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Carnivore conservation in practice: replicated management actions on a large spatial scale

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Summary

1. More than a quarter of the world's carnivores are threatened, often due to multiple and complex causes. Considerable research efforts are devoted to resolving the mechanisms behind these threats in order to provide a basis for relevant conservation actions. However, even when the underlying mechanisms are known, specific actions aimed at direct support for carnivores are difficult to implement and evaluate at efficient spatial and temporal scales.

2. We report on a 30-year inventory of the critically endangered Fennoscandian arctic fox *Vulpes lagopus* L., including yearly surveys of 600 fox dens covering 21 000 km^2. These surveys showed that the population was close to extinction in 2000, with 40–60 adult animals left. However, the population subsequently showed a fourfold increase in size.

3. During this time period, conservation actions through supplementary feeding and predator removal were implemented in several regions across Scandinavia, encompassing 79% of the area. To evaluate these actions, we examined the effect of supplemental winter feeding and red fox control applied at different intensities in 10 regions. A path analysis indicated that 47% of the explained variation in population productivity could be attributed to lemming abundance, whereas winter feeding had a 29% effect and red fox control a 20% effect.

4. This confirms that arctic foxes are highly dependent on lemming population fluctuations but also shows that red foxes severely impact the viability of arctic foxes. This study also highlights the importance of implementing conservation actions on extensive spatial and temporal scales, with geographically dispersed actions to scientifically evaluate the effects. We note that population recovery was only seen in regions with a high intensity of management actions.

5. *Synthesis and applications.* The present study demonstrates that carnivore population declines may be reversed through extensive actions that target specific threats. Fennoscandian arctic fox is still endangered, due to low population connectivity and expected climate impacts on the distribution and dynamics of lemmings and red foxes. Climate warming is expected to contribute to both more irregular lemming dynamics and red fox appearance in tundra areas; however, the effects of climate change can be mitigated through intensive management actions such as supplemental feeding and red fox control.

Key-words: Alopex, arctic, climate, extinction, population cycles, restoration, SEFALO, Vulpes

Introduction

During the last centuries, several species have suffered severe population declines with increased risk of extinction.

According to the IUCN Red List, 27% of the world's carnivores are threatened (IUCN 2012). Considerable research efforts are devoted to resolve the mechanisms behind these threats to provide relevant conservation actions. However, even when the underlying mechanisms are known, specific actions aimed at direct support for carnivores are difficult

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to evaluate and implement at efficient spatial and temporal scales. For example, it is unclear to what extent management actions have resulted in recovery of the Iberian lynx *Lynx pardinus* (Palomares *et al.* 2011; Simon *et al.* 2012), and evaluation of red fox *Vulpes vulpes* baiting in Australia indicated no effect on abundance of the targeted prey species (Walsh *et al.* 2012). Moreover, wild dogs *Lycaon pictus* in Kenya have recovered (Woodroffe 2011), but the underlying mechanism is unclear. The spatial and temporal scales of these studies illustrate the problems of conducting and scientifically evaluating conservation actions. We provide an example where long-term sustained conservation actions were tested scientifically and also resulted in significant growth of the threatened population.

Climate change is an important factor driving population declines, and interactions with other factors may further increase extinction risks (Brook, Sodhi & Bradshaw 2008). It is thus unclear to what extent forecasted changes in climate will increase threats against populations and species, although models predict high extinction rates (Thomas *et al.* 2004). Climate-induced changes are considered to be greater in the Arctic biome compared to temperate and tropical biomes. Arctic species are highly adapted to Arctic conditions, and climate-induced changes, such as invasion of boreal species from the south, can have profound effects on species' ecology and evolution (Post *et al.* 2009; Callaghan *et al.* 2011) with cascading consequences on both herbivores and predators (Ims & Fuglei 2005).

The Fennoscandian mountain tundra is a unique ecoregion from a global perspective (Brooks *et al.* 2006). It is shaped by a combination of high altitude and latitude with considerable fragmentation by forested valleys (Herfindal *et al.* 2010). Climate change is expected to alter the Fennoscandian mountain tundra through decreased snow cover and increased primary productivity (Ims & Fuglei 2005), which would decrease the extent of tree-less tundra and further increase the degree of fragmentation.

