 2008). The effects of climate change are most pronounced in Arctic and sub-Arctic areas, where warming is occurring at a rate faster than anywhere else on Earth (IPCC 2023). Resident species are particularly exposed to increased competition from expanding boreal-forest species when tundra-like habitats contract while boreal-forest habitats expand (Elmhagen et al. 2015; van Beest et al. 2021). In conjunction with food subsidies associated with human activity, spill-over into tundra habitat by expanding boreal-forest species may increase (Elmhagen et al. 2015). As a result, high-quality feeding habitats for resident Arctic predators can be expected to attract larger boreal-forest predators with typically higher energy demand, resulting in an increasing intraguild predation risk (Fuglei and Ims 2008; Elmhagen et al. 2015, 2017; but see Lai et al. 2022). For many species, range shifts may alleviate the negative effects of climate change and anthropogenic land use (Guo et al. 2018), but for species living at the tail-end of terrestrial habitats, such as Arctic or alpine environments, further expansion might not be possible, leaving no option but to seek refuge locally. Climate-tracking species and local species often have a shared evolutionary history and may have overlapped in the past (Urban 2020). Thus, climate trackers or trackers of anthropogenic land-use change might be able to coexist with tundra-natives in environments with high food abundance even in the long term, especially if productive refugia can effectively prevent competitive exclusion (Urban 2020; Bonnet-Lebrun et al. 2022). Conversely, populations displaced to low-productive habitats may go extinct if food resources are too scarce (Linnell and Strand 2000).

In the last century, the treeline has advanced uphill by an average of 70–90 m in Fennoscandian tundra (Fuglei and Ims 2008; Kullman and Öberg 2009; Callaghan et al. 2013), which may ultimately result in a total reduction of mountain tundra by 75–85% by the end of this century (Moen et al. 2004). Thus, the available habitat for tundra specialists is decreasing due to tree and shrub encroachment, while the available habitat for boreal-forest species is increasing. Under such circumstances, the balance between resource abundance and conflict with expanding species may eventually reach a threshold at which resident species consistently experience strong negative effects on reproductive output, even in habitats with high food abundance. However, although general northward range shifts have been documented in several taxa (Perry et al. 2005; Hickling et al. 2006; Hitch and Leberg 2007; Chen et al. 2011; Kwon et al. 2014; Elmhagen et al. 2015), there are relatively few examples of increased contact between climate-tracking and native species causing major negative fitness consequences for the native species (Alexander 2015). This could possibly be explained by adaptations to sympatry acquired during the historical overlap of species occupying adjacent ranges (Urban 2020).

Arctic species are generally expected to fare less well at their southern distribution limits (MacArthur 1972). The Fennoscandian population of the Arctic fox (*Vulpes lagopus*) experiences interference competition and intraguild predation from the dominant red fox (*Vulpes vulpes*), a boreal-forest species which has expanded its range in Arctic and sub-Arctic areas due to anthropogenic habitat change and increased food subsidies from human activities (Elmhagen and Rushton 2007; Killengreen et al. 2011; Stickney et al. 2014; Gallant et al. 2020 Rød-Eriksen et al. 2020). In Europe, winter harshness limits red fox abundance (Hersteinsson and MacDonald 1992; Selås and Vik 2006; Bartoń and Zalewski 2007; Pasanen-Mortensen et al. 2013) and a warming climate is expected to mediate further expansion of red foxes as boreal forest replaces tundra, thus further intensifying conflict (interference competition and intraguild predation) with Arctic foxes (Hersteinsson and MacDonald 1992; Elmhagen et al. 2015, 2017).

In Sweden, red foxes inhabiting the border between tundra and boreal forest breed at or below the treeline (Dalén et al. 2004), and the red fox has been recorded taking over previous Arctic fox dens at lower elevations across Fennoscandia (Elmhagen et al. 2002; Frafjord 2003), forcing the Arctic fox to retreat further from the treeline to less productive habitat at higher elevations (Elmhagen et al. 2002; Tannerfeldt et al. 2002; Frafjord 2003; Herfindal et al. 2010). While there may be additional negative effects of living close to the tundra/boreal border, the red fox is the only potential competitor/predator that is strongly associated with the treeline in this system, as other large predators such as golden eagles (*Aquila chrysaetos*) and wolverines (*Gulo gulo*) are breeding both in mountain tundra and boreal forests (Persson 2010; Tjernberg 1981).

Although the red fox is widely regarded as the main antagonist for the Arctic fox, it is presently not known if exclusion by interspecific conflict only occurs in productive areas near the treeline or if negative consequences of red fox presence affect Arctic foxes at high-quality territories at higher altitudes as well. Moreover, the effects of habitat quality on Arctic fox reproductive success under fluctuations in shared food sources have not been fully examined.

By investigating the reproductive success at Arctic fox dens under variable prey availability and at different distances to the treeline, we can gain insights into habitat effects on reproductive success in tundra-native species under threat from expanding boreal species. Moreover, differences in reproductive output among Arctic fox dens located in different habitats may reveal the current ecological status of Arctic biomes in a changing climate and inform Arctic fox conservation programmes.

Studies of the effect of habitat characteristics on reproduction among central-place foragers, such as Arctic foxes, can provide fundamental insights into how the landscape use of a species affects reproduction. Central-place foragers are limited to searching for food in the vicinity of their den site since they must carry food back to their young (Zapata et al. 1998). The Fennoscandian Arctic fox is a central-place forager that depends on a limited number of den sites in landscapes where the ground substrate does not allow for easy establishment of new dens (Dalerum et al. 2002; Tannerfeldt et al. 2003). Furthermore, the Fennoscandian subpopulations are unsaturated; therefore, there are numerous uninhabited dens available for reproduction (natal dens) in any given year (Frafjord 2003; Killengreen et al. 2007). With a finite number of dens in an unsaturated population, occupied dens and the surrounding habitat could be expected to reflect the territories where the trade-off between resource abundance and predation risk is perceived as optimal (Szor et al. 2008). If Arctic foxes have higher reproductive success in dens far from the treeline compared to those located in more high-productive areas near the treeline, further reduction of the mountain tundra biome through tree and shrub encroachment will likely negatively impact reproduction and the viability of the population.

