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Research article

Consequences of repeated sarcoptic mange outbreaks in an endangered mammal population

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Diseases and parasites are important drivers of population dynamics in wild mammal populations. Small and endangered populations that overlap with larger, reservoir populations are particularly vulnerable to diseases and parasites, especially in ecosystems highly influenced by climate change. Sarcoptic mange, caused by a parasitic mite *Sarcoptes scabiei*, constitutes a severe threat to many wildlife populations and is today considered a panzootic. The Scandinavian arctic fox *Vulpes lagopus* is endangered with a fragmented distribution and is threatened by e.g. red fox *Vulpes vulpes* expansion, prey scarcity and inbreeding depression. Moreover, one of the subpopulations in Scandinavia has suffered from repeated outbreaks of sarcoptic mange during the past decade, most likely spread by red foxes. This was first documented in 2013 and then again 2014, 2017, 2019, 2020 and 2021. We used field inventories and wildlife cameras to follow the development of sarcoptic mange outbreaks in this arctic fox subpopulation with specific focus on disease transmission and consequences for reproductive output. In 2013–2014, we documented visual symptoms of sarcoptic mange in about 30% of the total population. Despite medical treatment, we demonstrate demographic consequences where the number of arctic fox litters plateaued and litter size was reduced after the introduction of *S. scabiei*. Furthermore, we found indications that mange likely was transmitted by a few arctic foxes travelling between several dens, i.e. 'super-spreaders'. This study highlights sarcoptic mange as a severe threat to small populations and can put the persistence of the entire Scandinavian arctic fox population at risk.

Keywords: climate change, conservation biology, mange outbreak, panzootic, *Sarcoptes scabiei*, wildlife disease

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Introduction

Pathogens are important drivers of population dynamics in wild mammals. When multiple host species overlap, the rate of transmission is expected to increase as the total density of hosts, regardless of species, is higher (Hethcote 2000). Several endangered populations have become extinct or undergone severe declines due to larger sympatric reservoir populations of other species that maintain the pathogens within the populations' e.g., canine distemper virus (CDV) in black footed ferret *Mustela nigripes* (Williams et al. 1988), rabies in Ethiopian mane wolf *Canis simensis* (Sillero-Zubiri et al. 1996, Randall et al. 2006), rabies and canine distemper virus (CDV) in African wild dog *Lyacon pictus* (Gascoyne et al. 1993, van de Bildt et al. 2002). In these cases, pathogens are not the underlying cause of the small population size but can be the definite cause of extinction.

Climate change causes shifts in the geographic distribution of wildlife populations (Gilg et al. 2012, Elmhagen et al. 2015), with boreal species, such as the red fox, moose and roe deer, expanding their range into northern ecosystems. Such range expansion is predicted to increase the geographic range of diseases and parasites e.g. tick-borne pathogens, CWD and *Echinococcus* spp., as well as the risk of transmission from recently established species to native species (Prenter et al. 2004). Cross-specific transmission of diseases and parasites from boreal to tundra species have been documented in several cases (Welch et al. 1990, Kutz et al. 2009, Feldman et al. 2017). The role of pathogen outbreaks is hence expected to become even more important as climate change progresses, especially in northern ecosystems (Welch et al. 1990, Kutz et al. 2009, Feldman et al. 2017).

Sarcoptic mange is a highly contagious skin disease, caused by the parasitic itch mite *Sarcoptes scabiei*. The mites burrow through the skin of the infected animal, forming tunnels into which antigenic material (e.g. eggs, faeces, shed exoskeletons, digestive secretions) is deposited, causing intense irritation to the skin (Soulsbury et al. 2007). The development from egg to adult takes ca two weeks and heavy infections can build up rapidly, with densities up to 5000 mites cm^{-2} in some species (Bornstein et al. 2001). *Sarcoptes scabiei* is transmitted via direct contact or indirectly (Arlian and Vyszenski-Moher 1988), dependent on host density, sociality and environmental factors (Browne et al. 2022). Climate change is predicted to increase outbreaks of sarcoptic mange in wildlife populations (Niedringhaus et al. 2019). Outbreaks can impact severely on wildlife populations worldwide through lowered individual fitness and negative population development, especially in a scenario where the parasite is transmitted from a reservoir population to a small, threatened or genetically deprived population (Escobar et al. 2022). This can be exemplified by the endangered San Joaquin kit fox *Vulpes macrotis mutica* that was exposed to a long-term epidemic (2013–2020) of sarcoptic mange, which reduced the population by approximately 50% (Cypher et al. 2017, Foley et al. 2023). In Scandinavia, *S. scabiei* caused a large epizootic of sarcoptic mange in the red fox *Vulpes vulpes* 1975–1985, which led to 50% decrease of the population size (Lindström and Mörner 1985). The decline was driven by reduced survival in both adults and juveniles (Willebrand et al. 2022). Since the large outbreak in 1975–1985, the infection has remained within the red fox population but on a relatively low level. The epizootic primarily affected the red fox but also wolves *Canis lupus*, lynx *Lynx lynx* and arctic foxes *Vulpes lagopus* were infected (Mörner 1992). Sarcoptic mange outbreaks can also bring sub-lethal consequences, such as reduced reproductive capacity. For example, sarcoptic mange affect the reproductive ability through reduced ovulation and pregnancy rates in coyotes *Canis latrans* (Pence and Windberg 1994).