The arctic fox *Vulpes* syn. *Alopex lagopus* belongs to this environmentally unique ecoregion. The arctic fox in Fennoscandia is specialized on small rodents (voles and lemmings; Elmhagen, Tannerfeldt & Angerbjörn 2002), and its population dynamics are intimately connected to the 3- to 5-year rodent population cycles (Angerbjörn *et al.* 1995; Henden *et al.* 2009). Arctic fox reproduce almost exclusively in the increase and peak phase of the rodent cycle (Tannerfeldt & Angerbjörn 1998). In parallel with climate change, the amplitude and regularity of these cycles have diminished (Loison, Strand & Linnell 2001; Ims, Henden & Killengreen 2008; Elmhagen *et al.* 2011), with severe impacts on the viability of the Fennoscandian arctic fox population (Ims & Fuglei 2005; Henden *et al.* 2009). Furthermore, the larger red fox is favoured by climate warming. During the last century, it has increased its range above the tree line where it competes with the arctic fox for resources (Hersteinsson & Macdonald 1992; Tannerfeldt, Elmhagen & Angerbjörn 2002) and by direct inter-

specific interactions, including intraguild predation (Frafjord, Becker & Angerbjörn 1989; Pamperin, Follmann & Petersen 2006). Arctic and red foxes have similar fundamental food niches (Frafjord 2000), but the red fox can exclude the arctic fox from the most productive den sites with higher availability of alternative prey at low rodent densities (Elmhagen, Tannerfeldt & Angerbjörn 2002) as well as monopolizing carrion resources in the winter (Killengreen *et al.* 2012). In Finland, red fox establishment on the mountain tundra coincided with a rapid decline of the arctic fox population (Fig. 2a; Kaikusalo, Mela & Henttonen 2000), and a similar trend has been recorded in the Swedish population (Tannerfeldt, Elmhagen & Angerbjörn 2002). However, these recent shifts in the relative abundance of the two fox species in the mountain tundra have coincided with the dampening of rodent cycles (Ims, Henden & Killengreen 2008). Therefore, such time trends alone cannot be used to disentangle the relative importance of competition and changes in prey dynamics for the demography of arctic fox populations.

In 2009, IUCN classified the arctic fox as one of 10 flagship species for climate change as a future population decline is expected due to shrinking Arctic habitats, red fox expansion and fading rodent cycles (IUCN 2009). Although still an abundant species in most of its distribution range, the arctic fox is critically endangered in Fennoscandia and considered a priority species according to the EC Habitat directive. In the mid-19th century, the arctic fox was common in Fennoscandia (Hersteinsson *et al.* 1989), but a profitable trade with arctic fox fur in the end of the 19th century led to intense human hunting pressure and the population drastically declined to only a few hundred individuals (Zetterberg 1945). The arctic fox was therefore protected by law in 1928 in Sweden, 1930 in Norway and 1940 in Finland. Despite this, the population size remained low, and the situation deteriorated further during the 1980s and 1990s (Angerbjörn *et al.* 1995). According to recent genetic analyses, the Fennoscandian arctic fox is today fragmented into four isolated subpopulations with little or no gene flow between them (Dalén *et al.* 2006). There are 10–50 individuals in each subpopulation, and the risk of negative effects related to the low population size is substantial (Dalén *et al.* 2006). Genetic and demographic effects connected to population smallness have been dealt within previous papers, and we will here focus on ecological factors likely to have prevented population recovery despite 80 years of protection. Several interacting factors may have been involved, but low abundance of rodent prey in combination with interspecific interactions with red foxes are considered to be the most prominent causal factors (Hersteinsson *et al.* 1989).

Since 1999, large-scale conservation actions have been implemented in several regions of the Fennoscandian mountain tundra with the goal to mitigate the threats of red fox increase and food resource decline (in terms of rodents). The actions comprised red fox culling and supplementary feeding of arctic foxes, partly performed within

the conservation project Save the Endangered Fennoscandian Alopex (SEFALO). In this study, we combine and analyse long-term data sets on arctic fox population dynamics and conservation actions from all three Fennoscandian countries, Norway, Sweden and Finland. Our analysis aimed to assess the allocation of management actions and their effects on the arctic fox populations. We were particularly interested to test how the two types of management actions worked in conjunction with the expected key driver of arctic fox population dynamics – the phases of the small rodent cycle (Fig. 3a). For this purpose, we employ a statistical approach that allowed us, based on large-scale and long-term monitoring data, to quantify simultaneously the relative effects supplementary feeding, red fox control and rodent population phases. This study was conducted at a currently retracting edge of the arctic fox global distribution. In a broader perspective, we believe that inferences from our study can provide general insights into species with similar problems.

Materials and methods

FIELD SURVEYS

To investigate the dynamics of the breeding arctic fox population, we used two different data sets. First, to describe the long-term dynamics based on systematic field surveys of arctic fox in Fennoscandia on a national level, we used national long-term data sets with yearly number of litters from 1982 to 2011 (Table 1, Fig. 2). Secondly, to estimate effects of management actions in conjunction with the rodent cycle phases, we used regional data sets from 10 of 13 geographical regions surveyed from 2000 to 2011 (Table 1). The three excluded regions were in Finland where arctic foxes were functionally extinct during the study period, but surveys were carried out to monitor potential reestablishment. The number of arctic fox litters was based on summer inventories of known arctic fox dens during July and August. These are all established field methods used for 40 years (e.g. Angerbjörn *et al.* 1995; Kaikusalo & Angerbjörn 1995; Herfindal *et al.* 2010). Dens were screened for signs of fox activity (e.g. faeces, runways in the grass,

smell). For the regional data set, we observed active dens for *c.* 24 h or until arctic fox cubs were observed, to define the breeding status. In Finland, visual observations were complemented with DNA analysis of scats (following Dalén *et al.* 2006) in order to evaluate the presence of arctic foxes even though no litters were found. In some regions, we also surveyed active den sites in late winter where a den was considered active if it had open entrances in the snow and if the fox species could be identified by visual observation, remote cameras, tracks or DNA analysis of faeces.