Inland Arctic fox populations (the ‘lemming fox’ ecotype, (Bræstrup 1941) typically display cyclic population dynamics since they rely on cyclic small rodents (Elmhagen et al. 2011), particularly the Norwegian lemming (*Lemmus lemmus*) (Elton 1924; Angerbjörn et al. 2001), which in turn is habitat-specific, except at extreme population peaks (Le Vaillant et al. 2018). The difference in foraging quality around Arctic fox dens could hence be considered spatially stable but temporally pulsed. Suitable lemming habitat should therefore strongly influence Arctic fox breeding success. Norwegian lemmings are strictly breeding in tundra habitats; however, competition in lemming-rich areas is likely more intense closer to the treeline, as most predators in both the tundra and in the boreal-tundra border zone rely heavily on lemmings (Ims and Fuglei 2005; Krebs 2010).

During years with limited lemming densities, alternative prey species with relatively stable population dynamics become important food sources for tundra predators (Ims and Fuglei 2005). Although lemmings are the preferred prey and essential for the onset of breeding in Fennoscandian Arctic foxes, alternative prey has been shown to improve the chance of successful breeding in other cyclic Arctic fox populations when small rodent availability is low (Ehrich 2017). In Fennoscandia, alternative prey such as ptarmigans and hares, as well as small rodents other than lemmings such as grey-sided voles (*Craseomus ruficanus*), field voles (*Microtus agrestis*), tundra voles (*Microtus oeconicus*) and bank voles (*Clethrionomys glareolus*), decrease with elevation and are hence more abundant closer to the treeline and in the birch forest (Stoessel et al. 2019; Ecke and Hörnfeldt 2021). In particular, birds have been identified as important alternative prey for Fennoscandian Arctic foxes (Elmhagen et al. 2000; Wilkinson 2023), and especially waders and waterfowl have been found to constitute a higher proportion of Arctic fox diets during lemming low years in other Arctic fox populations (Dalerum and Angerbjörn 2000; Ehrich 2017; McKinnon and Bety 2009). Moreover, waders in the Swedish tundra are probably not top-down controlled, and population sizes do not vary significantly over time (Svensson et al. 1984), making them a potentially reliable subsidiary food source for sustaining reproductive effort during lemming low years. However, as there is dietary overlap between Arctic foxes and red foxes (Elmhagen et al. 2002; Stoessel et al. 2019; Wilkinson et al. 2023), it is likely that bird-rich areas at lower elevations, as well as lemming-dense areas further from the treeline, are associated with higher interspecific conflict.

In this study, we investigated the factors that influenced reproductive success in the Arctic fox, using a long-term dataset of yearly den inventories (2000–2020). We investigated the hypothesis that Arctic foxes are more likely to successfully breed in dens offering the best trade-off between low risk of interspecific conflict and high food availability. To that end, we analysed the difference in a range of landscape factors between occupied dens successfully producing Arctic fox litters, and dens that were either unoccupied or had signs of (Arctic) fox activity but no successful reproduction. We predicted that:

I) In lemming low years, breeding should predominantly occur in dens far from the treeline, where interspecific conflict should be lower. Moreover, Arctic foxes attempting to breed in dens located in areas with a higher proportion of wetlands and waterbodies should have higher reproductive success, since these areas may provide subsidiary food resources such as waders or waterfowl when lemmings are scarce.

II) In lemming peak years, interspecific conflict should be lower since shared food resources are more abundant. Therefore, while Arctic fox reproductive success should generally be higher in dens located further from the treeline, the effect of distance to the treeline should be weaker. Similarly, Arctic fox reproductive success should be higher in dens located in areas with a larger proportion of lemming habitat during peak years. We expect the same patterns for lemming increase years, albeit weaker.

Material and methods

Study areas

This study was conducted in the sub-Arctic areas of Helagsfjällen, Jämtland county (≈62°54′ N, 12°27′ E), and Vindelfjällen, Västerbotten county (66°00 N, 16°00E), Sweden. The Helags population inhabits an area of 3,400 km^2 (Norén et al. 2016) consisting mostly of typical Fennoscandian mountain tundra. Productivity is low, and the ground surface is characterised by grass heath, dry heath, fens, and bogs at elevations between 900 and 1,200 m above sea level (m.a.s.l.). Rocky terrain is common at higher elevations, reaching up to the highest peak at 1,797 m.a.s.l. The forest line is at 850–900 m.a.s.l., with roughly a 100 m wide band of birch bordering the tundra with spruce-dominated boreal forest at lower elevations (Borgström 1979). Located 400 km further north, the Vindelfjällen population inhabits an area of 2,000 km^2, similar to Helags in terms of ground cover but with a slightly lower treeline averaging around 800 m.a.s.l. and the highest peak at 1,611 m.a.s.l (Staafjord 2012). Norwegian lemming density is generally higher in the Vindelfjällen area than in Helags (Ecke and Hörnfeldt 2021). See Table 1 for a summary of geographical differences.

Study species

In Fennoscandia, new Arctic fox dens are rarely established since the best locations for digging have likely already been used (Zetterberg 1927). Extant dens can, therefore, be several hundred years old and are used multiple times by consecutive generations (Dalerum et al. 2002; Tannerfeldt et al. 2003; Frafjord 2003). Although inactive or seldom-used dens can be found at all elevations in Fennoscandia, active dens are generally located above the treeline (Linnell et al. 1999; Dalerum et al. 2002; Frafjord 2003) and the climate-tracking treeline and subsequent red fox expansion have led to the abandonment of dens at lower elevations (Linnell et al. 1999; Elmhagen et al. 2002; Frafjord 2003).