From a conservation perspective, medical treatment or vaccination of endangered populations is an important tool to avoid extinction parallel to other actions in order to improve the viability of an endangered population (Woodroffe 1999, Knobel et al. 2008, Sillero-Zubiri et al. 2016, Woodroffe et al. 2021). However, treatment of wild populations compared to domestic animals is challenging since the wild animals are free ranging and the population size and distribution is often unknown (Barnett and Civitello 2020). The treatment or vaccination of wild populations have been conducted through capture with immobilisation or non-invasively through feeding or bait (Knobel et al. 2008, Sillero-Zubiri et al. 2016, Gilbert 2019, Woodroffe et al. 2021). Capture is connected to both logistical and ethical issues but with the advantage that the number of treated individuals and received dose is known (Gilbert 2019). On the other hand, non-invasive strategies such as baiting have the advantage that the method often is relatively simple to conduct but it is less certain whether the treatment is reaching its target and the number of treated individuals (Wobeser 2002). Given the widespread occurrence and potential consequences of sarcoptic mange, efficient strategies for treatment are of fundamental importance for management and conservation of wildlife (Rowe et al. 2019). The treatment of sarcoptic mange in domestic animals or wild species in captivity is effective but demands repeated treatments since the eggs survive the treatment (León-Vizcaíno et al. 2001). An individual treated for mange does not receive immunity and can be re-infected multiple times (Rowe et al. 2019).

The Scandinavian arctic fox is endangered and is listed as a priority species according to the EC Habitats Directive. Intensive conservation actions, including red fox culling and supplementary feeding have been successful and the population has increased during the last 20 years (Angerbjörn et al. 2013, Wallén et al. 2023). However, the population is still endangered and fragmented with limited gene flow between the subpopulations (Hemphill et al. 2020, Cockerill et al. 2022), as well as reduced genetic variation and inbreeding depression (Hasselgren et al. 2021). Another potential threat is outbreaks of diseases and parasites. A minor outbreak of sarcoptic mange occurred in 1986–1987 in one of the four subpopulations, around the mine in Stekenjokk, Borgafjäll, southern Lapland, Sweden (Fig. 1a). Approximately 25 arctic foxes and a number of red foxes lived around the mine and utilised remains from the kitchen and a close by reindeer