Small rodents were systematically snap-trapped each summer in five regions (Henttonen & Kaikusalo 1993; Framstad 2011; Ims, Yoccoz & Killengreen 2011). In an additional four regions, snap-trapping was carried out in some summers. For years and regions where trapping was not carried out, we approximated the rodent phase from nearest trapping region (always <200 km away), that is, close enough to assume similarity given the scale of synchrony of Fennoscandian rodent cycles (Henden *et al.* 2009; Elmhagen *et al.* 2011). We used the between-summers pattern of changes in the number of rodents trapped per 100 trap-nights (trap-index) to classify rodent abundance in each region into four phases. (1) low phase (following a peak or decline, trap-index: 0.07 ± 0.17, $N = 21$); (2) increase phase (increasing rodent density between low and peak phase, trap-index: 2.03 ± 1.28, $N = 7$); (3) peak phase (highest abundance of small rodents, trap-index 8.07 ± 8.36, $N = 24$); and (4) decline phase (drastic decline after a peak or increase, trap-index: 0.40 ± 0.48, $N = 15$). We used this classification in the analyses rather than raw data on lemming abundance because differences in trapping design did not allow for direct quantitative comparisons. In the 2000s, the small rodent cycle was dominated by a 3-year period, where the low phase was followed by an increase phase (Hörnfeldt 2004; Elmhagen *et al.* 2011), that is, we had phases 1, 2 and 4. Note that the rodent cycle is somewhat different from the fox cycle, especially in the decline phase, because high food availability during winter causes many arctic foxes to reproduce although 90% of the cubs die of starvation during summer (Meijer *et al.* 2008).

MANAGEMENT ACTIONS

We focused our actions on red fox culling in winter and supplementary feeding of arctic foxes. In Finland, red fox appearance

Table 1. Description of study areas and management actions. Area is defined by the outline between the den sites, Known dens is number of primary arctic fox dens, Natal dens is number of dens used for reproduction at least once during the monitoring period

Region	Country	Area (km²)	Known dens	Natal dens 1980–2011	Average no. culled red foxes (range)	Start of actions	Average no. of fed dens (range)
Børgefjell NO	Norway	1139	30	17	No action	–	No action
Indre Troms	Norway	1320	25	6	No action	–	No action
Saltfjellet	Norway	1539	49	9	No action	–	1 (0–1)
Varanger	Norway	1675	33	6	92 (0–158)	2005	No action
Borgafjäll SE	Sweden	1676	45	25	19 (0–32)	2000	11 (3–22)
Helags	Sweden	1920	68	26	35 (0–86)	1999	13·5 (0–25)
Padjelanta	Sweden	1984	48	13	No action	–	No action
Rousto	Sweden	2448	49	10	3 (0–12)	Scattered	2 (0–9)
Sitas	Sweden	1680	23	6	1·5 (0–6)	Scattered	1 (0–6)
Vindelfjällen	Sweden	2205	115	33	7 (0–45)	Scattered	3 (0–10)
Käsivarsi	Finland	937	48		10 (0–36)	1999	No action
Pöyrisjärvi	Finland	630	16	1	38 (16–61)	1999	No action
Utsjoki	Finland	2050	57	2	82 (43–190)	1999	No action

on the mountain tundra coincided with a decreasing arctic fox population (Kaikusalo, Mela & Henttonen 2000; Fig. 2). Hence, red fox culling during winter at traditional arctic fox territories was initiated by local authorities in Finland and Sweden around 2000 (especially in Helags and Borgafjäll SE) and in the Varanger area in Norway 2005 (Fig. 1, Table 1). The cull was organized by rangers in local authorities (county board administrations in Sweden; Statskog Fjelltjenesten and Statens Naturoppsyn in Norway; Finnish Park and Forestry Service). They all had special permits from relevant national authorities (Swedish Environmental Protection Agency in Sweden, the Norwegian Directorate for Nature Management in Norway and Ministry of Environment in Finland). Culling was done with the utmost caution to reduce the stress for the hunted red foxes and to not disturb other wildlife.