The Arctic fox typically digs dens in sand- and gravel-dominated terrain features, such as moraines and sandbanks (Macpherson 1969; Prestrud 1992). In our study system, an unestablished Arctic fox usually settles in a den during early spring, with cubs born in May. Once a den is chosen, Arctic foxes typically remain at the same den site throughout the summer and often throughout the winter unless disturbed (Angerbjörn et al. 1997). Red fox activity near a natal Arctic-fox den can lead to den abandonment, and cubs are sometimes killed by red foxes (Tannerfeldt et al. 2002). If undisturbed, Arctic foxes seldom change natal dens but stay in the same den for consecutive years (Angerbjörn et al. 2004). During lemming population peaks, Arctic foxes can give birth to up to 18 cubs (Tannerfeldt and Angerbjörn 1998), while small or no litters are born in lemming low years (Angerbjörn et al. 1995; Strand et al. 1999).

Intense conservation actions have been implemented in Sweden since 1999 (Angerbjörn et al. 2013). These measures include supplemental feeding at all active dens (which includes almost all litters born since 2000), red fox culling, yearly den inventories, and ear tagging of individual Arctic foxes (Angerbjörn et al. 2013). Following these conservation efforts, combined with the increased regularity of lemming cycles, the population in Helags increased from 4 to 48 breeding individuals during the period 2000–2015 (Norén et al. 2016; Hasselgren et al. 2018) and from 2 to 34 in Vindelfjällen (Wallén et al. 2023). Since the initiation of the conservation actions, there have been 5 and 6 rodent cycle peaks in Helags and Vindelfjällen, respectively, although with varying amplitudes (Ecke and Hörnfeldt 2021). Notably, while supplementary feeding has increased overall litter size, it has not reduced the impact of the lemming cycle on the number of Arctic fox litters (Meijer et al. 2013).

Data collection

Since the Arctic fox relies on dens for reproduction, occupied dens are often used to estimate population sizes (Angerbjörn et al. 1995). During the study period from 2000 to 2020, we conducted yearly summer inventories (July and August) of dens in the core areas of the two study sites: Helags (n_{dens}=60) and Vindelfjällen (n_{dens}=66) (Table 1). To

Table 1 Geographic and population differences between study areas

Parameter	Helags	Vindelfjällen
Area	3,400 km²	2,000 km²
Treeline elevation (metres above sea level)	850–900	800
Highest peak (metres above sea level)	1797	1611
No. dens surveyed annually	60	66
Litters born during the study period 2000–2020	222	75

detect successful breeding, we surveyed all dens from late June to late August in both study areas in all years throughout the study period. If there was a sign of Arctic fox activity likely originating from the present year, i.e. visual observation of Arctic foxes, fresh scats, trampled grass, freshly dug or freshly cleared out burrows or fresh prey remains, the den was monitored for at least 24 h or until the presence of cubs was confirmed (see Angerbjörn et al. 2013 for more details) and subsequently classified with "successful reproduction" if cubs were observed. Breeding attempts without successful reproduction can be hard to determine from traces alone, since such traces may originate from winter use or red fox activity. Thus, if we detected no signs of Arctic fox activity or no cubs emerged from the den despite signs of Arctic fox activity, the den was registered as "unoccupied and/or no successful reproduction".

To determine the phase of the lemming cycle, we snap-trapped rodents at six sites throughout the core population area at Helags following the method of Krebs et al. (2002) (see ethical permits in the Declarations section below). Two Krebs lines, each consisting of 60 baited snap traps, were deployed evenly in groups of 3 over a 300 m transect for 48 h and checked twice. The number of catches was then calculated per 100 trap nights, with a total of 1440 trap nights per year. As we lacked data for several years at the start of the study period for Vindelfjällen, we instead used lemming indices from the yearly trapping surveys conducted by the county administrative board in Västerbotten and the Swedish University of Agricultural Sciences (Ecke and Hörnfeldt 2021). Although these surveys have a lower sampling effort in tundra habitat compared to our trapping, the captures of Norwegian lemming can reflect trends above the treeline since this species is a tundra specialist. In Helags, Norwegian lemming captures are much rarer, but the combined species data from Ecke and Hörnfeldt showed the same pattern for Helags as our own surveys, except for 2015 where we detected a strong initial increase in rodent abundance indicative of a peak, while Ecke and Hörnfeldt (2021) registered a weaker signal. Despite starting as a peak year, there was a drastic decline in rodent density later in the summer (Choi et al. 2019; Erlandsson et al. 2022). Such stochastic changes to phases in the rodent cycle are not uncommon in our study areas, and the cycle may vary between 3 and 5 years. Based on the number of catches and changes relative to the preceding year, the rodent cycle was divided into four phases for each area separately: low, decrease, increase, and peak (following Erlandsson et al. 2022). However, no or few Arctic foxes breed during the low phase of the lemming cycle, making the sample size too low for statistical analysis. Therefore, we pooled the decrease and low phases into one phase (low). Landscape explanatory variables were then extracted for areas around all dens using national land cover data (Table S1).