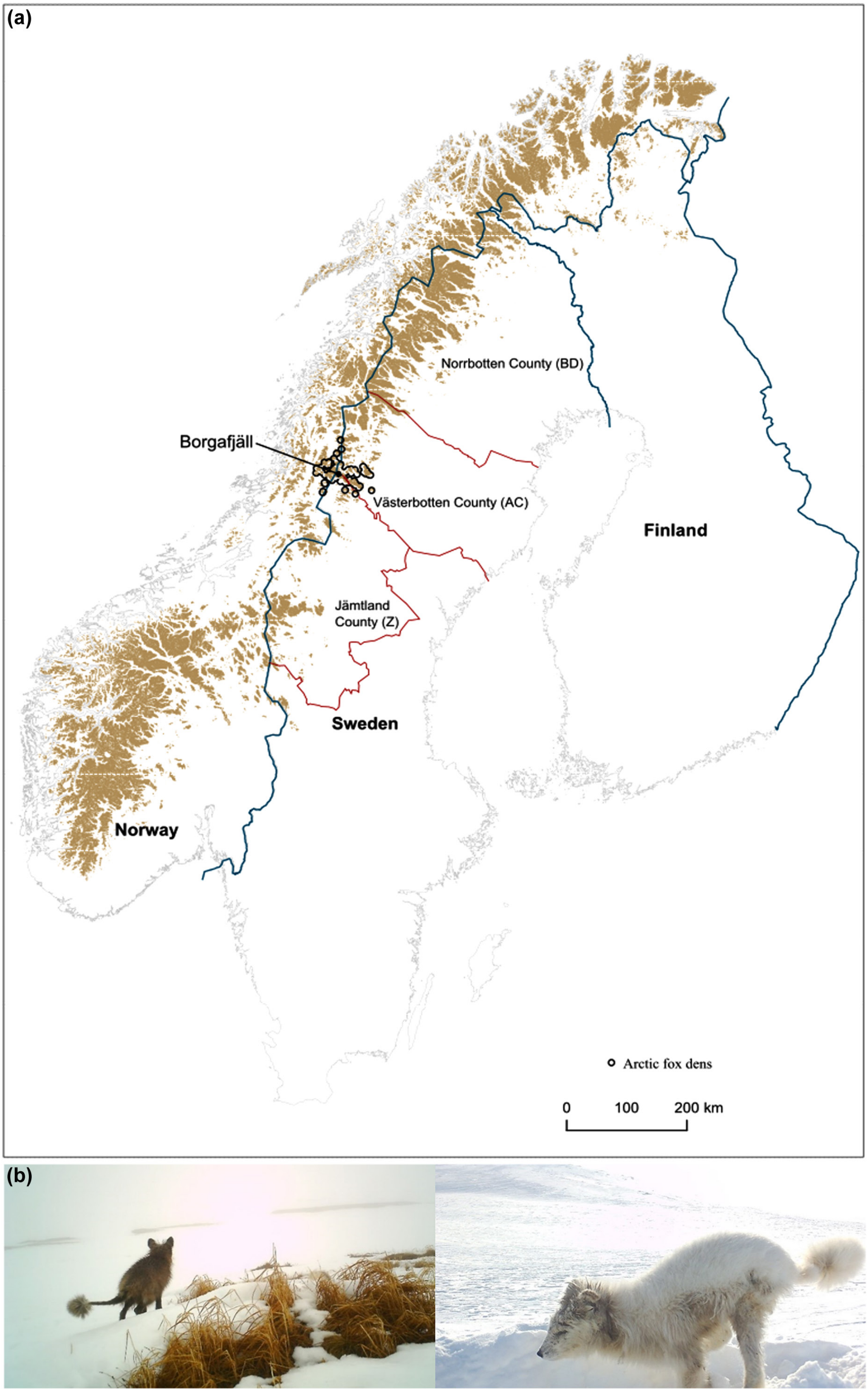

Figure 1. (a) Scandinavia with the subpopulation Borgafjäll marked, (b) wildlife camera photos of infected arctic foxes in Borgafjäll.

slaughterhouse. In 1987, 21 arctic foxes were caught, of which four showed clear symptoms of sarcoptic mange and were treated several times with the active substance Ivermectin. One year after the treatment, no arctic foxes showed symptoms of sarcoptic mange (Mörner 1992).

However, in April 2013 arctic foxes in the same subpopulation were yet again observed with sarcoptic mange, most likely introduced by sympatric red foxes. Red foxes are commonly regarded as the primary reservoir for *S. scabiei* in northern Sweden (Mörner 1992), no other potential vectors have been observed in the vicinity of arctic fox dens. A treatment program was initiated in May 2013 by putting out bait injected with Dectomax every third week during three months at all inhabited den sites. In July 2013, no arctic foxes with symptoms of sarcoptic mange were observed, but in December 2013, new observations of arctic foxes with clear symptoms of mange initiated a second period of treatment. Sarcoptic mange was documented yet again in 2017, 2019, 2020 and 2021. This triggered a rapid response with medical treatment that held the spread at bay. Little is however known about the long-term effects of these repeated outbreaks. For instance, there are indices of demographic consequences in response to the outbreaks, e.g. reduced reproduction and population growth rate. The aim of this paper was to explore the demographic consequences of sarcoptic mange outbreaks in an endangered arctic fox population. We specifically focus on the dynamics of transmission, reproductive output and population development using a long-term data set obtained through field monitoring and wildlife cameras placed at active den sites. Furthermore, we also describe the treatment process and discuss the conservation implications.

Material and methods

Study population

The sarcoptic mange epizootic occurred in the Swedish subpopulation Borgafjäll (65°2′00″N, 14°20′00″E) located at the border between Jämtland and Västerbotten counties in Sweden (Fig. 1a). The area consists of 1676 km^2 sub-Arctic tundra and is surrounded by valleys with boreal forest. The arctic fox population in Borgafjäll has been under conservation actions since 2001, including supplementary feeding and red fox culling (Angerbjörn et al. 2013). Feeding stations containing commercial dog pellets are placed in close connection to active den sites. Since the conservation actions started, the number of litters has increased two-fold from early in the century until today (Wallén et al. 2023).

Disease appearance and diagnosis

The first suspected case of sarcoptic mange was observed the 14 April 2013. This individual was euthanized and sent to the Swedish Veterinary Institute (SVA) for autopsy which confirmed the diagnosis of sarcoptic mange (U130513-0007). In December 2013, a mountain rescue group reported a suspected case of sarcoptic mange that was observed at an old hut. Due to severe weather conditions, field work could not be initiated directly but new cases of sarcoptic mange was confirmed in January 2014. In January, two weeks of trapping was conducted in order to collect blood samples and monitor symptoms of infected individuals. In total, six individuals were captured and sampled. Blood samples were collected on Nobuto blood sampling paper and was analysed by SVA using sarcoptic ELISA test. Two of six adults that were captured in January 2014 were seropositive to *S. scabiei*. One of the seropositives had clear symptoms of sarcoptic mange while the second individual was considered as symptom free. In July 2014, eight juveniles and three adults were sampled at five different den sites, all were zero negative.