Arctic foxes at inhabited dens were fed during winter with commercial dog food deposited in containers (50 kg Dogman Dinner; 21% protein, 10% fat, energy content 14 000 KJ kg^{-1}) or remains from reindeer slaughter. The intensity of feeding varied between regions with a high intensity in two Swedish regions (Helags and Borgafjäll SE) where food was available from December to May. In Finland and Varanger, intensive red fox culling took place but no supplemental feeding. In other Swedish areas (Vindelfjällen, Arjeplog, Sitas, Rousto), logistic problems caused actions to be conducted at low intensity (0–3 fed dens) and only in some years. No actions were performed in Børgefjell NO, Indre Troms and Padjelanta, and these areas are considered as control regions.
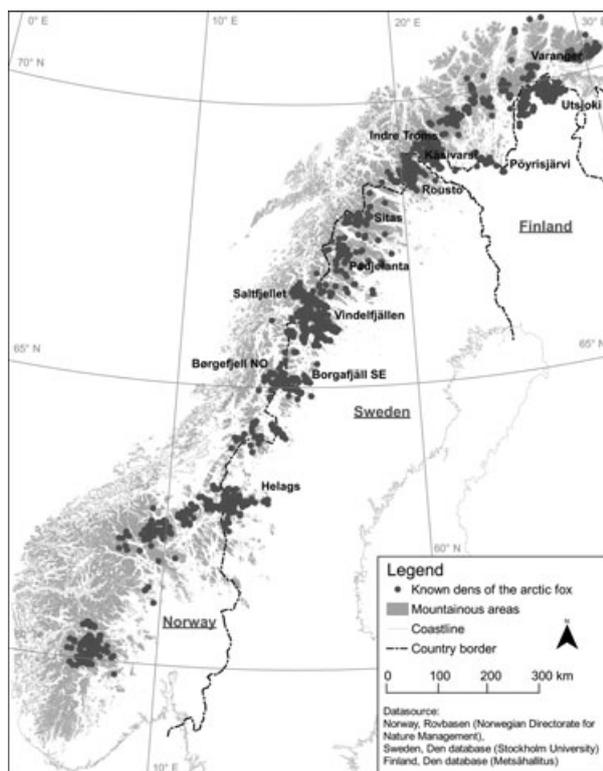

Fig. 1. Dark grey areas represent the known distribution of arctic fox dens in Fennoscandia, from Herfindal *et al.* 2010. Light grey shows the mountain tundra and thus historically suitable arctic fox habitat. Names refer to the 13 different regions, described in Table 1.

STATISTICAL ANALYSES

Statistical analyses are based on data from 10 regions in Sweden and Norway (Fig. 1) with extant arctic foxes in 2000–2011. We used structural equation modelling, specifically path analysis, to test the effect of conservation actions on arctic fox reproduction, while controlling for the effect of rodent availability by including rodent phase in the analysis. Structural equation models are based on *a priori* knowledge to evaluate complex hypotheses on how ecosystem components are related to each other, including sequential relationships between variables (Grace 2008). Our study system involved a number of potential sequential relationships. Rodent phase is closely related to the number of arctic fox litters born (Angerbjörn *et al.* 1995; Strand *et al.* 1999), but the effect could be indirect, that is, mediated by the number of arctic foxes establish in winter as indicated by the number of active dens (Angerbjörn *et al.* 1991). Rodent phase could also affect the extent of winter feeding if high rodent availability increases arctic fox establishment at non-fed dens and rangers respond by feeding also at these dens. It could also impact the number of red foxes culled, as rodent phase can affect the number of red foxes that breed in the mountain tundra (Elmhagen *et al.* 2011).

Following Fox (2002), we first constructed a full model including all potential relationships between variables, based on the *a priori* knowledge above (Fig. 3). We then tested for causal relationships by using covariance matrices and their inverse, the concentration matrices (Højsgaard, Edwards & Lauritzen 2012), that is, identifying significant pathways between the variables. We compared the full model to simpler models through stepwise backwards elimination of non-significant pathways. We accepted the model with the smallest Bayesian Information Criterion (BIC) as the best model. The models were fitted by maximum likelihood and models were rejected if their covariance structure differed from that of the data. The models were fitted in R with the sem library (Fox 2002). All variables but rodent phase were log-transformed as the sem library assumes linear relationships and normal distributions. We compared model selection with BIC to model selection with AICc, where the latter penalize less for model overfitting. The estimates and confidence intervals of important parameters were very similar, suggesting that the evaluation based on BIC was robust.

We tested two different full models. In the first (grand) study, we tested the relative effect of rodent phase, feeding and red fox culling on the number of arctic fox litters born in each area and year ($N = 115$). The data representing each variable in each area and year were (i) rodent phase (1–4), (ii) number of dens provided with supplementary food, (iii) number of red foxes culled in winter and (iv) number of arctic fox litters born. Rodent phase was an exogenous variable, that is, not affected by the other variables, while the actions and number of litters were endogenous variables, that is, assumed to be affected by other variables. In the second (seasonal) study, we included an additional endogenous variable representing (v) number of active arctic fox dens in winter in each area and year. The seasonal model used a subset of the data in the grand model ($N = 91$) and included only areas and years where winter surveys had been carried out. For all models, we also run the analysis with data on red fox culling and number of supplementary fed dens standardized by region area. Because regions were of similar size relative to the variation in action effort, standardization by area did not have significant impacts on the best models (number of pathways included and/or parameter estimates), and we therefore present the first analysis based on raw data.