Explanatory variables

At each den site, our model included: distance to the treeline, probability of lemming presence (from Le Vaillant et al. 2018), bog area and water area, where we used a variance inflation factor (VIF) value of 3 as a threshold for collinearity between predictor variables (see Online Resource 1 for collinearity assessments and Table S1 for file origins). We used distance to the treeline as a proxy for the influx of boreal competitors. Since red foxes spill over into tundra habitat from boreal forest, elevation or distance to treeline (which are highly correlated) are often used as proxies for red fox territories in studies of Arctic fox and red fox interactions in Fennoscandia (Dalerum et al. 2002; Herfindal et al. 2010; Erlandsson 2019; Erlandsson et al. 2022). Stoessel et al. (2019) also found that the red fox abundance in mountain tundra areas decreased with increasing altitude, whereas the Arctic fox abundance increased, especially during winters after a lemming peak. When measuring distances from dens to the treeline, we excluded groups of trees not connected to continuous lowland forests. Fennoscandian Arctic fox territories cover approximately 45 km^2 for males and 16 km^2 for females (Landa et al. 1999), although females may become even more stationary if food availability is high close to the den (Angerbjörn et al. 1997). As reproducing foxes act as central place foragers, we chose a 1500 m radius around each den to calculate the mean probability of lemming presence, total bog area and total water area. The probability of lemming presence during increase-years around each den was calculated using a raster model developed by Le Vaillant et al. (2018) based on Normalised Difference Vegetation Index (NDVI) (500 × 500 m scale), elevation (50 m), and slope aspect. Each cell of the raster specifies the probability that lemmings are present. We only included probability of lemming presence calculated for increase years, since they best reflect optimal lemming habitat (Le Vaillant et al. 2018). Although lemmings are less habitat-specific in summers of peak years, the main population increase occurs in mid- to late winter, and the shift to summer habitat does not occur until snowmelt (Tast 1991). Thus, except for the most extreme peak years, lemmings are most likely still tied to high-quality habitat in late winter when Arctic foxes start the breeding season. From the raster model, we calculated the mean probability of lemming presence around each den by extracting probabilities from all cells within the 1500-metre radius. One group of prey that is less sensitive to terrestrial variation in primary productivity is birds that rely on aquatic prey and aquatic subsidies such as insects emerging from water. We used the area of bogs and waterbodies around each den as proxies for this group of species, as for example many wader species breed in wet habitats (Cunningham et al. 2016). All GIS computations were performed using R version 4.0.5 (R Core Team 2021) with packages sp version 1.2-6 (Bivand et al. 2013), rgdal version 1.3-1 (Bivand et al. 2022) raster version 3.5–15 (Hijmans 2022) and rgeos version 0.6.4 (Bivand and Rundel 2021).

Statistical analyses

To investigate potential spatial differences in reproductive success under varying levels of prey availability, we divided the dataset by phase of the lemming cycle: low (including both decrease and low years), increase, and peak. We modelled the reproductive success of a den as a binary response variable where, for each year, dens classified as "unoccupied and/or no successful reproduction" where specified as 0 and dens classified with "successful reproduction" where specified as 1, using generalised linear mixed models (GLMM) with a binomial distribution and a logit link function. We standardised all continuous variables by rescaling to mean = 0 and SD = 0.5, as recommended by Gelman (2008) and Grueber et al. (2011). We then fitted all possible combinations of the selected variables describing habitat quality, with random intercepts for den-identity, along with an intercept-only (null) model, for both the Helags and Vindelfjällen populations in separate population-phase-specific analyses. We used r packages "lme4" version 1.1.29 (Bates et al. 2015) to fit the model containing all predictor variables and the "dredge" command in package "MuMIn" version 1.46.0 (Bartoń 2018) to fit models with all predictor-variable combinations. Due to limited reproductions in low and increase years for Vindelfjällen (8 and 21 litters respectively), these phases were excluded from the final analyses. We then used the Akaike information criterion adjusted for small sample size (AIC_c) to determine which models containing the combination of predictor variables best described dens likely to yield successful Arctic fox reproductions.

There was no clear best model for any of the four analyses (Helags low, increase, and peak, and Vindelfjällen peak phases), and models with a ΔAIC_c score <2 may explain the data equally well (Burnham and Anderson 2002). Therefore, we averaged the parameter estimates of models with a ΔAIC_c score <2, so that each selected model contributed proportionally to its likelihood weight. To compare the among-predictor contribution to the variance in the response variable, we calculated the relative importance of each predictor variable using the sw command in r-package "MuMIn" 1.46.0 (Bartoń 2018). Together with standardised parameter estimates, we were then able to compare the effects of predictor variables on differences in Arctic fox reproductive success between territories. To assess the impact of two outlier low years when Arctic fox reproductive success was uncharacteristically high, we analysed the Helags low phase again with these two years excluded. See Online Resource 1 for goodness of fit assessments.

Results

In Helags, we identified 7 lemming increase years, 4 peak years and 10 low years (Fig. 1a), where the years 2000–2017 phases correspond to the classification by Erlandsson et al. (2022). In Vindelfjällen, we identified 6 increase years, 6 peak years, and 9 low years (Fig. 1b). Throughout the study period, litters were produced at 35/60 surveyed dens in Helags and 23/66 in Vindelfjällen (Fig. S1). There were in total 222 recorded litters in Helags and 75 recorded litters in Vindelfjällen. In Helags, the number of litters born was evenly divided among the phases of the lemming cycle (low = 30%, increase = 37%, peak = 33%), whereas in Vindelfjällen most litters were born during peak years (peak = 61%, increase = 28%, low = 11%).

Successful Arctic fox dens increased in Helags with increasing distance to the treeline during all phases of the lemming cycle (Table 2; Fig. 2a), with a relative importance value of 1.00 for each phase. The mean den distance to the treeline was 5 km, ranging from 0.4 km to 12.7 km. With an increase of 5 km from the mean den distance to the treeline, the expected probability of a Helags den producing a litter was 2–3 times larger compared to the probability at the mean den distance. For Helags, the expected probability of successful reproduction at the mean den distance +5 km was 0.16, 0.31 and 0.54 for low, increase and peak years, respectively. At the treeline, the expected probability of reproduction was small for all phases, but slightly higher in the peak phase with 0.07 compared to 0.02 and 0.01 for the increase and low phases, respectively. However, the confidence intervals of these predictions overlapped (Fig. 2).

In Vindelfjällen, the number of Arctic fox litters in low and increase phases were too few to analyse (8 and 21 litters respectively). But following the pattern from Helags, the number of litters increased with increasing distance from the treeline during the peak phase (relative importance 1.00, Table 2; Fig. 2a). The mean den distance to the treeline was 3.3 km in Vindelfjällen, ranging from 0.6 km to 9.1 km. With an increase of 5 km from the mean den distance to the treeline, the expected probability of a den producing a litter during the peak phase was 0.35, which is roughly ten times higher than the probability at the mean den distance to the treeline.