Field monitoring

The population has been monitored yearly since 2004 (Fig. 2). In July, data on the number of reproductions and litter size was collected through direct observations by visiting active den sites (2004–2012), through both direct observations and wildlife cameras (2013–2015) and through wildlife cameras (2016–2021). In addition to this, information about active dens is collected by rangers at county administrative boards throughout the year. To detect symptoms of sarcoptic mange,

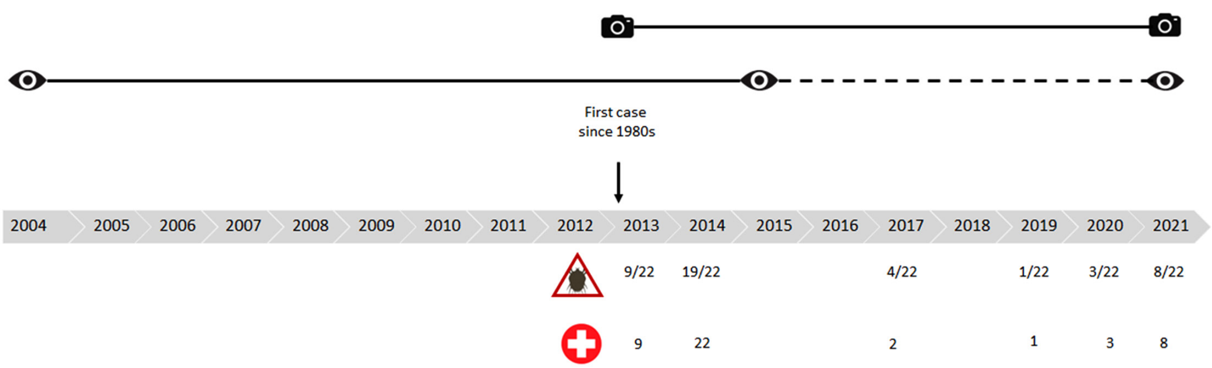

Figure 2.Timeline showing the monitoring regime, number of infected den sites (triangle) and number of dens obtaining medical treatment (cross). For monitoring approach, [eye symbol] represents visual observations and [camera symbol] wildlife cameras. Solid lines show intensive monitoring and dashed lines less intensive monitoring.

arctic foxes at inhabited active den sites were visually examined on distance using binoculars to detect symptoms of sarcoptic mange (Fig. 1b). We also used wildlife cameras to record individuals with symptoms of sarcoptic mange (Fig. 1b).

Litter size was assessed by visiting dens and by counting the number of cubs visually observed. All dens were visited at least once during July, i.e. the time when cubs usually emerge up on the dens and were monitored for 12–24 h. No movement between dens was observed during the study period. During 2016–2021, litter size was primarily estimated using wildlife cameras placed on dens. Two cameras were placed to cover the den and the maximum number of cubs observed at the same time was counted. Cameras were usually active between late June and late August.

Small rodent abundance on the Swedish tundra is monitored through systematic snap trapping in July. The classification into 'low', 'increasing', and 'peak' phases is based on the direction of change and follows Meijer et al. (2013).

Wildlife cameras

During 2013–2014, we identified arctic foxes with severe symptoms of sarcoptic mange using wildlife cameras on all den sites (n = 22) (Fig. 1b). The cameras were set to be triggered by motion and took three photos every third minute when triggered. The photos were analysed for red or arctic foxes with or without symptoms of sarcoptic mange that was used as a measurement of activity of infected arctic foxes. All photos were then classified into 'visits' in order to be able to compare the occurrence of infected individuals independent of the duration of the visit. A 'visit' was considered as unique if no photos with animals had been triggered during the last 20 min. By this, an individual that spent 6 h in front of the camera contributed to only one visit, despite several hundreds of photos. Cameras were active during three periods; May–June 2013, September–November 2013 and February–April 2014. Due to logistical restrictions and harsh climate, the cameras were not always active for the same number of days, mainly dependent on the snow conditions. The minimum number of working days for a camera during one period were 20.

During fur moulting in May, we could estimate the minimum number of individuals by fur characters and thereby determine the number of individuals at specific den sites. In July, no individual identification was possible due lack of individual markers in the fur.

During 2016–2021, the population was monitored by the county board administration through wildlife cameras. This recorded arctic fox activity, reproduction, litter size and arctic and red foxes with visual signs of sarcoptic mange. However, data on the detailed dynamics of transmission across den sites were not recorded during this period.

Medical treatment

The medical treatment was designed by veterinarians, inspired by the oral bait vaccine approach used on African wild dogs (Knobel et al. 2002). Since capture and direct treatment was infeasible, we provided a non-invasive treatment through meat or sausage injected with Dectomax or Nexgard with the active substance Doramectin or Afoxolaner. A minimum of five pieces were put out on each den site, hidden in the entrances or feeding stations. The provided dose was determined to avoid the risk of a single individual overdosing. The pieces were hidden in order to avoid consumption by birds. Feeding stations are designed to prevent entrance by other species (e.g. red fox, wolverine) and the risk of being consumed by non-target species is thus minimal. The treatment was initiated immediately after diagnosis of sarcoptic mange (Fig. 2) and was repeated at the infected inhabited den sites every two to three weeks until no signs of mange was recorded, with treatment cycles ranging from one to six times. All treatments were conducted by the county board administration in Västerbotten and Jämtland. Dens or feeding stations that received medication were monitored through wildlife cameras and directly by field personnel. In 2023, individuals were identified based on ear-tags and fur characteristics at dens where medicine was provided, in order to assess the treatment's effectiveness.

Statistical analysis

We tested for difference in the proportion of arctic foxes with sarcoptic mange observed at visits between years using a general linear model (GLM). The relationship between geographic distance from the core area (i.e. the area where mange was first detected) was correlated to the proportion of visits from arctic foxes with clear symptoms of sarcoptic mange.