Results

LONG-TERM POPULATION DEVELOPMENT

The overall fluctuations of the breeding population of Fennoscandian arctic foxes, as reflected by the 30-year data set on the number of litters (Fig. 2), demonstrate a strong short-term relationship to rodent cycles and some clear long-term trends. The arctic fox went through a severe decline in Fennoscandia at the end of the 20th century, and the entire population might have been as small as 40–60 animals. In Finland, the arctic fox had the last recorded breeding in 1996 (Fig. 2) but still have about 5–10 yearly sightings. In Sweden, the arctic fox was close to extinction around 1998–2000 (Fig. 2), but recovered thereafter. In Norway, there was a stable but very small population during the same period, mainly comprised of the subpopulation in Børgefjell NO (Figs 1 and 4). Based on the number of arctic foxes surviving the low phase in 2009 and reproducing in the peak year of 2011, we estimated the current minimum population size to 135 adult foxes in Sweden and 80 in Norway.

REGIONAL-SCALE EFFECT OF CONSERVATION ACTIONS

The regional population trends in 2000–2011 show that arctic foxes recovered in some regions, but not in others (Fig. 4). The recovery was partly related to the return of regular rodent cycles (Elmhagen *et al.* 2011) and partly to conservation actions. Path analyses (Fig. 3) showed that both supplementary feeding and red fox control had a positive impact on the number of arctic fox litters born. In the grand study, the best model explained 41·7% of the variation in the number of arctic fox litters, which was positively affected by feeding, red fox control and rodent phase. The intensity of actions, that is, the number of fed dens and red foxes culled, was independent of rodent phase (Fig. 3).

The best model with a seasonal perspective (i.e. including information about winter activity on dens) explained 56·7% of the variation in the number of arctic fox litters.
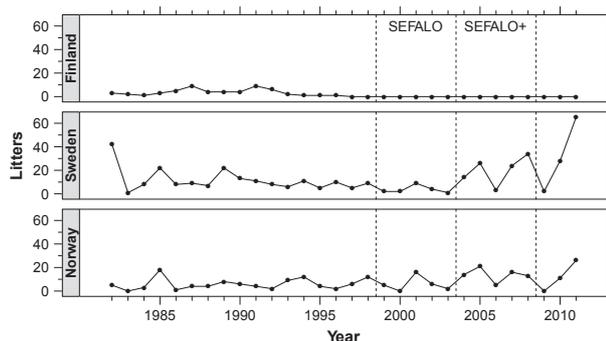

Fig. 2. The number of arctic fox litters in Sweden, Norway and Finland from 1982 to 2011. Note that the numbers for Norway do not include the southern population which is built up from captive breeding and release of arctic foxes, measures that were initiated in these areas from 2007 (Landa *et al.* 2011).

Feeding and red fox control increased the number of active arctic fox dens in winter, which in turn increased the number of litters. Rodent phase had a strong and positive direct impact on the number of litters and a weak indirect effect by increasing the number of active dens. As in the grand study, action intensity was independent of rodent phase (Fig. 3).

The results of the path analysis thus demonstrate statistically significant effects of red fox hunting, supplemental feeding and rodent abundance on the number of reproducing arctic foxes. Differences between arctic fox populations in regions with, on the one hand, low-intensity or no conservation actions and, on the other hand, high-intensity actions became particularly evident when considering the number of fox litters born in rodent pre-peak years (Fig. 4b). In these phases of the rodent cycle, most adult foxes should be breeding. In the regions Helags and Borgafjäll SE, where both food supplementation and red fox culling were intense, the number of arctic fox litters born in rodent increase years increased steeply during the study period and approximately doubled between each peak year of the 3-year rodent cycle (Fig. 4). In Varanger, where only red fox culling was implemented, the number of litters increased over the two 5-year rodent cycles represented in our data set (Fig. 4b). In contrast, there was no increase in the number of arctic foxes in the regions with little or no actions (Fig. 4b). Finland had no case of arctic fox reproduction and only a few single foxes were observed annually, despite intensive surveys and red fox culling.

To summarize, the programme was conducted over a large geographical scale with striking differences in ecological conditions, arctic fox population dynamics and management intensity, between regions. Despite this, we identified three major factors, viz. rodent dynamics, supplemental feeding and red fox culling, that influence the viability of the arctic fox population.