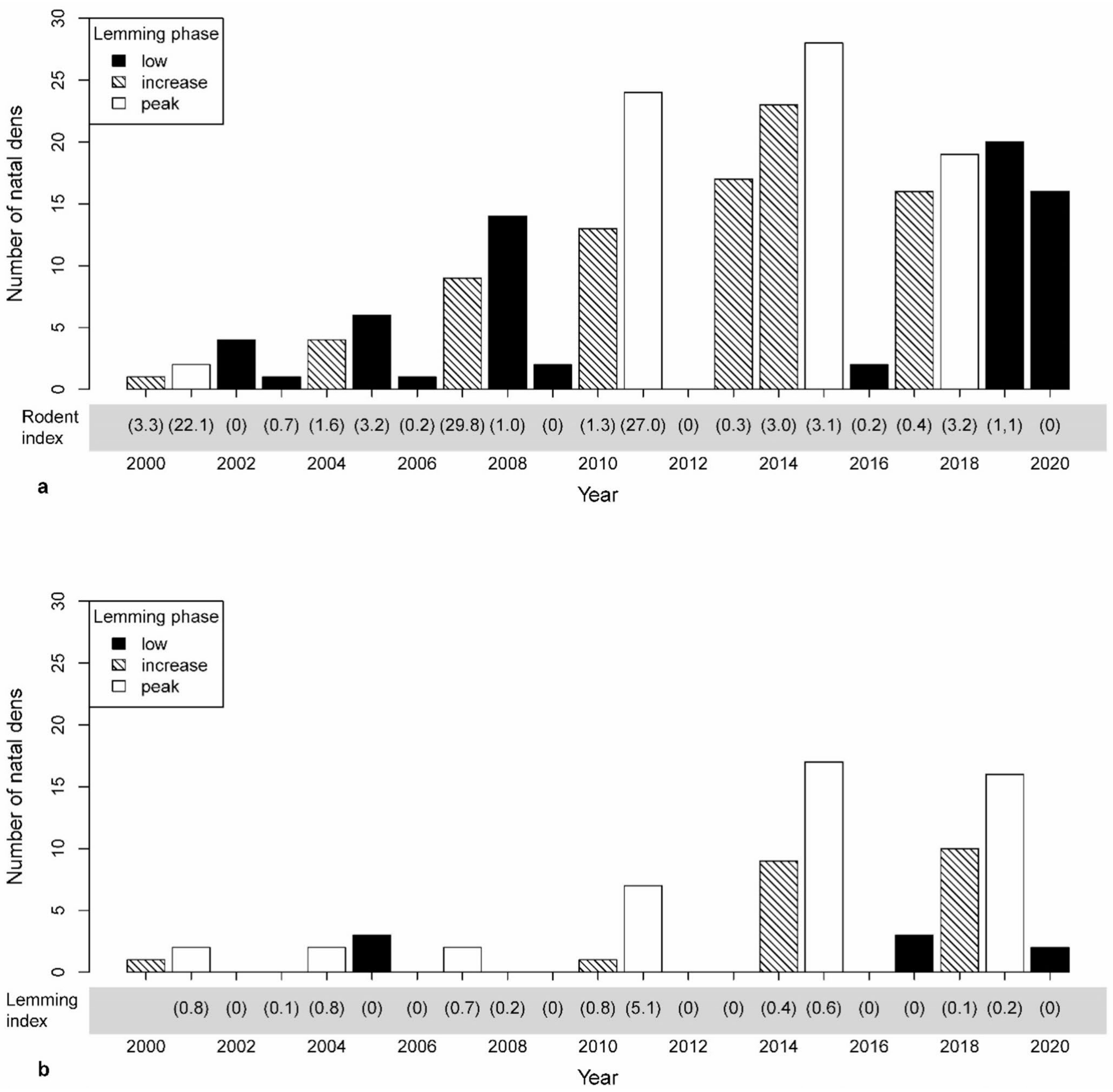

Fig. 1 Number of Arctic fox natal dens and rodent/lemming trapping indices per year, with bar colours representing phase of the lemming cycle for **a**; Helags and **b**; Vindelfjällen. The only year without recorded litters in Helags (2012) was a lemming low year. Of years with no successful reproductions in Vindelfjällen, 2003 and 2006 were lemming increase years, 2002, 2006, 2008, 2009, 2012, 2013 and 2016 were lemming low years

Contrary to our predictions, the effect of distance to the treeline was not stronger during the low phase compared to the increase and peak phase in Helags (Table 2). However, reproductive success was uncharacteristically high in the low years of 2019 and 2020 when 36 litters were born in total, compared to 30 litters in 7 low years prior to 2019. Re-analyses without those years showed that the effect of distance to the treeline was stronger in low years prior to 2019: 2.48 (CI = 0.58, 4.38), which was also stronger than the effect of distance to the treeline in increase years: 2.18 (CI = 0.83, 3.53) and peak years: 1.84 (CI = 0.29, 3.38), although the confidence intervals for the three phases overlapped. In addition, we also recorded successful breeding in 4 dens that had previously only been used during peak years. After the 2020 breeding season, there were only 4 dens that had been exclusively used during lemming peak years (Fig. S1).