We also recorded the number of litters over the study period, divided into before and after the first mange appearance (2013). We accounted for prey abundance by including small rodent phases (classified as 'low', 'increase' and 'peak'). We tested the association between the probability that a den was producing a litter in relation to the mange period (before versus after) and the rodent phase (classified as 'low', 'increase' and 'peak') in a log-linear analysis. To obtain a robust sample, we only included dens with at least three or more reproductions and with at least 10 of 19 years of inventories. In order to decrease the sensitivity to rodent abundance, we illustrated reproduction in a three-year moving average. We compared these data with a neighbouring subpopulation, Helags (data from Wallén et al. 2023). These two subpopulations were of similar size before the appearance of mange. They are also comparable in terms of area and conservation actions (Angerbjörn et al 2013).

To investigate if the litter size changed in response to sarcoptic mange outbreaks, we used linear mixed models (LMM) fitted with maximum likelihoods, using litter size as response variable and period (before versus after) as a binary fixed effect explanatory variable. We accounted for prey abundance by including small rodent phase (classified as 'low', 'increase' and 'peak') as a fixed effect explanatory variable. Den site was included as a random variable. Further, we also tested for a difference in litter size between years with documented sarcoptic mange (2013–2014, 2017, 2019–2021) and years with no records of mange (2015–2016, 2018) within the later time period (2013–2021). For this, we used the same approach as above, but used years with and without documented sarcoptic mange as a binary fixed effect explanatory variable.

Results

Transmission

In April–June 2013, arctic foxes with sarcoptic mange symptoms were observed at 9 out of 22 den sites (41%). The infected individuals were primarily observed in the central area (Fig. 3a). No individuals with symptoms of sarcoptic mange were observed during the summer field monitoring period (July–August 2013) and only one individual with symptoms was observed during September–November 2013. In February–March 2014, arctic foxes with sarcoptic mange had expanded towards both east and west, and were observed at 19 out of 22 den sites (86%). No individuals with symptoms of sarcoptic mange were observed during the summer field monitoring period (July–August 2014). There was a similar geographic distribution of den sites with infected individuals between 2013 and 2014 (Fig. 2–3), indicating the continued presence of the infection in the population after the first medical treatment. In 2014, an additional 10 den sites were found to be inhabited by infected individuals. These additional den sites were the closest ones to the outbreak epicentre in 2013. The den sites without infected arctic foxes were all located at a relatively isolated distance from the other den sites, with more than 15 km separating them from the nearest infected den site.

At den sites with arctic foxes exhibiting symptoms of sarcoptic mange in May–June 2013, 17% (CI ± 3%) of the den visits were from arctic foxes with visible symptoms of sarcoptic mange (Fig. 3a). At the den sites with infected individuals in 2013, the proportion of visits with infected individuals were higher in 2014 (March–April), 33% (CI ± 4%) ($p = 0.00021$, $F = 13.80$). Including all den sites with infected individuals in 2014, the average proportion of visits with infected individuals were 24% (CI ± 4%) (Fig. 3b).

In 2013, 13 of approximately 45 individuals (28.6%) were identified with symptoms of sarcoptic mange. During February–March 2014, 19 of approximately 60 individuals (31.6%) could be individually identified with symptoms. Further, the proportion of visits by individuals with severe symptoms decreased with distance from the core area, i.e., the area where sarcoptic mange was first diagnosed (Fig. 3; $F = 4.73$, $p = 0.038$). Based on individual identification, five individuals with sarcoptic mange were observed at more than one den site, indicating a high mobility between the den sites. The most active individual was observed at six den sites, with just more than 8 km between the den sites that are furthest apart (Fig. 3c).

Arctic foxes with symptoms of sarcoptic mange were recorded at one to eight den sites in 2017, 2019–2021 (Fig. 3c–d). In 2017, at least three individuals with symptoms of sarcoptic mange were recorded. For 2019–2021, data for individual identification were not available.

Effect of medical treatment

Medical treatment was provided to all dens with signs of mange; that is nine dens in 2013 and 22 dens in 2014.