Discussion

Boreal species are increasing in abundance in Arctic areas, probably due to an ongoing change in climate (Callaghan *et al.* 2004). Moreover, some lemming populations in Arctic and subarctic areas display disrupted dynamics (Kausrud *et al.* 2008; Ims, Yoccoz & Killengreen 2011) with long periods without distinct high-amplitude peaks. The influx of boreal species, such as the red fox (Kaikusalo & Angerbjörn 1995), can be expected to be especially pronounced in Fennoscandia where the subarctic mountain tundra is fragmented by boreal valleys. Such phenomena can be generic for ecotones between biomes in eras of climate change. The simultaneous appearances of changes that include invasive species, disrupted food resource dynamics and loss of habitats are likely to have a strong impact on endemic biota. In case of the Arctic tundra, the fate of the arctic fox under impacts of increasing red fox and declining lemming populations has been particularly flagged (IUCN 2009). Although shrinking
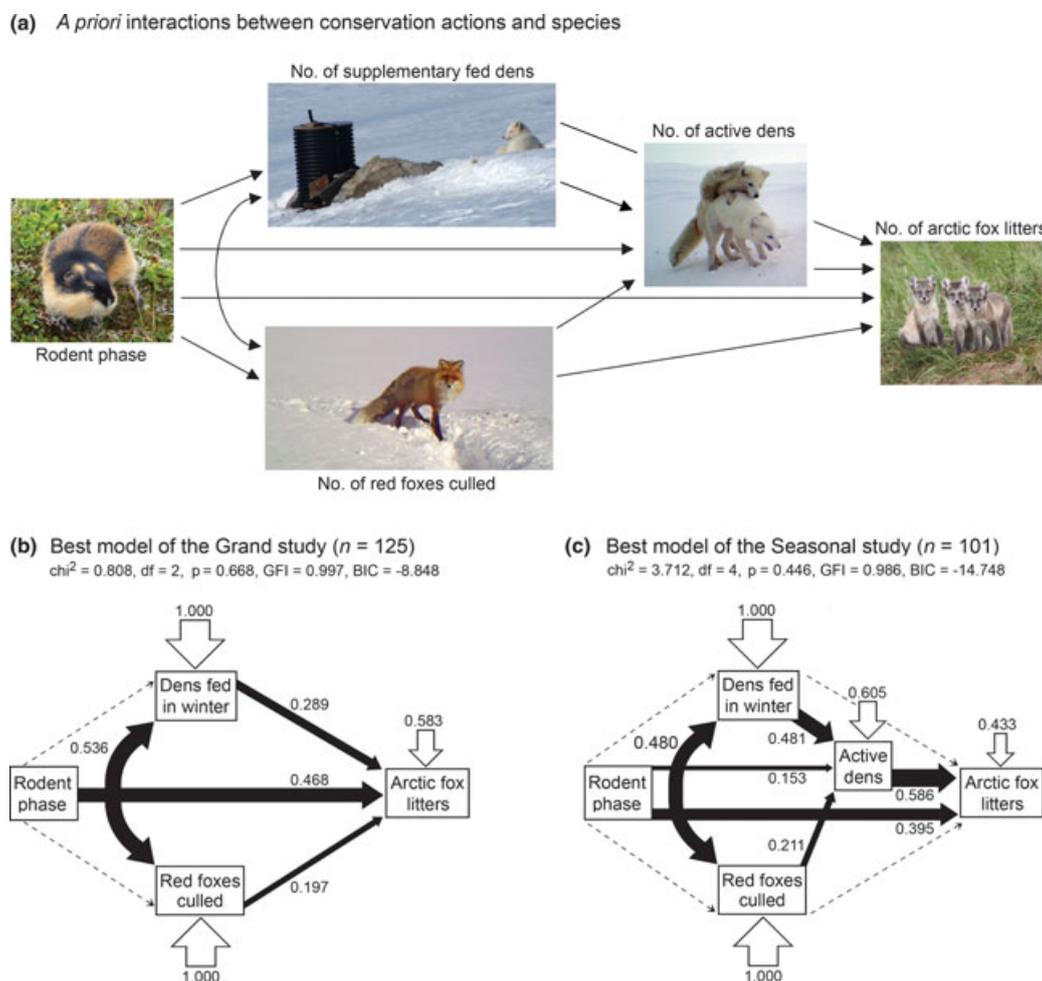
Fig. 3. *A priori* interactions between conservation actions and species (a) and best models for the (b) grand and (c) seasonal study. In both models, winter feeding and red fox control had a positive impact on the number of arctic fox litters born, but these impacts were completely mediated by a positive effect on the number of active dens in the seasonal study. Rodent phase had a positive impact on the number of litters in both models. Black single-pointed arrows indicate causal pathways and standardized path coefficients. Standardized path coefficients can be interpreted as correlation coefficients and partial correlation coefficients. For unstandardized estimates (regression coefficients, partial regression coefficients) and their details, see Appendix S1 (Supporting information). The black double-pointed arrows indicate unresolved correlation between actions. Outlined arrows indicate residual errors for response variables. Pathways included in the full model, but not retained in the best model, are indicated by dashed lines. GFI, Goodness-of-fit Index; BIC, Bayesian Information Criterion.