Table 2 Model-averaged parameter estimates on the logit scale with 95% confidence intervals for landscape characteristics' effects on Arctic fox (*Vulpes lagopus*) den reproductive success at different phases of the lemming cycle, low phase (decrease phase and low phase combined), increase phase and peak phase, for the Helags and Vindelfjällen populations. Predictor variables were centred at the mean and scaled to 0.5 standard deviations before analysis. Unconditional standard errors and the Akaike-weight relative importance of each variable to other variables within the same phase are also reported

	Parameters	Estimate	95% CI	Unconditional SE	Relative Importance
Helags					
	Low phase				
	Intercept	-3.34	-4.13, -2.54	0.41	
	distance to treeline	1.83	0.57, 3.09	0.64	1
	area bogs	-0.27	-1.47, 0.94	0.61	0.28
	prob. lemming presence	0.09	-0.53, 0.7	0.31	0.18
	area water	-0.08	-0.73, 0.57	0.33	0.17
	Increase phase				
	Intercept	-2.51	-3.27, -1.75	0.39	
	distance to treeline	2.18	0.83, 3.53	0.69	1
	area bogs	-1.41	-3.63, 0.81	1.13	0.8
	prob. lemming presence	0.35	-0.87, 1.57	0.62	0.41
	area water	-0.04	-0.57, 0.49	0.27	0.16
	Peak phase				
	Intercept	-1.2	-1.67, -0.73	0.24	
	distance to treeline	1.73	0.8, 2.67	0.48	1
	prob. lemming presence	1.1	0.2, 2	0.46	1
	area water	-0.18	-0.89, 0.52	0.36	0.39
	area bogs	-0.24	-1.22, 0.75	0.5	0.37
Vindelfjällen					
	Peak phase				
	Intercept	-3.19	-4.12, -2.25	0.48	
	distance to treeline	1.84	0.29, 3.38	0.79	1
	prob. lemming presence	0.32	-0.93, 1.57	0.64	0.38

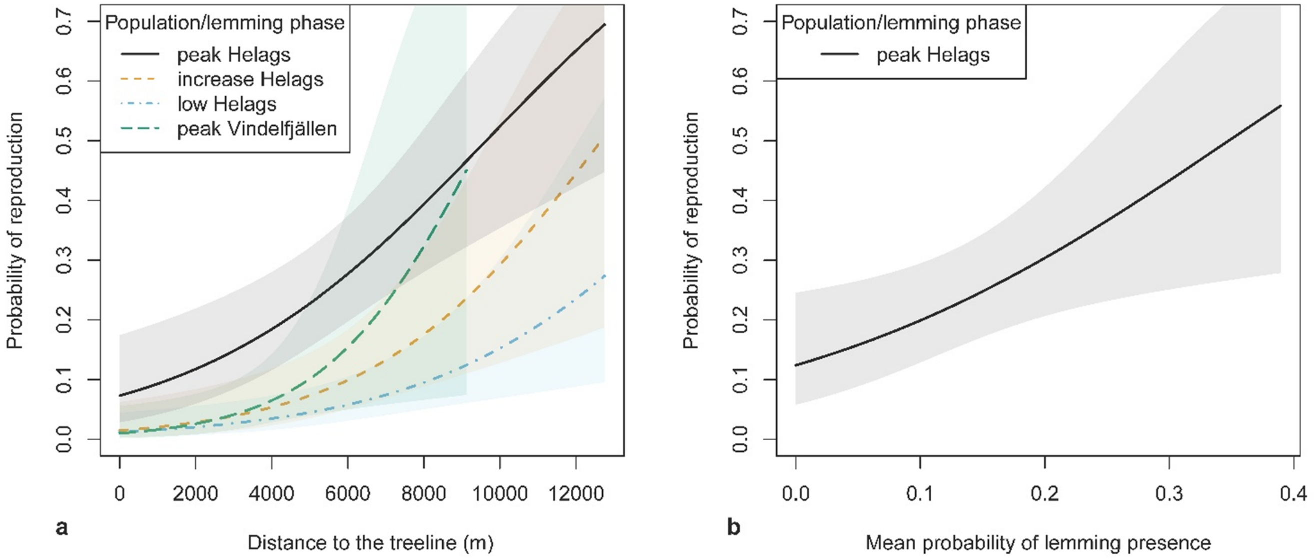

Fig. 2 The expected change in probability of reproduction in dens in the Helags and Vindelfjällen Arctic fox populations with **a;** increasing den distance to the treeline and **b;** increasing mean probability of lemming presence in 1500 m buffers around each den. The mean probability of lemming presence was extracted from a raster model developed by Le Vaillant et al. (2018). Parameter estimates with confidence intervals overlapping zero are not shown

Table 3 Models with ΔAICc <2 retained for model averaging analysis, with log likelihood, Akaike weights and marginal and conditional R^2. The Model column indicates the analysed population and phase, with predictor variables retained for each model. Intercept-only models contain a fixed intercept. All models, including intercept-only models, were fitted with random intercepts for den identity

Model	logLik	AICc	ΔAICc	Akaike weight	R^2m	R^2c
Low phase Helags						
dist. treeline	-179.45	364.94	0	0.35	0.066	0.222
area bog, dist. treeline	-178.55	365.18	0.239	0.311	0.084	0.224
dist. treeline, prob lemming	-179.04	366.14	1.202	0.192	0.072	0.224
area water, dist. treeline	-179.3	366.67	1.734	0.147	0.066	0.221
intercept only	-185.56	375.14	10.206	0.002	0	0.198
Increase phase Helags						
area bog, dist. treeline	-187.04	382.16	0	0.422	0.225	0.322
area bog, dist. treeline, prob lemming	-186.69	383.51	1.348	0.215	0.228	0.317
dist. treeline, prob lemming	-187.79	383.67	1.505	0.199	0.241	0.331
area bog, area water, dist. treeline	-186.96	384.05	1.886	0.164	0.241	0.324
intercept only	-198.49	401	18.835	0	0	0.305
Peak phase Helags						
dist. treeline, prob lemming	-121.58	251.34	0	0.378	0.225	0.322
area water, dist. treeline, prob lemming	-120.95	252.16	0.824	0.25	0.228	0.317
area bog, dist. treeline, prob lemming	-121.03	252.32	0.986	0.231	0.241	0.331
area bog, area water, dist. treeline, prob lemming	-120.47	253.31	1.972	0.141	0.241	0.324
intercept only	-138.11	280.27	28.937	0	0	0.305
Peak phase Vindelfjällen						
dist. treeline	-122.4	250.86	0	0.616	0.076	0.276
dist. treeline, prob lemming	-121.85	251.81	0.947	0.384	0.082	0.278
intercept only	-128.62	261.26	10.403	0.002	0	0.247