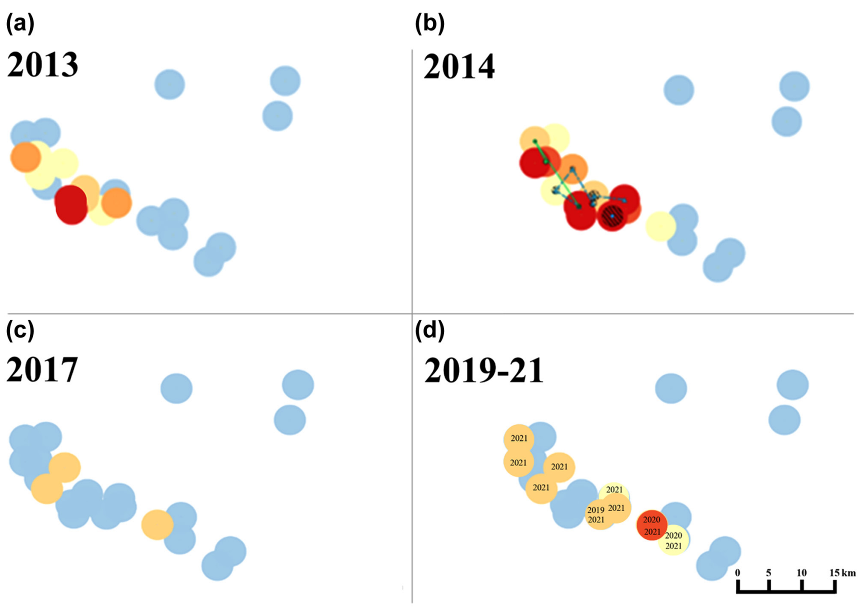

Figure 3. The expansion of den sites with visits of arctic foxes with visual symptoms of sarcoptic mange in (a) 2013, (b) 2014 (c) 2017 and (d) 2019–2021 where blue represents no visits, yellow 0–0.1, light orange 0.1–0.2, orange 0.2–0.3 and red 0.4–1. Arrows in (b) show the movement of the most active infected individual observed at six different den sites (super-spreader). Numbers in (d) show which year sarcoptic mange has been documented at a specific den site.

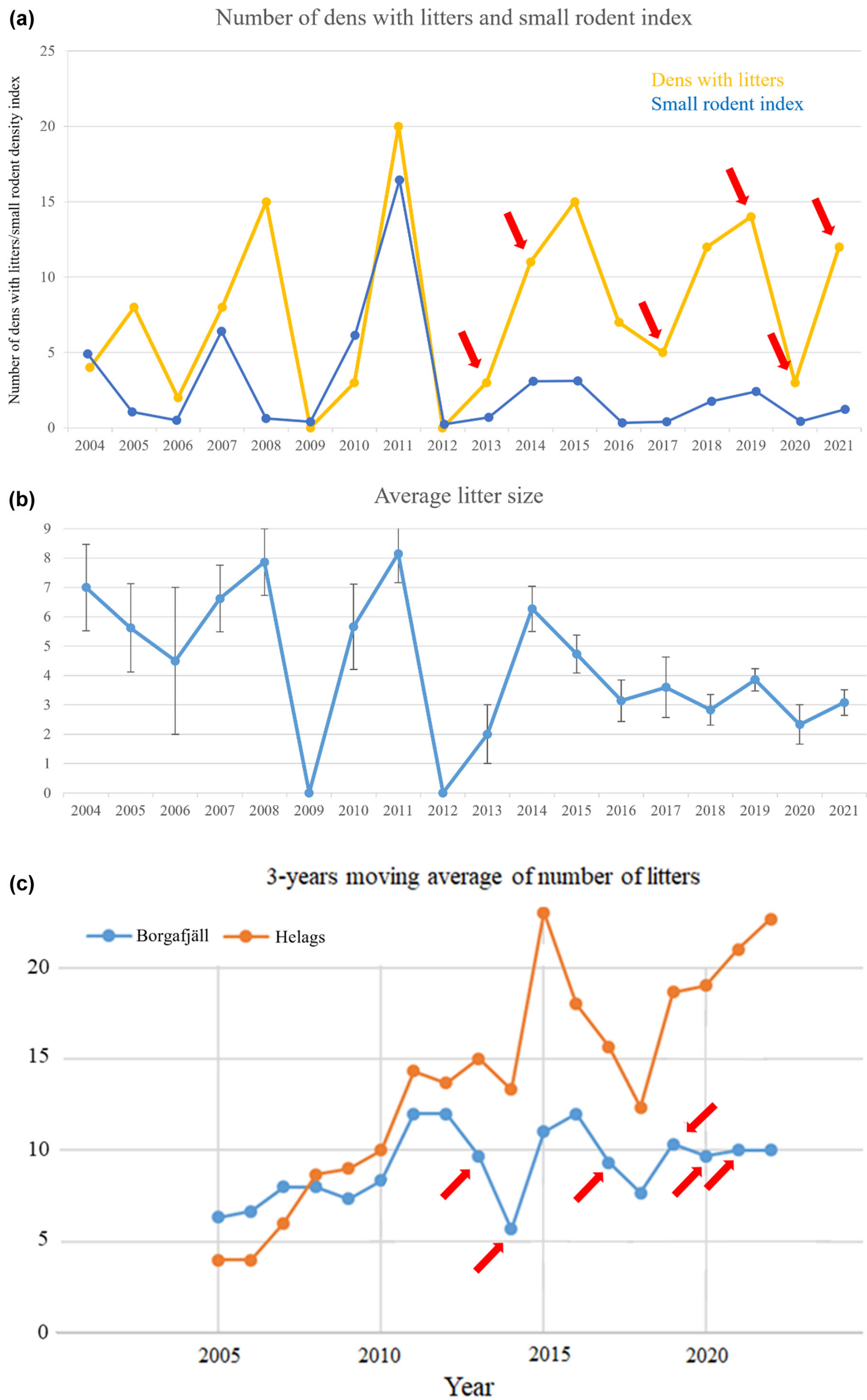

Figure 4. (a) Population development illustrated by number of litters per year and small rodent index (Ecke and Hörnfeldt 2023) (b) Average litter size, and (c) Number of litters in a 3-year moving average in the subpopulation with mange (Borgafjäll) compared to a subpopulation with no mange (Helags). Arrows indicate years with mange infestation.