range of the arctic fox and the expanding range of red fox might be a circumpolar phenomenon (Hersteinsson and Macdonald 1992), the situation from Fennoscandia has been most illustrative (Hersteinsson *et al.* 1989) and the present paper's account on the long-term population development contributes substantially further to this. We can now summarize the Fennoscandian case as follows: the arctic fox in Fennoscandia was widespread with high abundance up to 100 years ago (Zetterberg 1945) but has since become extirpated in several parts of its previous distribution range and was close to extinction at the end of 20th century. In Finland, where the population declined rapidly in the 1990s, no litters have been born since 1996 and only single foxes are observed on an irregular basis, despite intensive red fox culling. The influx of red foxes was especially strong in northern Finland, where the subarctic tundra is at lower altitude than in Sweden

and Norway and thus closer to the forest zone. Furthermore, the absence of lemming peaks was also of longer duration in Finland than in the other regions (Henttonen & Kaikusalo 1993).

In Sweden and Norway, the population was on the verge of extinction during 1998–2000 with about 50 reproductive foxes coupled to a lack of lemming peaks in most parts of its distribution range. However, in Børgefjell (Norway), lemming cycles were locally retained (Framstad 2011) and a small population of arctic foxes remained throughout the 1990s. The return of lemming and vole cycles across large tracts of the mountain tundra after 2000 (Elmhagen *et al.* 2011; Ims, Yoccoz & Killengreen 2011) may have rescued the arctic foxes from extinction in Fennoscandia.

However, although the return of regular rodent cycles appears to have stopped the decline in regions without management actions, there is still no arctic fox recovery
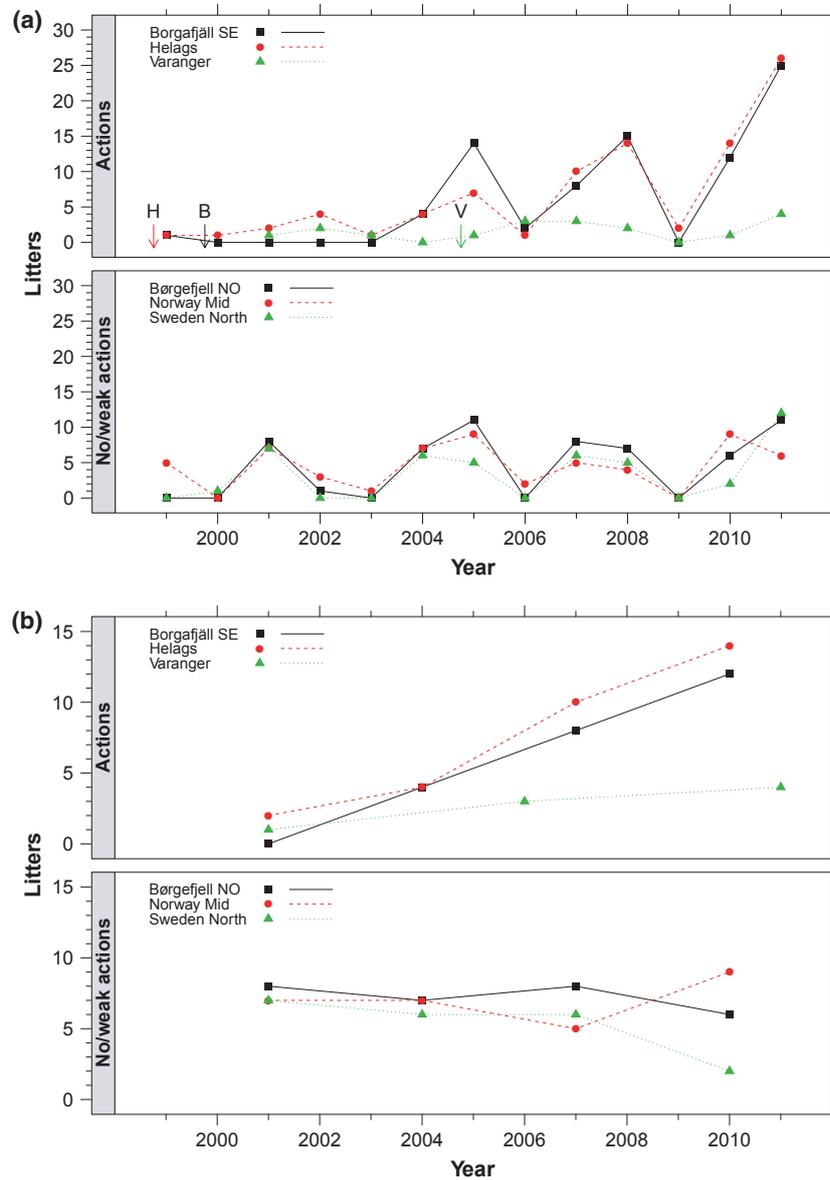
Fig. 4. (a) Number of arctic fox litters from 2001 to 2011 in Helags, Borgafjäll SE, Varanger and Børgefjell NO. Note that Sweden North and Norway mid represent the data from the four Swedish regions Rousto, Padjelanta, Sitas and Vindelfjällen and the two Norwegian regions Saltfjellet and Indre Troms, respectively (see Table 1). (b) Number of arctic fox litters during the increase year for the fox cycle.

in these areas. In contrast, there has been an increase in the arctic fox population size in areas where conservation actions were implemented during the last decade. Our results indicate that this recovery is due to a combined effect of the newly returned rodent cycles and the conservation actions outlined above.