In Helags lemming peak years, successful Arctic fox reproduction increased in dens with a higher probability of lemming presence (relative importance = 1.00, Table 2; Fig. 2b) but the point estimate of the standardised predictor variables was smaller for probability of lemming presence than the point estimate for distance to the treeline (1.1 vs. 1.7) suggesting a weaker effect of probability of lemming presence compared to distance to the treeline. The grand mean probability of lemming presence for all dens was 0.17, where the expected probability of reproduction was 0.23. With a doubling of the mean probability of lemming presence, the expected probability of reproduction would also double (0.48) during the Helags peak phase. There was no detectable effect of the mean probability of lemming presence on reproductive success for peak years in Vindelfjällen (Table 2). The confidence intervals of all other parameters for all phases in both populations spanned zero, indicating no effect. None of the null models (only intercept and den identity random effect) had a ΔAIC_c score <2, but the delta-method conditional pseudo-R^2 for models with a ΔAIC_c score <2 were generally quite close to the conditional pseudo-R^2 values for the null models (Table 3), which suggests that den-identity explained most of the variance in reproductive success. See Table 3 for a summary of models retained for model averaging (models with a ΔAIC_c score <2).

Discussion

Our results indicate that Arctic fox reproductive success was higher at dens far from the treeline in both the Helags and Vindelfjällen populations during all analysed phases of the small rodent cycle. Given that Arctic fox natal den distance to the treeline is a representative proxy for distance to red fox territories, these results may indicate that the presence of red foxes causes higher rates of failed reproduction near the treeline, or that Arctic foxes avoid attempting to breed at lower elevations altogether. Regardless of the causal mechanism of the lower reproductive success in dens near the treeline, future climate-change-induced treeline expansion may likely cause reduced Arctic fox reproductive success, as fewer dens may successfully produce litters. We predicted that the mean probability of lemming presence around dens would have the strongest effect on Arctic fox reproduction during peak years, while having an intermediate effect during increase years and a weak effect during low years. We found some evidence for an effect of mean probability of lemming presence on reproductive success in Helags during the peak phase, which supported our predictions. However, contrary to our expectations, we detected no effect during the increase or low phases.

Lemming abundance is generally considered the primary factor influencing Fennoscandian Arctic fox reproductive success (Elton 1924; Angerbjörn et al. 1995; Elmhagen et al. 2011). However, many other carnivores, such as red fox, wolverine, and golden eagle, also prey on lemmings when the abundance is high (Rød-Eriksen et al. 2023), creating an intricate ecological community (Ims and Fuglei 2005; Legagneux et al. 2012) where lemming-rich territories may be associated with increased intraguild predation risk (Gilliam and Fraser 1987; Brown 1992, 1999). That we did not find a clear positive association between the probability of lemming presence and Arctic fox reproduction during low and increase years in Helags may suggest that breeding in lemming-rich areas can be risky due to an increased presence of top or intraguild predators (Rød-Eriksen et al. 2023). If local basal prey densities are sufficiently high to attract predators that prey on both basal prey species and mesopredators, mesopredator breeding success would likely decrease in those areas, with the potential long-term risk that they become effectively excluded. A parallel phenomenon has been observed in other mesopredators (e.g. rough-legged buzzards (*Buteo lagopus*) (Potapov 1997), bottlenose dolphins (*Tursiops aduncus*) (Heithaus and Dill 2002) and common buzzards (*Buteo buteo*) (Björklund et al. 2016), which avoid areas rich in shared prey to reduce exposure to intraguild predators. Arctic fox reproductive success would then generally be higher in resource-poor areas with less interspecific conflict (Dalén et al. 2004). We did not detect an effect of the mean probability of lemming presence on Arctic fox reproductive success in the peak phase in Vindelfjällen, where the above-treeline density of red foxes is higher during lemming peak years (Wilkinson et al. 2024). The absence of a relationship between the mean probability of lemming presence and Arctic fox reproductive success could suggest that negative effects on breeding apply in lemming-rich territories even at high prey availability. Alternatively, lemming densities are sufficiently high to sustain breeding Arctic foxes in lower-quality lemming habitat territories during Vindelfjällen peak years.

In contrast to Vindelfjällen, Helags Arctic foxes reproduced more successfully in territories with an increased probability of lemming presence during lemming peak years, but this effect appeared weaker than the effect of distance to the treeline (Table 2). Since red foxes are known to expand into tundra in peak years (Henden et al. 2010; Wilkinson et al. 2024), and red foxes, wolverines, and golden eagles are known to increase their predation rate on lemmings (Rød-Eriksen et al. 2023), interspecific conflict could potentially increase if lemming densities are low enough that lemmings remain habitat-specific. If high-risk territories are used despite a higher predation pressure, foraging quality in those territories is expected to be considerably higher, which has been demonstrated empirically in foraging experiments conducted on various species such as creek chubs (*Semotilus atromaculatus*) (Gilliam and Fraser 1987), European starlings (*Sturnus vulgaris*) (Olsson et al. 2002) and Nubian ibex (*Capra nubiana*) (Kotler et al. 1994). Alternatively, the predation risk for Arctic fox juveniles becomes sufficiently reduced in peak years as larger predators switch to prey on lemmings (Erlandsson et al. 2017), which are less habitat-specific during these periods, leading predators to be less tied to areas with high-quality lemming habitat (Rød-Eriksen et al. 2023). Consequently, the relaxed conflict and simultaneous increase in prey availability in the peak phase could reduce costs and increase the benefits of breeding in territories with high-quality lemming habitats, which could explain the positive effect of lemming presence probability on Arctic fox reproductive success in peak years in Helags.