Stationary individuals could be followed over time and the symptoms seemed to halt when the treatment was initiated. After moulting (May–June) no symptoms could be observed in the infected individuals. Regarding the treatment's effectiveness, our observations yielded promising results: In 2013, when individual identification was possible, three out of five identified infected foxes recovered from sarcoptic mange. Additionally, 50% of den sites documented with mange during spring successfully produced litters, constituting half of the total number of litters. Notably, no signs of sarcoptic mange were observed among visually inspected cubs during ear-tagging. One individual who was found dead in August 2013 did not have clear symptoms of sarcoptic infection but adult mites of *S. scabiei* were found on the animal during autopsy (SVA U130822-0314).

During 2017, 2019, 2020 and 2021, between one and eight den sites were provided with treatment. Through follow-up via wildlife cameras, no arctic foxes with symptoms of sarcoptic mange were observed six weeks after medication.

Effects on reproduction

The demographic consequences of sarcoptic mange outbreaks were explored on the number of produced litters over time (Fig. 4a), and average litter size (Fig. 4b). The number of litters was strongly related to the abundance of small rodents ($\chi^2 = 63.4$, df $= 1$, $p < 0.001$; Table 1, Fig 4a) but also showed a significant difference between the years before the first mange (2013) and the period after ($\chi^2 = 4.27$, df $= 1$, $p = 0.039$). The three-year moving average of the number of litters suggests that the number of litters are plateauing compared to the earlier period (Fig. 4c).

The yearly litter size varied considerably between years, related to the small rodent abundance (Fig. 4c). Litter size however showed a significant difference from an average of 7.2 (SE $= 0.49$) cubs before the first documented outbreak (2004–2012) to 3.9 (SE $= 0.25$) cubs after the first documented outbreak (2013–2021) (LMM: $\chi^2 = 30.7$, $p < 0.001$, df $= 1$, Table 2). Also, there was a trend towards an effect of small rodent phase on litter size (LMM: $\chi^2 = 5.02$, $p = 0.081$, df $= 2$, Table 2). However, we did not document a difference in litter size between years with documented sarcoptic mange (2013–2014, 2017, 2019–2021) and years without mange (2015–2016, 2018) (LMM: $\chi^2 = 0.0185$, $p = 0.89$, df $= 1$). During this time period, however, we found a trend towards an effect of small rodent phase on litter size (LMM: $\chi^2 = 5.604$, $p = 0.061$, df $= 2$, Table 2).

Table 1. Probability of a den having a litter (breeding) in a subset of 15 dens, where all dens had a minimum of ten years of inventories and at least four litters during this 19-year period divided into before versus after the first appearance of mange 2013. The data were analysed in a log-linear analysis.

Effect	df	χ^2	p-value
Breeding vs rodent phase	2	63.42	0
Breeding vs before or after mange	1	4.27	0.039
Rodent phase vs before or after mange	2	12.25	0.002

Discussion

The aim of this paper was to assess the transmission and demographic consequences of repeated sarcoptic mange outbreaks in an arctic fox subpopulation. This case study has shown that it is possible to implement non-invasive treatment to promote individual recovery as well as to prevent further transmission. It is likely that without treatment, the infection would have had a considerably larger impact on the population. Previous outbreaks of mange in other fox populations have decreased the population size drastically. In Bristol, 95% of the red foxes died from sarcoptic mange, and in Sweden around 50% (Mörner 1992, Soulsbury et al. 2007). In the San Joaquin kit fox, a population decline estimated to 50% in response to sarcoptic mange was recorded. (Cypher et al. 2017, Foley et al. 2023). Based on this, we conclude that without treatment, the small arctic fox population in Borgafjäll would probably have decreased to critically low levels. However, to accurately quantify the impact of the treatment, an experimental comparison with an infected but untreated population would have been ideal. Unfortunately, due to the conservation status of the study population, such a comparison was neither possible nor desirable. Alternatively, a simulation could have been conducted, but it would be beyond the scope of this paper.

The persistence and strategy for treatment should however be reflected upon. The treatment of sarcoptic mange differs from precautionary vaccination against e.g. rabies or canine distemper virus since it is a treatment of already infected individuals that can be re-infected after the treatment. Further, medication of sarcoptic mange is generally only targeting adult mites, nymphs and larvae, while the eggs in the epidermis can continue to develop. How long Doramectin or Ivermectin, the most common active substances used for treatment of sarcoptic mange, are active in arctic foxes or other canid species is unclear. In commercial swine, Doramectin has been found to be effective for a minimum of 12 days after treatment, inflicting that one treatment would be enough (Arends et al. 1999). The treatment in Borgafjäll was repeated every 2–3 weeks depending on the weather conditions. This timespan might have been too long, since eggs can develop and become adults in 12 days if the conditions are favourable. Further, since the medication was distributed non-invasively, individuals can have missed occasions of treatment which further expands the time for the eggs to develop into adults. Moreover, the finding of an infected female without clear symptoms suggests that infected individuals might go unnoticed.