In this large-scale conservation programme, we have shown that it is possible to halt the decline and even reverse the negative trend for the arctic fox. By combining intensive conservation actions in the form of red fox culling and supplementary feeding, the arctic fox populations increased considerably. However, without the return of regular lemming cycles (Elmhagen *et al.* 2011; Ims, Yoccoz & Killengreen 2011), it is likely that the actions would have been less successful. This study adds to previous work showing that supplementary feeding can have a positive effect on the demography of mammals (Boutin 1990), including arctic foxes (Angerbjörn *et al.* 1991), and

demonstrates the efficiency of supplemental feeding on a large scale in conservation management. However, the abundance of natural food resources (i.e. small rodent abundance) also had a strong effect that was independent of the supplemental feeding. This suggests that the natural food source may have a very important role that artificial feeding cannot fully compensate. To what extent this result is specific to the arctic fox or more general for other facultative specialist predators needs to be verified by similar studies on other species.

Regarding the relationship between the two fox species, previous studies have provided anecdotal evidence for intraguild predation and competition from red foxes on arctic foxes (Frafjord, Becker & Angerbjörn 1989; Pamperin, Follmann & Petersen 2006). The results presented here, however, provide a strong indication that this interaction has population-level consequences for the arctic fox, and thus support the Hersteinsson

and Macdonald (1992) hypothesis that arctic foxes are limited by red fox presence. However, the relationship between the fox species was not affected by the climate warming in Canada (Gallant *et al.* 2012) where red foxes did not increase in abundance. One important difference might be the importance of domestic reindeer as a food source for red foxes in Fennoscandia whereas this is absent in Canada. The mechanism behind the intraguild relationship is still unclear; for example, we did not have any quantitative evidence for the impact of direct killings.

Overall, the combined actions and return of the rodent cycles had a significant effect across a large geographical scale, resulting in a doubling of the breeding population over each cycle. This trend suggests no density-dependent mechanisms so far. Because the main aim of the SEFALO project was to urgently maximize the support to the arctic fox population, there was limited scope for implementing a rigorous experimental design with fully crossed and random allocation of treatment combinations. Nonetheless, the existence of 10 geographical regions, where actions were implemented at different intensity, allowed us to estimate the relative contribution of the rodent cycle and the two types of management actions. It should be noted that the haphazard distribution of action levels across time and regions to some extent limits the inferences that can be drawn from our quasi-experimental approach (c.f. Shaddish, Cook & Campbell 2002). However, compared to proper field experiments, the spatial scale of this study is rather large (*c.* 21 000 km^2). In general, community ecological experiments very rarely cover such large areas, and it is also unusual to run the experiments for 10 years. Our study could maybe best be compared with studies that also lacks true replicates such as the Iberian lynx and re-introduction of wolves in Yellowstone (e.g. Arjo & Pletscher 1999; Palomares *et al.* 2011) or removal of pigs in California (Bakker *et al.* 2009).

In conclusion, the results presented here suggest that (i) it is possible to halt and even reverse a decline in a threatened carnivore population by the use of long-term sustained conservation actions; (ii) extensive spatial and temporal population surveys associated with geographically dispersed conservation actions provide ample opportunities for assessing the efficiency of the management actions even in an ecosystem with considerable natural fluctuations (i.e. the rodent cycle). The arctic fox in Fennoscandia is exposed to both direct and indirect effects of climate change (Ims & Fuglei 2005) and probably represents an early example of future trajectory of other arctic populations across the Holarctic. Consequently, the conservation actions presented and evaluated here can provide guidelines for conservation in other ecoregions, and also insights of value for the management of endangered carnivore species in regions beyond the Arctic. In particular, our study highlights the importance of natural food resource dynamics, which may overrule management interventions. With respect to the particular situation of

the Fennoscandian arctic fox, the results of this study emphasized a need for continued actions in Fennoscandia to secure the population's viability. Without management actions, the Fennoscandian arctic fox population appears to be too large in suitable tundra habitats to allow for long-term persistence. However, our study also points to the paramount importance of rodent peak years for the maintenance of the arctic fox, at least in regions where access to other natural food resources is low. A priority for future monitoring, research and management efforts is therefore to carefully take into account the fate of arctic rodents (in particular lemmings) when attempting to find optimal solutions to conserve the arctic fox in a warming climate.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Unstandardized parameter estimates for structural equation models.

Table S1. Estimates for the grand study.

Table S2. Estimates for the seasonal study.