We predicted that Arctic fox reproductive success would be higher in areas richer in alternative prey during low years, and possibly in increase years, when lemmings are scarce. However, we did not detect an effect of bog or water area where wader and waterfowl nesting densities could be expected to be higher. It is important to note that these proxies are rough representations of concentrations of water-associated prey, and the increase in prey availability may not scale linearly with increasing wetland/water area. Therefore, it is conceivable that a more fine-scaled predictor variable (such as the Le Vaillant et al. 2018 lemming raster model used in this study) could have captured a positive response. Future work could therefore focus on developing presence-probability models for alternative prey, which could further improve our understanding of Arctic fox reproductive success during years with low lemming densities. Another possible explanation for this null result is that flat bogs do not provide a suitable habitat for lemmings (Kausrud et al. 2008; Le Vaillant et al. 2018), forcing Arctic foxes to face a trade-off between main and alternative prey, where a strong lemming focus remains dominant.

Normally, no or few Arctic foxes reproduce during the low years of the lemming cycle when competition, predation, and the risk of cubs starving to death are higher. Investing in reproduction during these years would require access to territories providing an optimal risk/foraging ratio. Hence, the dens with reproductions during the low phase could be expected to be of the highest quality. Indeed, the most frequently used dens produced litters irrespective of the lemming phase (Fig. S1). In Helags, 4 dens solely had reproduction during peak years (Fig. S1). Before the uncharacteristically successful breeding seasons of the low years 2019 and 2020, 8 dens had had reproductive success solely recorded during peak years. These dens should therefore be of lower quality because litters were only produced when the breeding population was relatively large and prey abundance was high. Additionally, before 2019, the positive effect of distance to the treeline was stronger during the low- and increase phases than during the peak phase, in line with our predictions. This could be interpreted as an indication that dens further from the treeline not only had higher reproductive success but were also preferred as a first choice when the breeding population was small and intraspecific competition for dens was low. However, our field methods do not safely allow us to separate dens utilised for winter shelter from natal den selection when no cubs emerge, making breeding site preference hard to disentangle from reproductive failure.

Low-productive refugia are likely important for the long-term survival of Arctic foxes, since red foxes have a much higher energy demand due to their larger size (Hersteinsson and MacDonald 1992) and are therefore restricted to more productive patches of tundra (Elmhagen et al. 2002; Herfindal et al. 2010; Stoessel et al. 2019). Although lemmings are not favoured by a warming climate (Kausrud et al. 2008; Gauthier et al. 2024), many other potential prey species are expected to increase as a result of higher primary productivity (Elmhagen et al. 2015), thereby expanding the potential distribution of predators in Arctic and sub-Arctic areas. While all tundra and tundra-expanding boreal-forest predator species benefit from lemming peaks, Arctic fox reproductive success is directly linked to lemming abundance (Ims and Fuglei 2005). A general increase of boreal-forest prey species following higher primary productivity and advancing treeline (Elmhagen et al. 2015), coupled with a simultaneous dampening of the lemming cycle, should therefore disproportionally favour generalist predators, especially in the lemming low and increase phases. Indeed, conservation actions such as red fox culling and supportive feeding of Arctic foxes have substantially increased the number of reproducing adults in Helags (Angerbjörn et al. 2013).

Anthropogenic food subsidies following infrastructure development have increased red fox presence in tundra habitats in Fennoscandia and elsewhere (Stickney et al. 2014; Elmhagen et al. 2017; Gallant et al. 2020; Rød-Eriksen et al. 2020), but human settlements are small in our study areas. While red fox expansion into tundra areas in Helags and Vindelfjällen may have been driven by a combination of land use change and warming temperatures (Elmhagen et al. 2015), its current range is likely limited by lynx predation and winter harshness (Pasanen-Mortensen et al. 2013). Given the low levels of present infrastructure development in our study areas, we believe that warming winter temperatures and treeline encroachment will be the main drivers of red fox expansion into tundra habitat in the foreseeable future.

Arctic species are well-adapted to reproduce in extreme environments where few other species survive, but they are generally inferior competitors in species-rich ecosystems (Ims and Fuglei 2005). Conversely, generalist species are more likely to adapt to increasing winter temperatures and expand their ranges poleward (Elmhagen et al. 2015; Sokolov et al. 2016; Warret Rodrigues and Roth 2023). A key feature of animal populations threatened by extinction due to interspecific conflict is exclusion from prime foraging grounds to low-productivity refugia (Linnell and Strand 2000). Our results show that Arctic fox reproductive success in Fennoscandia is dependent on the possibility of breeding far from the treeline, where productivity is lower, which will be increasingly harder as continued climate warming causes further reductions in tundra habitat by treeline expansion. Since treeline expansion will likely be accompanied by a further expansion of red fox distributions, efficient conservation efforts such as red fox culling and Arctic fox supplemental feeding (Wallén et al. 2023) may need to be intensified compared to present-day levels if extinction of the Fennoscandian populations is to be avoided. The rapid changes facing Arctic and sub-Arctic environments require careful management actions to balance the need of fringe environments as climate refugia for southern species, as well as the continuous functioning of endemic Arctic and sub-Arctic communities.

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Author contributions THF, KN and RE conceived and designed research. KN and RE supervised, AA, JW, KN, and RE collected field data. AA and KN acquired funding. THF compiled and analysed data. THF, KN and RE wrote the manuscript, AA and JW commented on the manuscript.

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Data availability The Arctic fox is classified as endangered in Sweden despite protection since the 1920s. Therefore, we cannot deposit the data used for this work in a public repository since it may be used to locate Arctic fox dens.

Code availability R-scripts without data are available on request.

Declarations

Ethics approval All relevant institutional and national regulations regarding animal care and use were adhered to. The trapping and handling of animals were ethically reviewed and received legal approval from Umeå djurförsöksetiska nämnd and the Swedish Environmental Protection Agency, under Swedish law and legislation. Permits number: 412-35-99 Nf, 412-4191-03 Nf, 412-5362-04 Nf, 412-7884-07 Nf, NV-01959-14, NV-02547-17, 30-1698/04, A65/99, A39-00, A49-01, A111-03, A74-05, A130-07, A131-07, A36-11, A36-11, A37-11, A1814, A19-14.

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