To understand the dynamics of pathogen outbreaks, the mechanism for transmission is a key factor. Our data suggest that the spread of the sarcoptic infection occurs by individuals visiting several den sites. All the den sites with individuals showing symptoms were located within five km from each other, compared to an average home range of 25 km^2 (Angerbjörn et al. 1997). Several individuals were caught on wildlife cameras at multiple den sites, and one infected individual was observed at six different den sites. This individual

Table 2. The relationship between litter size and i) period and small rodent phase, and ii) sarcoptic mange occurrence and small rodent phase. Data was analysed through linear mixed models (LMM).

Model	df	χ^2	p-value
Litter size ~ Period + Rodent phase + 1/Den site			
Litter size vs period	1	30.7	< 0.001
Litter size vs small rodent phase	2	5.02	0.081
Litter size ~ Sarcoptic mange occurrence + Rodent phase + 1/Den site			
Litter size vs sarcoptic mange occurrence	1	0.0185	0.89
Litter size vs small rodent phase	2	5.604	0.061

can be considered as a potential 'super spreader' and illustrates how a single individual can have a large impact on the transmission within the population by functioning as a vector. With super spreaders, movements between den sites will enable the infection to spread easily between den sites and individuals, even if population density is low. This suggests that the transmission within the arctic fox population is not necessarily density dependent, which is supported by similar findings of sarcoptic mange transmission in the red fox (Devenish-Nelson et al. 2014). The repeated occurrence of sarcoptic mange in this population shows many similarities to the long-term occurrence (2013–2020) of sarcoptic mange in the San Joaquin kit fox population (Foley et al. 2023). In that system, the role of direct and indirect den transmission was highlighted as an important factor that could increase the likelihood of sarcoptic mange spreading and persisting in a population (Montecino-Latorre et al. 2019). Another aspect that needs to be considered to understand the transmission dynamics is the role of supplementary feeding stations contributing to transmission. Supplementary feeding stations can attract both infected and uninfected animals, increasing the likelihood of direct and indirect contact between individuals and thus facilitating the spread of sarcoptic mange. We have observed that closing feeding stations during outbreaks can lead to increased movement of arctic foxes. Typically, arctic foxes tend to remain close to their dens, particularly when food is available nearby. A deeper understanding of how feeding stations may facilitate infections is necessary to fully comprehend the transmission dynamics of sarcoptic mange among arctic foxes. This has been highlighted as an important factor in transmission of sarcoptic mange in raccoon dogs (Süed et al. 2014) and should be evaluated also for the arctic fox. Furthermore, studies are needed to quantify the frequency of infected red foxes in the area and to identify any potential alternative vectors. Despite this, we remain confident in our assumption that red foxes are the main vector responsible for the reoccurring introductions of the parasite into the arctic fox population. This is based on wildlife camera photos of infected red foxes near arctic fox dens as well as culled infected red foxes in the study area.

We found evidence for the repeated sarcoptic mange outbreaks causing sub-lethal, demographic consequences in the population, manifested as decreased reproduction. Based on a long-term data set, we demonstrate that the production of litters has plateaued following the emergence of sarcoptic mange in the population (Fig. 4). Furthermore, the average litter size declined after the appearance of sarcoptic mange in the population. Taken together, this suggests that as a consequence of the reappearing sarcoptic mange, the population growth levelled out and smaller litters were produced, which will hamper the chances for the population to reach a viable population size. There was no difference in average litter size after sarcoptic mange had appeared in the population. This indicates that the demographic effects of sarcoptic mange will persist over multiple years, as evidenced by the levelling out of litter production. Furthermore, arctic fox reproduction is strongly connected to the small rodent dynamics, which is apparent also under a disease outbreak.

Conclusions

Outbreaks of diseases and parasites constitute a severe threat to small and fragmented populations. Sarcoptic mange is expected to increase under climate change, especially when multiple host species overlap. We showed that the sarcoptic mange is transmitted between dens by infected arctic foxes visiting multiple dens and we found that around 30% of the population was infected when transmission rates were highest. Non-invasive treatment strategies were successful in terms of individual recovery and preventing further transmission. However, the reappearance of sarcoptic mange may suggest that the effect of treatment was short-term and that the infection remains in the population, or that individuals become reinfected by e.g. red foxes. We also showed reduced reproduction, which confirms that sarcoptic mange can bring both lethal and sub-lethal consequences to a small population over multiple years. Given records of high mortality rates in closely related species and sub-lethal effects in this population, we conclude that outbreaks of sarcoptic mange should be regarded a serious threat to population recovery and the future persistence of the endangered Scandinavian arctic fox.

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Author contributions

Johan Wallén: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal). **Rasmus Erlandsson**: Investigation (supporting); Visualization (equal); Writing – review and editing (supporting). **Malin Larm**: Data curation (equal); Investigation (equal); Visualization (supporting); Writing – review and editing (supporting). **Tomas Meijer**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (supporting). **Karin Norén**: Conceptualization (equal); Formal analysis (equal); Funding acquisition (lead); Writing – original draft (equal); Writing – review and editing (equal). **Anders Angerbjörn**: Conceptualization (equal); Formal analysis (equal); Funding acquisition (lead); Visualization (equal); Writing – original draft (equal).

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